

REPRODUCTIVE ECOLOGY AND HABITAT ASSOCIATIONS
OF FLORIDA'S CRESTED CARACARAS

By

JOAN L. MORRISON

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To Clyde and all the rest.

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	iv
LIST OF TABLES	ix
LIST OF FIGURES	xii
ABSTRACT	xiv
CHAPTERS	
1 STUDY OVERVIEW	1
Introduction	1
Study Species -- History and Background	2
Study Area	5
Study Organization	5
2 BREEDING ECOLOGY OF FLORIDA'S CRESTED CARACARAS .	9
Introduction	9
Study Area and Methods	10
Nest Location and Visitation	10
Reproductive Success	11
Productivity and Components of Variation	12
Environmental Data	13
Statistical Analyses	13
Results	14
Territorial Occupancy and Breeding Rates	14
Breeding Behavior and Site Fidelity	14
Nest Building and Incubation	15
Length of the Breeding Season and Timing of Broods	15
Number of Broods Per Year	16
Clutch Size	16
Broods	16
Reproductive Success, Productivity and Components of Variation .	17
Performance and Laying Date	17
Nest Failure, Egg, and Chick Mortality	18
Discussion	18
Weather, Timing, and Length of the Breeding Season	19
Clutch Size	20

Timing and Number of Broods	20
Mortality	21
Breeding Strategy and Variation in Reproductive Parameters	21
Comparison With Other crested caracaras	22
3 EFFECTS ON PRODUCTIVITY AND POTENTIAL COSTS OF DOUBLE BROODING IN CRESTED CARACARAS	41
Introduction	41
Study Area and Methods	43
Results	46
Extent of Occurrence of Double Brooding	46
Timing of Broods	47
Productivity and Nesting Success	47
Parental Care and Post-fledging Survival	48
Potential Costs to Adults	48
Effects on Population Growth and Persistence	48
Influence of Factors	48
Discussion	48
4 HABITAT ASSOCIATIONS AND PRODUCTIVITY OF CARACARAS ON CATTLE RANCHES	64
Introduction	64
Study Area	65
Methods	65
Land Ownership/Land Use	65
Home Range Estimation and Spatial Dispersion of Territories	66
Landscape-level Habitat Selection by Breeding Pairs	68
Caracaras and Cattle Ranches	70
Results	70
Land Ownership/Land Use	70
Home Ranges and Spatial Dispersion of Territories	70
Landscape-level Habitat Selection by Breeding Pairs	71
Caracaras and Cattle Ranches	72
Discussion	72
5 SYNTHESIS AND CONCLUSIONS	92
LITERATURE CITED	96
BIOGEOGRAPHICAL SKETCH	108

LIST OF TABLES

<u>Table</u>		<u>page</u>
2-1	Breeding chronology and intervals, in weeks, between broods for Florida's crested caracara population, 1994 - 1996.	24
2-2	Multiple nesting in Florida's crested caracara population, 1994 - 1996. Early nests are those that initiated egg-laying before the median week of egg-laying for the entire sample, each year.	25
2-3	Reproductive success parameters for Florida's crested caracaras, 1994 - 1996. Nestling survival to fledging (number of fledglings/number of eggs laid), fledgling survival to independence (number of young alive at end of post-fledging dependency period/number fledged), and egg success (proportion of eggs laid that produced independent young) for eggs from known size clutches.	26
2-4	Estimates of Mayfield nest success probabilities for breeding pairs of crested caracaras in south-central Florida, 1994 - 1996.	27
2-5	Measures of annual productivity (mean \pm SE) and Index of Productivity for crested caracaras in south-central Florida, 1994 - 1996. See text for calculation of Index of Productivity. Productivity per successful pair includes young from re-nesting attempts.	28
2-6	Variability in reproductive parameters for crested caracaras during 3 years in south-central Florida. CV = coefficient of variation (standard deviation/mean). Productivity/successful pair includes young from re-nesting efforts. $n = 98$ clutches.	29
2-7	Seasonal decline in breeding performance (mean \pm SE) for known-size clutches and for all nest attempts of crested caracaras in south-central Florida, 1994 - 1996. Early nests initiated egg-laying before the median week of egg-laying each year, late nests initiated egg-laying after the median week.	30
2-8	Fates of eggs from known-size clutches for crested caracara nests in south-central Florida, 1994 - 1996.	31
2-9	Failure of crested caracara nests in south-central Florida, 1994 - 1996.	32
3-1	Occurrence and timing of nesting attempts between years for crested caracaras in south-central Florida. NA = not applicable for that year.	53
3-2	Clutch size (mean \pm SE) and nesting success (SD in parentheses) between nest types for crested caracaras in south-central Florida, 1994 - 1996. The same letter indicates significant differences between nest types. ND = no	

	data on clutch sizes of first or second nests in 1994 because these nests were found after hatching.	54
3-3	Estimated parameters for evaluating contribution of double brooding to population growth for crested caracaras in south-central Florida. Parameters estimated from data collected during 1994 - 1996.	55
3-4	Estimation of population size and annual growth rate for two hypothetical populations of crested caracaras in south-central Florida, one in which all pairs only produce a single brood each year, and one in which approximately 10% of pairs successfully produce two broods each year.	56
3-5	Statistics for logistic regression analysis of the influence of timing of initiation of the first brood (INITWK) and the number fledged in the first brood (NUMFRST) on the occurrence of double brooding in crested caracaras in south-central Florida, 1994 - 1996. $n = 16$ double-brooded pairs, 103 single-brooded pairs.	57
3-6	Statistics for logistic regression analysis of the influence of double brooding the previous year (DBPREV), fledging date (WKPREV) and number fledged the previous year (NUMPREV) on the occurrence of double brooding in crested caracaras in south-central Florida, 1994 - 1996. $n = 11$ double-brooded pairs, 34 single-brooded pairs.	58
4-1	Variables included in development of the logistic regression model describing caracara home ranges. Unless noted, all variables are expressed as proportions of the total area of the home range that was vegetated with natural or semi-natural* vegetation.	76
4-2	Landownership and major land use for crested caracara territories in south-central Florida, 1994 - 1996. $n = 65$ territories.	77
4-3	Size and vegetation composition of crested caracara home ranges. Home ranges are defined as the 99% kernel contour estimated using a 0.85 smoothing factor. $N =$ number of radiolocations used to estimate home range size.	78
4-4a	Matrix of percent overlap of 60% contours (core areas) for 9 adjacent pairs of breeding crested caracaras on the MacArthur Agro-Ecology Research Center, Highlands County, south-central Florida. Birds in rows are overlapped by birds in columns.	79
4-4b	Matrix of percent overlap of 60% contours (core areas) for 4 adjacent pairs of breeding crested caracaras along the Kissimmee River, Highlands and Okeechobee counties, south-central Florida. Birds in rows are overlapped by birds in columns.	79

4-5a	Matrix of percent overlap of 99% contours for 9 adjacent pairs of breeding crested caracaras on the MacArthur Agro-Ecology Research Center, Highlands County, south-central Florida. Birds in rows are overlapped by birds in columns.	80
4-5b	Matrix of percent overlap of 99% contours for 4 adjacent pairs of breeding crested caracaras along the Kissimmee River, Highlands and Okeechobee counties, south-central Florida. Birds in rows are overlapped by birds in columns.	80
4-6	Parameter estimates for model produced using logistic regression analysis that best distinguished between known caracara home ranges and available units throughout the study area. Variables include pine forest (PINEFOR), mixed forest (MIXFOR), wax myrtle (WAXMYRT), woodland (WOODL), and contiguous pasture (CONTIGP).	81
4-7	Parameter estimates for model that best distinguished between known caracara home ranges and available units throughout the study area and that did not include forest variables. Variables include native grassland/prairie (GRASSL), wax myrtle (WAXMYRT), improved pasture (IMPPAST), and contiguous pasture (CONTIGP).	82
4-8	Predicted probabilities of use for test caracara home ranges calculated using logistic regression models that best distinguished between caracara home ranges and available units throughout the study area.	83

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1-1	Distribution of the crested caracara in North and Central America. 7
1-2	Current known breeding range of the crested caracara in Florida. The study area encompassed much of this range 8
2-1	Location of study area for crested caracaras in south-central Florida. Study area encompassed much of the species' current known breeding range in Florida. 33
2-2	Mean monthly rainfall and breeding chronology of crested caracaras during 3 years in south-central Florida, 1994 ($n = 33$ nest attempts), 1995 ($n = 62$ attempts), 1996 ($n = 62$ attempts). 34
2-3	Relationship between month of first nest initiation and occurrence of renesting by crested caracaras following either an early failure or a successful first brood, south-central Florida, 1994 - 1996. 35
2-4	Distribution of clutch sizes by year, for crested caracara nests in south-central Florida, 1994 - 1996. 36
2-5	Mean number of fledglings and independent young per nest for each clutch size during each year for crested caracaras in south-central Florida, 1994 - 1996. n indicates number of clutches. 37
2-6	Relationship between mean clutch size and month of nest initiation for 98 known-size clutches of crested caracaras in south-central Florida, 1994 - 1996. Number of clutches is shown above each month. 38
2-7	Mayfield probability of nest success (\pm SD) by month for crested caracaras in south-central Florida, 1994 - 1996 ($n = 157$ nest attempts). 39
2-8	Relationship between productivity per nest attempt ($n = 157$ attempts) and month of nest initiation for crested caracaras in Florida, 1994 - 1996. Number of nest attempts is shown above each month. 40
3-1	Timing of nest initiation throughout the breeding season for crested caracaras in south-central Florida, 1994 - 1996. 59
3-2	Length of the interbrood interval in relation to number fledged from the first nesting attempt for double brooded crested caracaras in south-central Florida, 1994 - 1996. $n = 16$ pairs. 60

3-3	Proportion of nests initiated in each month that were successful, for crested caracaras in south central Florida, 1994 - 1996.	61
3-4	Mean number of young fledged per pair for pairs of crested caracaras nesting in south-central Florida, 1994 - 1996. Number of pairs is shown above each column.	62
3-5	Kaplan-Meier survival functions estimated for juvenile crested caracaras from first, second, and single broods in south-central Florida, 1994 - 1996. ...	63
4-1	Study area for evaluating landscape-level habitat selection by breeding pairs of crested caracaras in Florida, 1994-1996.	84
4-2	Relationship between occupancy, initiation of breeding attempts, and land ownership for 37 crested caracaras territories in south-central Florida, 1994 - 1996.	85
4-3	Mean (\pm SE) number of radiolocations for 25 breeding adult crested caracaras in relation to distance from the nest. $n = 1283$ total radiolocations.	86
4-4	Distributions of radiolocations of 25 breeding adult crested caracaras in relation to distance from the nest during breeding and non-breeding seasons in south-central Florida, 1994 - 1996.	87
4-5	Distribution of distances between nests of neighboring pairs of successfully breeding crested caracaras in south-central Florida, 1994 - 1996. $n = 30$ pairings.	88
4-6	Relationship between proportion of improved pasture in home range and home range size for 25 crested caracara home ranges in south-central Florida, 1994 - 1996.	89
4-7	Relationship between the amount of improved pasture in the home range and total number of young fledged during 1994 - 1996, for crested caracaras in south-central Florida.	90
4-8	Home ranges of the crested caracara on study area in south-central Florida. ...	91

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By

Joan L. Morrison

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I studied the reproductive ecology and habitat associations of the crested caracara (*Caracara plancus*) in Florida. Listed as Threatened, this population is believed to be in decline due to habitat loss. Results from observations conducted at 155 nests during 3 years indicated that Florida's caracaras may be doing better than previously believed, particularly on privately owned cattle ranches, where most nesting pairs were found. Pairs nesting on ranches exhibited higher site fidelity, annual breeding rates, and nesting success, and produced more young overall.

The breeding cycle is strongly tied to the annual precipitation cycle. Although the modal clutch size was 2, clutch sizes of 3 produced the most independent young during all years. Pairs can make several nesting attempts per year. Individuals that successfully raise two broods in a year may realize higher lifetime reproductive success. Fledglings from early-season nests had the highest probability of survival to recruitment. Home range size and nesting density estimated using radiotelemetry were considerably smaller and higher, respectively, than previously published estimates for this population.

Caracaras are highly territorial near the nest but apparently tolerate conspecifics in foraging areas.

I investigated landscape-level habitat selection by breeding pairs of crested caracaras using GIS analysis and logistic regression modeling. Results indicated a positive association between caracara home ranges and improved pastures, particularly with large areas of contiguous pasture. The size of individual caracara home ranges was inversely correlated with the proportion of improved pasture in the home range.

Caracaras frequently occupy areas in close association with humans and are generally tolerant of moderate levels of human activities. Because of the caracara's strong site fidelity, a conservation strategy for Florida's population should be based on protecting known nest sites and should focus at a regional scale. Management plans must address effects of loss and degradation of nesting and foraging habitat, particularly conversion of pastures to citrus and sugar cane. Because most suitable habitat is in private ownership, habitat protection must involve cooperative efforts between land management agencies and private landowners. This research has focused attention on the importance of cattle ranches to Florida's native wildlife by using the caracara as an example of how humans, agriculture, and native wildlife can coexist.

CHAPTER I

STUDY OVERVIEW

Introduction

One of the most profound and widespread impacts of humans on the landscape is alteration of natural habitats. Fragmentation and loss of natural habitats have been implicated in the decline or extinction of many species (Askins et al 1990, Wilcox and Murphy 1985). Consequences of these habitat changes may include reduced reproductive success or survivorship owing to loss of suitable breeding and foraging habitats, altered dispersal and other behavioral patterns, and increased predation pressure within remaining habitat patches (Whitcomb et al. 1981, Wilcove et al. 1984, Hagan and Johnston 1992, LaHaye et al. 1992, McKelvey et al. 1993, Herkert 1994, Lens and Dhondt 1994, Dunning et al. 1995, Redpath 1995, Robinson et al. 1995, Matthysen and Currie 1996). Formerly contiguous populations are fragmented into disjunct subgroups if individuals are unable to disperse among isolated patches that are embedded in an inhospitable matrix (Opdam et al. 1985, Sjögren 1991, Fahrig and Merriam 1994).

The effects of fragmentation or loss of natural habitats on small, isolated, or peripheral populations are of particular concern. These populations have high conservation value because they often show some degree of genetic, behavioral, and/or morphological divergence from central populations (Levin 1970, Lawton 1993, Lesica and Allendorf 1995). Geographically isolated populations are subject to higher risk of extinction owing to demographic, environmental, and genetic stochasticity (Shaffer 1981). It is reasonable to expect that effects of habitat loss and fragmentation acting in concert with isolation and small size pose serious threats to peripheral populations.

Fragmentation and loss of natural habitats are occurring at a rapid rate throughout peninsular Florida. Because of its geographic position and glacial history, Florida has a rich biodiversity (Neill 1957, Myers and Ewel 1990). The peninsula is a mosaic of

habitat islands and small, often disjunct populations of species, many of which have differentiated at least at the subspecies level from their closest relatives in the western U.S. Continued fragmentation and conversion of natural habitats combined with geographic isolation currently jeopardizes chances for the long-term persistence of many species in Florida.

Study Species -- History and Background

The crested caracara (*Caracara plancus*) is a medium-sized tropical raptor that occupies open habitats, typically grassland, prairie, rangeland, savanna, and desert. Its current geographic distribution covers most of South and Central America, through parts of northern Mexico, and into the southern U.S. (del Hoyo et al. 1994). Its current North American distribution is limited to disjunct populations in Texas, Arizona, Cuba, and Florida (Figure 1-1).

Fossil records and the distribution of these populations suggest that the caracara may have been more widespread throughout southern North America during the Pleistocene (Howard and Miller 1933, Brodkorb 1964, Chandler and Martin 1991, Vuilleumier 1985). This epoch was characterized by extensive periods of reduced rainfall. During these times, grassland and savanna habitats presumably reached their maximum extent across the continent. Especially during the glacial cycles when sea levels were lowest, an extensive subtropical savanna corridor may have extended around the Gulf of Mexico, facilitating the exchange and movement of western biota eastward into Florida (Neill 1957, Webb 1977, Webb and Wilkins 1984). Ancestors of the extant caracara may have expanded northward through Central America during the biotic interchange, followed by continued expansion throughout the Gulf region and into peninsular Florida.

As a consequence of numerous glacial cycles, repeated fluctuations in sea level, and associated climate and habitat changes, the geographic ranges of many North and Central American species eventually became divided and reduced in size. Many species having western affinities, including the caracara, were ultimately restricted to small

populations in Florida (Woolfenden and Fitzpatrick 1984). Today, conservation efforts throughout Florida are increasingly focusing on these populations because of their isolation, small size, and disjunct distributions.

The extant Florida population of the crested caracara (*C.p. audubonii*) occurs in the south-central peninsula. Described by early ornithologists as inhabiting much of the central peninsula (Scott 1892, Phelps 1912, Howell 1932, Bent 1937, Nicholson 1929, 1930), its historic distribution probably conformed closely to the original location of the major prairie ecosystems (Davis 1967). Representatives of this ecosystem included the Kissimmee prairie, which extended north and westward from Lake Okeechobee in association with the Kissimmee River floodplain, and the DeSoto prairie, which extended westward from the southernmost portion of the central ridge. These prairies constituted vast expanses of low, open, nearly treeless grasslands, with sparse cabbage palm hammocks and scattered patches of shrubs and saw palmettos (Harshberger 1914).

The current breeding range of the caracara in Florida encompasses parts of about 10 counties within this presumed historic range (Kale et al. 1992, Stevenson and Anderson 1994) (Figure 1-2). The grassland and prairie ecosystems in this region are now only limited in extent (Abrahamson and Hartnett 1990). Extensive areas of the original prairies have been converted to improved pastures, which are dominated by non-native grasses and are intensely managed to produce forage for cattle. What remains as natural and semi-natural habitat in this region is rapidly being converted for agricultural and urban development.

The status of Florida's crested caracara population has long been a subject of concern. Apparent steep declines in numbers during the late 1960s and early 1970s (Funderberg and Heinzman 1967, Heinzmann 1970) first focused attention on this population. Results of surveys of historic territories in the late 1980s suggested that this population may be undergoing a long-term decline concomitant with accelerated habitat loss (Millsap 1989). Layne (1995), however, stated that during the period 1972 to 1991,

the adult population appears to have been stable. Current published estimates for this population are approximately 400-500 individuals statewide (Layne 1995, 1996).

Because of its restricted range, apparent small population size and history of decline, Florida's crested caracara population was listed as federally Threatened in 1987 (U.S. Fish and Wildlife Service 1987a), followed by a similar state listing (Wood 1990). The current paucity of demographic and ecological information precludes accurate assessment of this population's status or trends, however. Habitat fragmentation and loss are assumed to threaten population persistence, but little data exist with which to test this hypothesis. In 1989, a federal recovery plan was accepted for Florida's caracara population (U.S. Fish and Wildlife Service 1989), but there was little biological information from which to develop appropriate recovery goals.

Management of wildlife populations and development of suitable conservation strategies require in-depth knowledge of a species' life history and population dynamics. The caracara apparently now occurs primarily on privately-owned cattle ranches in this region, undoubtedly contributing to the paucity of biological information. Confrontations between land management agencies and private landowners have escalated in recent years, particularly over issues relating to threatened and endangered species (Lewis 1995, Bean and Wilcove 1997). Landowners are hesitant to permit access to their lands, particularly when a threatened or endangered species is involved. This poses a major dilemma for conservation of a species that occurs regularly on private lands.

The purpose of this research was to provide basic ecological information on Florida's caracara population, particularly information that is relevant for management. Although caracaras apparently persist on cattle ranches, their exact distribution throughout the region, their habitat requirements, and their productivity on cattle ranches are poorly known. Goals of this research included improving knowledge of the caracara's breeding biology, determining land uses compatible with its survival, and assessing relationships between caracaras and cattle ranches. This knowledge is critical for developing guidelines for long-term population monitoring and management.

Study Area

The study area in south-central Florida encompassed much of the crested caracara's current breeding range. Included were all or parts of Highlands, Glades, Okeechobee, Osceola, DeSoto, Polk, Hendry, and Indian River counties (Figure 1-2), an area totaling approximately 20,891 km². The landscape in this region is a mosaic of habitats, primarily grasslands and pastures interspersed with cropland, citrus groves, dairies, pine flatwoods, freshwater marshes and lakes, oak scrub, hardwood hammocks, and urban developments. Over half of this area is in private ownership. Primary land uses are cattle ranching, citrus production, and other agricultural crops. The land in public ownership is managed for a variety of uses including recreation, military training, hunting, natural areas, and river floodplain management.

Study Organization

My research examined the reproductive ecology and habitat associations of Florida's crested caracaras. I focused on (1) documenting reproductive strategies and productivity during 3 breeding seasons; (2) determining spatial requirements and dispersion of breeding pairs, (3) evaluating habitat selection of breeding pairs throughout the landscape, and (4) assessing density and productivity of caracaras on cattle ranches. Results and conclusions are organized into four chapters.

Chapter 2 details the breeding biology and discusses reproductive strategies of Florida's crested caracaras. I examine territorial occupancy, breeding rates, and various reproductive parameters for the sample population. Specifically, I test the hypothesis that caracaras, like other large raptors, have low reproductive rates and low productivity. I also examine relationships between breeding chronology and environmental parameters. Finally, I examine factors that may influence overall productivity in this population.

In Chapter 3, I examine the incidence, determinants, and potential costs of double brooding in this population, a strategy previously unknown for this species. I also discuss potential implications of double-brooding for individual and population productivity.

I examine spatial requirements and evaluate habitat selection of breeding pairs across the south-central Florida landscape in Chapter 4. I estimated home ranges using radiotelemetry then used resource selection techniques to develop a model that describes habitat and landscape features important to breeding pairs in selection of a territory. In this chapter I also examine density of breeding pairs on cattle ranches and compare productivity among caracaras nesting at sites where the major land use is or is not cattle ranching.

Chapter 5 contains a synthesis of the conclusions and findings from this research. I present an evaluation of the current status of this population within the context of its historical background and my research results. I also provide recommendations for conservation efforts, management, and monitoring of this population.



Figure 1-1. Distribution of the crested caracara in North and Central America.

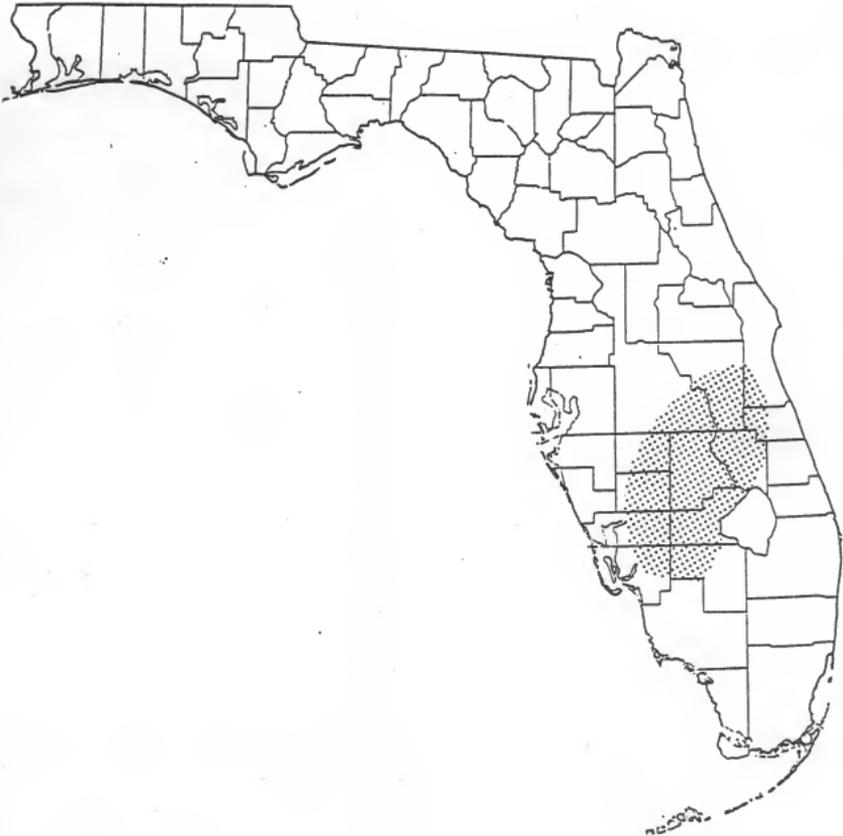


Figure 1-2. Current known breeding range of the crested caracara in Florida. The study area encompassed much of this range.

CHAPTER 2

BREEDING ECOLOGY OF FLORIDA'S CRESTED CARACARAS

Introduction

The crested caracara (*Caracara plancus*) is one of nine species in the subgroup Caracarinae (caracaras), family Falconidae (del Hoyo et al. 1994). Although some species are widely distributed throughout Central and South America, caracaras as a group have been little studied. The crested caracara is the only species that reaches North America. Breeding populations occur in Texas (Oberholser 1974), southern Arizona (Levy 1988, Ellis et al. 1988), and Florida (Howell 1932, Stevenson and Anderson 1994). The breeding ecology of this species is poorly known throughout its range, although populations in Texas (Dickinson and Arnold 1996) and Baja California Sur, Mexico (Rivera-Rodríguez and Rodríguez-Estrella, unpubl. data), have received recent attention.

Florida's crested caracara population is of conservation concern because it is isolated from other populations, has a restricted range, and apparently is of small size (Funderberg and Heinzmann 1967, Heinzman 1970, Millsap et al. 1990). Nesting habitat throughout its historic range has been greatly reduced by conversion of grassland habitats for urban and agricultural development, and this habitat loss is expected to continue. This population is currently listed as Threatened by the U.S. Fish and Wildlife Service and the state of Florida. Despite this listing, published information is limited to descriptions of its natural history and distribution (Nicholson 1929, Howell 1932, Bent 1937, Sprunt 1954, Stevenson and Anderson 1994, Layne 1996).

The intent of this research was to study the breeding ecology of Florida's crested caracaras, particularly to provide data useful for conservation and management of this population. Specific objectives were to (1) determine breeding chronology, (2) assess relationships between breeding and environmental variables, (3) relate breeding ecology to annual population productivity, and (4) assess variation in reproductive parameters.

Study Area and Methods

I studied the breeding ecology of crested caracaras during 3 years in south-central Florida (Figure 2-1). The landscape is a mosaic of habitats, primarily grasslands and pastures interspersed with cropland, citrus groves, dairies, pine flatwoods, freshwater marshes and lakes, oak scrub, hardwood hammocks, and urban developments. Primary land uses are cattle ranching, citrus production, and other agricultural crops. Breeding pairs of crested caracaras occupy open grasslands and pastures. These habitats are characterized by large expanses of low-growing (< 0.5 m in height) ground cover of grasses and forbs and are dotted with numerous shallow ponds, wetlands, and marshes, and single or small clumps of live oaks (*Quercus virginiana*), cabbage palms (*Sabal palmetto*), and cypress (*Taxodium sp.*).

Southern Florida has a humid, subtropical climate with a distinct annual cycle of temperature and precipitation (Chen and Gerber 1990). During the rainy season, June through September or October, temperatures are warm and relatively uniform, averaging about 28°C. Convective rains and thunderstorms occur almost daily, and monthly rainfall averages more than 60 cm. Monthly rainfall during the dry season, usually from November through May, averages around 20 cm. During the dry season, air temperatures are cooler but rarely drop below freezing. Daily high temperatures rarely exceed 20°C, but in May, temperatures as high as 38°C have been recorded.

During the three years of this study, I monitored 33, 62, and 62 nesting attempts in 30, 48, and 55, (65 different) territories, respectively. I color-banded 49 adult caracaras representing 41 territories. I also color-banded and radiotagged 189 nestlings between 7 and 8 weeks of age while they were still in the nest or just after they fledged, when they could be captured easily on the ground.

Nest Location and Visitation

I located active nesting territories by visiting known historic sites (Layne unpubl data, Millsap 1989) and by conducting observations at sites where I had seen adult caracaras. I found nests by observing the behavior of adults and by covering entire areas

on foot and searching individual trees. I conducted monthly observations throughout the year in known territories to assess site fidelity of adults and to look for nesting activity. Although I found most nests in 1994 after hatching, I followed nest progress before laying in most territories in 1995 and 1996.

Once found, I checked nests weekly to determine their fate. I determined clutch size, hatching date, brood size, and chick age using a mirror attached to an extendible pole. Each nest was assigned a week of initiation based either on the known time of egg laying or on back-dating from known hatching or fledging dates (assuming an incubation period of approximately 32 days and a nestling period of approximately 8 weeks). I then calculated week of initiation from the first week of September, which I assigned as the first week of the breeding season each year, based on the earliest known egg laying during all 3 years. I defined breeding season length each year as the number of weeks during which I found nests with eggs. Early nests were defined as those in which egg laying was initiated before the median laying week each year, late nests were those in which egg laying was initiated after the median laying week.

Following nest failures, I continued to check these territories at least monthly for signs of renesting. I also regularly searched all territories that had successfully fledged one brood in a breeding season, for second nests. After fledging, I monitored chicks weekly by telemetry to determine survival.

Reproductive Success

I estimated probabilities of nest success using Mayfield's method (Mayfield 1961, Johnson 1979) for all nest attempts during all years ($n = 157$ attempts). I estimated weekly rather than daily probabilities of nest success (Mayfield 1961), because of the length of the caracara's breeding cycle. I defined a successful nest as one in which at least one fledgling survived to independence, because conclusions based on reproductive output measured at fledgling independence can differ strongly from those measured at fledging (e.g. Haukioja 1970). I defined independence as the end of the post-fledging dependency period (PFDP), the first 8 weeks post fledging. Before reaching

independence, young remained near the nest and were dependent on their parents for food. I calculated nest success for the incubation, nestling, and post-fledging periods, using lengths of 4, 8, and 8 weeks, respectively. I compared Mayfield nest success probabilities between periods and years using a Z-test (Hensler and Nichols 1981).

Measures of reproductive success also included clutch size, nestling survival to fledging, fledgling survival to independence, and egg success (the proportion of eggs laid that produced independent young). For these analyses, I used a subset of the total nests with known clutch size ($n = 98$ nests representing 50 territories). I compared these measures of reproductive success among years using Mann-Whitney and Kruskal-Wallis nonparametric tests (Sokal and Rohlf 1995).

Along with nesting success, territorial occupancy and breeding rates are often used as indicators of the stability and productivity of a population (Steenhof 1987, Newton 1979). Relatively unbiased estimates of these parameters may be derived by determining these rates over several years for a set of preselected territories (Steenhof and Kochert 1982). I identified 37 territories for which occupancy and breeding status were known in 1994 and tracked their status through the subsequent 2 years. I defined an occupied territory as one in which adult caracaras were seen on 3 or more visits to the territory. I considered a breeding attempt to be actual egg laying, not just nest construction. To assess changes in these rates between years, I used Cochran's Q-test (Sokal and Rohlf 1995).

Productivity and Components of Variation

I defined two measures of annual productivity: the number of independent young per nesting attempt and the number of independent young per successful pair. Productivity per successful pair included young from renesting attempts. To evaluate factors that influenced overall annual productivity, I calculated an Index of Productivity for each year using information from known clutch-size nests:

$$\text{Index of Productivity} = \frac{(C)(B)(S)}{N}$$

where C = mean annual clutch size, B = length of the breeding season each year, S = annual egg success, and N = length of the breeding cycle (Ricklefs and Bloom 1977, van Riper 1995). Length of the breeding season was the average number of weeks each year when nests with eggs were found, and length of the breeding cycle was

$$N = b + e + y + n + f$$

where b = nest building (4 weeks), e = egg laying (0.5 weeks), y = length of incubation period (4.5 weeks), n = nestling period (8 weeks), and f = fledgling dependency period (8 weeks). All time estimates are average for the sample. Total length of the breeding cycle for the crested caracara in Florida is approximately 25 weeks.

To evaluate seasonal trends in reproductive performance, I compared clutch size, number of independent young per nesting attempt, and Mayfield nest success estimates for early (initiated egg laying before the median week of egg laying) and late (initiated egg laying after the median week of egg laying) nests for all 3 years. I assessed monthly trends in clutch size and number of independent young per nesting attempt using weighted regression for unequal sample sizes among categories (Sokal and Rohlf 1995).

To examine variation among reproductive parameters, I calculated the coefficient of variation (standard deviation/mean, Ricklefs 1973) in percent, for clutch size, number of independent young per nesting attempt, number of independent young per successful pair, and Mayfield nest success.

Environmental Data

For monthly rainfall analysis, I used data collected from 35 stations throughout the study area by the National Weather Service and the South Florida Water Management District. I averaged daily precipitation values for each month to obtain monthly average precipitation for all 35 stations. Values for all stations were then averaged to obtain monthly precipitation averages for the overall study area.

Statistical Analyses

Because each year's sample of territories contained a subset of the previous year's territories, data were not pooled across years, unless indicated. I conducted statistical

analyses using SigmaStat v. 2.0 (Jandel Scientific 1995). Statistical significance was evaluated at the $\alpha = 0.05$ level.

Results

Territorial Occupancy and Breeding Rates

Territorial occupancy rates for the subsample of 37 territories were 97% and 100% in 1994 and 1995, respectively, but were lower in 1996 (89%, $Q = 6.5$, $P < 0.05$). One territory was only occupied during 1995, and I could not confirm occupancy in 2 additional territories during 1996. Adult caracaras were seen in these areas, but no individuals were banded in these territories and no breeding activity was observed near the traditional nesting site, so these territories were considered unoccupied. Among known occupied territories, breeding rates remained high during all 3 years, at 100%, 97%, and 97%, respectively ($Q = 2.0$, $P > 0.25$).

Breeding Behavior and Site Fidelity

Pairs of breeding caracaras are apparently monogamous and remain together on the territory throughout the year, although they are not easily observed outside the breeding season. The beginning of the breeding season was signaled by several changes in the adults' behavior. Pairs were often observed around the traditional nesting site perching together, preening and allopreening, and sharing food. Adults were generally faithful to both mate and site. Thirty-nine of 49 banded adults, including both banded members of 5 pairs, were present in the same territory and reproduced there for at least 2 years. Although this represents an annual turnover rate of approximately 18%, I do not know the fate of the birds that disappeared. Re-pairing within a breeding season was observed only once, after disappearance of a banded female shortly after her single chick fledged. During the 1995 breeding season, an entire family abandoned its breeding territory about one month after the 2 chicks fledged, and moved to an area approximately 4 km from the nest. This new area was within the territory of another pair that had successfully fledged two young that same year. Radiotelemetry data for the female and 2

chicks that had relocated indicated that they did not return to their original nesting territory. This female nested successfully in the new territory during 1996.

Nest Building and Incubation

Both males and females build the nest. All pairs that built nests eventually produced a clutch. Building time ranged from 2 to 4 weeks ($n = 34$ pairs) and often, up to 2 months elapsed between nest completion and egg laying. Both parents developed a brood patch and incubated the clutch. Neither mate delivered food to the other during incubation, but one would remain on the nest while the other left the area to forage.

Length of the Breeding Season and Timing of Broods

Florida's caracaras' exhibit a prolonged breeding season (Figure 2-2). Chicks fledged from successful nests as early as mid-December, indicating that eggs had been laid during late September. The latest eggs were laid in July, in 1995, although these nests failed ($n = 2$; both were second attempts). Most young fledged during March and April. Chicks from late and second nests fledged as late as July.

Although yearly variation existed in onset and duration of the breeding season, the median week of egg laying for all nesting attempts ($n = 157$) was in late January each year and did not differ among years ($H = 4.14$, $P = 0.13$, Table 2-1). Secondary peaks of egg laying in March and April (Figure 2-2) represent territories where pairs made a second nesting attempt following a successful first brood ($n = 16$ pairs). The breeding season was longest in 1995, when nests with eggs were found during 40 weeks. Breeding season length in 1994 and 1996 was approximately 28 weeks (Table 2-1).

Although within-year variation existed in timing of nest initiation among pairs, between-year nesting intervals for individual pairs were remarkably consistent. The median year-to-year interval between egg laying for single brooded pairs was 50 weeks ($n = 41$ pairs, Table 2-1), thus individual pairs tended to initiate nests at about the same time each year.

Number of Broods Per Year

Multiple nesting within a breeding season occurred during all 3 years. Early nesting pairs regularly renested, either by attempting a second brood or after a first attempt failed (Figure 2-3). During 1995 and 1996, an average of 17.5% of early nests failed in the incubation or early nestling stages. Eighty percent of these pairs renested and half were successful (Table 2-2). Time between failure of the first nest and egg laying in the second nest ranged from 3 to 14 weeks ($n = 8$ pairs, Table 2-2).

Successful double brooding was recorded during all 3 years (Table 2-2). Although second nests failed more often and had smaller clutch sizes, pairs that successfully raised two broods during a season had higher annual productivity than pairs that raised only one brood. More pairs renested after early failure and attempted a second brood in 1995 than in other years (Table 2-2).

Clutch Size

For known-size clutches ($n = 98$), the overall mean was 2.23 eggs (Table 2-3). Modal clutch size was 2 eggs for all years. Mean clutch size was higher in 1994 ($H = 7.61, P = 0.02, n = 16$) owing to more clutches of 3 (Figure 2-4) but did not differ between 1995 and 1996 ($U = 1698, P = 0.98$). For the same females, clutch size decreased between first nests (2.18 ± 0.20) and replacement or second brood nests (1.91 ± 0.09 , paired t -test, $t = 2.19, P = 0.03, n = 11$ pairs).

Broods

Hatching was asynchronous. Eggs hatched one to two days apart. Both parents fed and cared for the young. Brood size at approximately 4 weeks after hatching averaged 82% of mean clutch size for all 3 years pooled ($n = 81$ broods, Table 2-3). Chicks occasionally fell out of nests (pers. obs.). Many chicks simply disappeared; some may have died from starvation. Over all years, only 38% of nests with 3-egg clutches fledged all 3 chicks. Nestlings were in the nest for 7 to 8 weeks, although the earliest recorded fledging occurred at age 42 days. After fledging, the young remained in the general area around the nest and were dependent on the adults for food for at least 2

months. Even after independence, some young remained in the territory until the adults begin breeding the following year.

Reproductive Success, Productivity, and Components of Variation

The overall Mayfield probability of nest success for all nest attempts ($n = 157$) was 0.74 (SD = 0.03, Table 2-4). Nest success was lower in 1995 than in 1996 ($Z = -4.83, P < 0.0001$). Nest success was also lower in 1995 than in 1994, but not significantly so ($Z = 0.73, P > 0.46$, Table 2-4). Lower nest success in 1995 was caused by higher failure rates of early nesting pairs and second brood attempts. Probabilities of nest success during all phases of the nesting cycle were similar within years (Table 2-4) except for the incubation period in 1994. The number of exposure weeks for the incubation period was less in 1994 than in other years because in that year, most nests were found after hatching. Early-season nest failures were likely missed in 1994.

Measures of productivity were lowest in 1995 (Table 2-5), owing to reduced egg success (Table 2-3) and nest success (Table 2-4). In all years, productivity per successful pair was enhanced because pairs successfully renested following early failure or raised second broods. Clutch sizes of 3 produced the most fledglings and independent young during all years (Figure 2-5). Two- and 3-egg clutches produced similar numbers of independent young. Most clutches of 1 failed (Figure 2-5).

Measures of productivity showed the highest variability among reproductive parameters (Table 2-6). Clutch size varied little and nesting success showed the least variability among parameters (Table 2-6).

Performance and Laying Date

All measures of breeding performance declined as the breeding season progressed each year (Table 2-7). Mean clutch size was negatively correlated with laying date ($r = -0.85, P < 0.01$, Figure 2-6) and the regression was significant ($F = 29.07, n = 98$). Approximately 76% of the variation in clutch size was due to month of nest initiation. The probability of a nest succeeding varied throughout the breeding season (Figure 2-7). During all years, pairs that initiated egg laying early in the breeding season had a higher

probability of nest success ($Z = -3.06$, $P < 0.001$, $n = 76$) than late nesting pairs ($n = 81$, Table 2-7), although the earliest nesting pairs generally had a lower probability of nest success (Figure 2-7). Timing of nest initiation also clearly affected productivity. The number of independent young per nesting attempt declined as the breeding season progressed ($r = -0.95$, $P < 0.01$, Figure 2-8) and again, the regression was significant ($F = 18.44$, $P < 0.005$, $n = 157$). Approximately 67% of the variation in productivity could be explained by month of nest initiation.

Nest Failure, Egg and Chick Mortality

Overall, 61.2% of all eggs that hatched from known-size clutches survived to fledging and 48.4% survived to independence (Table 2-3). The fate of most eggs that did not result in an independent young was unknown (Table 2-8). Total nest failure occurred most often during late incubation and near the time of hatching (Table 2-9). Overall, an average of 25% of nests failed each year (Table 2-9), but most early nesting pairs that failed renested, and approximately 50% of renesters were successful (Table 2-2). On average, 18% of pairs each year failed to produce any young despite a nesting attempt (Table 2-9).

Discussion

The reproductive rate of birds presumably represents the maximum number of young that individuals in a population can raise given the prevailing environmental conditions during a breeding period (Amadon 1964, Lack 1968, Ricklefs 1973). Raptors typically have lower reproductive rates than most birds (Newton 1979). Territorial occupancy rates vary widely, and a percentage of pairs annually may not attempt to breed or may abandon an attempt, often due to weather, food availability, or density dependent effects (Newton and Marquiss 1976, 1986, Village 1982, 1983, Kostrzewa 1996).

My results indicate territorial occupancy and breeding rates for Florida's crested caracaras that are higher than rates reported for most raptors. In a resident population where pairs are monogamous and remain on the territory year-round, individuals' familiarity with both territory and mate may facilitate successful annual breeding.

Although annual breeding rates were high, productivity varied considerably among pairs and years. In all years, factors associated with productivity included weather, timing and length of the breeding season, clutch size, timing and number of broods, and mortality of eggs and chicks.

Weather, Timing, and Length of the Breeding Season.

Many factors interact to modify the timing of reproduction in birds, particularly for tropical and subtropical species (Skutch 1950, Immelmann 1971, Ricklefs and Bloom 1977). Cues that function to initiate the crested caracara's breeding season in Florida are unknown. Food supply often is a proximate factor regulating both reproductive timing and effort (Perrins 1970, Newton and Marquiss 1981, Dijkstra et al. 1982, Daan et al. 1989). In tropical and subtropical regions, the abundance of food resources, and thus many birds' reproductive cycles, are closely tied to rainfall cycles (Skutch 1950). Florida's climatic cycle may provide predictable cues to resource availability for crested caracaras. The length and timing of the caracara's breeding season in Florida was strongly tied to the rainfall cycle (Figure 2-2). Reproduction occurred during the winter dry season, with the peak in egg laying following periods of decreasing precipitation in the fall. During the fall, as conditions become drier, fish and other prey become concentrated in ephemeral wetlands, ponds, and ditches (Kushlan 1990, Babbitt 1996). Caracaras often forage in these habitats and regularly kleptoparasitize other species feeding there (Rivera-Rodríguez and Rodríguez-Estrella 1992, pers. obs.). Seasonal and predictable abundance of prey during dry-down may enhance individual females' ability to attain body condition necessary for breeding.

Rainfall cycles may also influence the length of the breeding season. Higher precipitation during the winter of 1994-1995 (Figure 2-2) resulted in a higher water table at the beginning of the rainy season in summer 1995. I found nests containing eggs during a longer period in 1995 and more breeding attempts were recorded. Overall productivity for 1995 was lower, however, despite the longer breeding season and similar

mean clutch size. Lower productivity was due to reduced egg and nest success during that year (Tables 2-3 and 2-4).

Temperature cycles may also influence reproduction. High temperatures in the spring at the end of dry season may impose additional physiological stress on breeding adults, particularly on late nesters. In 1995, many second and late season (June-July) nests failed, and 3 clutches were found abandoned during incubation in May, when ambient temperatures reached $> 40^{\circ}\text{C}$ for several consecutive days.

Clutch Size

Similar to many avian species, the most productive clutch size for Florida's crested caracaras was larger than the modal clutch size, during all years. This is contrary to Lack's hypothesis (Lack 1954, 1966) but instead supports the hypothesis that females capable of laying a variable number of eggs lay clutches as large as they can produce (Klomp 1970, von Haartman's 1971, Högstedt 1980). Differences in territorial and individual quality may exist that translate into the ability of each female to lay the largest clutch possible.

Timing and Number of Broods.

A decline in all aspects of breeding performance with advance in laying date has been well-documented for birds (Lack 1968, Perrins 1970, Newton and Marquiss 1984, Daan et al. 1989, Verhulst and Tinbergen 1991). Timing of nest initiation clearly affects the reproductive performance of Florida's crested caracaras. Clutch size, probability of nest success, productivity, and probability of renesting all declined as the breeding season progressed. Differences in territory or individual quality can affect the timing of egg laying (Klomp 1970, Murphy 1978, Verhulst et al. 1995). Reduced nesting success late in the breeding season may be indicative of seasonal environmental changes, particularly declining food availability (Perrins 1970, Korpimäki and Lagerström 1988).

Although the ability to renest is clearly advantageous for many avian species (Smith and Roff 1980, Westmoreland et al. 1986, Guepel and DeSante 1990, den Boer-Hazewinkel 1987) most raptors do not normally hatch more than one clutch per season

(Newton 1979). The ability to renest enhances annual productivity and thus lifetime reproductive success of individual caracaras. About half of the pairs that renested following early failure ultimately did produce independent young during the same year. During all 3 years, pairs that successfully fledged two broods in a breeding season incurred higher productivity than pairs that fledged only one brood.

Mortality

Loss of eggs and chicks during the breeding cycle affected annual productivity. Less than half of all eggs from known-size clutches resulted in independent young. Most losses occurred before fledging and the cause of most losses was unknown. Most eggs lost during incubation disappeared at the time of hatching. With weekly nest checks, it was difficult to determine whether eggs disappeared or whether newly hatched nestlings were lost during the first week. Predation, possibly by crows and raccoons (Layne 1996, pers. obs.), and weather were suspected causes of egg and chick disappearance. Collisions with vehicles was the major cause of fledgling mortality. The loss of a relatively large number of fledglings due to vehicle collisions in 1995 contributed heavily to reduced overall productivity of the sample of breeding pairs during that year.

Breeding Strategy and Variation in Reproductive Parameters

Florida is characterized by both spatial and temporal environmental heterogeneity. Florida's crested caracaras exhibit much spatial and temporal variation in the timing of reproduction and reproductive performance by individual pairs. Clutch size and nesting success showed the least variation among years. Since clutch size is related to the number of young parents can raise (Lack 1954), there would be little advantage to varying clutch size unless future conditions were predictable (Cody 1971). The low coefficient of variation for nest success suggests that most pairs have a good chance at producing at least one independent young during any year. High variation in productivity may be attributable to variable food supply and a myriad of potential causes for loss of eggs and chicks. High variation in productivity is also partly due to the fact that

productivity was measured after the young had become independent and mortality factors had acted for a longer period.

Variable weather and resource conditions probably have been major factors in the evolution of observed life history patterns for Florida's crested caracaras. Winter weather is unpredictable in south-central Florida. Early nesting pairs, in particular, face a tradeoff. Although reproductive success is highest for early nesting pairs, the very earliest pairs incur a high risk of nest failure due to unpredictable winter storms and cold fronts (Figure 2-7). The strategy of multiple nesting may offset this risk. Pairs that successfully renest after failure or successfully double brood ultimately may have more young recruited into the breeding population. Despite the risk of failure due to weather, nesting as early as possible is advantageous because early nesting pairs generally fledge more chicks per nest and have the opportunity to make a second nesting attempt.

The plastic patterns of reproduction for Florida's crested caracaras presumably evolved because they are effective in this variable environment. Although caracaras may breed in any month of the year, the peak of egg laying in late January during all 3 years suggests an optimal time for reproduction. Fewer nests are initiated outside this period and they are less successful, although some do succeed. If unpredictable, catastrophic storms occur during the peak reproductive period, widespread nest failure may result. During these years, pairs that initiate nesting outside the "optimal" period may exhibit higher reproductive success. Such plasticity in spatial and temporal nesting patterns will result in successful nesting and productivity by at least some pairs during any particular year.

Comparison With Other Crested Caracaras

Information on the breeding biology and nesting success of other crested caracara populations is limited. Dickinson and Arnold (1996) and Rivera-Rodríguez and Rodríguez-Estrella (unpubl. data) have reported extended breeding seasons for crested caracaras in Texas and Baja California Sur, Mexico, respectively. Mean clutch size of crested caracaras in Texas was 2.14 ± 0.14 (SD) eggs, ($n = 7$ clutches, Dickinson and

Arnold 1996). Productivity was 1.14 ± 0.46 (SD) independent young per breeding pair ($n = 7$ attempts) and declined as the breeding season progressed (Dickinson and Arnold 1996). Rivera-Rodríguez and Rodríguez-Estrella (unpubl. data) reported productivity of 1.91 ± 0.08 (SE) fledglings per nesting attempt ($n = 22$ attempts) in Mexico. Double brooding was suspected at both sites. Second clutches were observed in June in Texas (Dickinson and Arnold 1996), and in August in Mexico (Rivera-Rodríguez and Rodríguez-Estrella, unpubl. data).

Table 2-1. Breeding chronology and intervals, in weeks, between broods for Florida's crested caracara population, 1994 - 1996. ND = no data.

Year	Length of breeding season (weeks)	Median week of initiation for all attempts	<i>n</i>	Median year-to-year interval for single brooded pairs	
					<i>n</i>
1994	28	21 (3rd wk Jan)	33	ND	
1995	40	22 (4th wk Jan)	62	52	18
1996	28	22 (4th wk Jan)	62	48	23

Table 2-2. Multiple nesting in Florida's crested caracara population, 1994 - 1996. Early nests are those that initiated egg-laying before the median week of egg-laying for the entire sample, each year.

Year	Number of territories	Early nests	Early nests that failed	Attempted renesting after failure	Successful	Interval between failed first nest and replacement nest in same year		
						Successful	Attempted second brood	Successful
1994	30	19	1	0	-	-	3 (10.0%)	3 (100%)
1995	48	26	7 (26.9%)	6 (85.7%)	3 (50%)	4 - 6 weeks	8 (16.7%)	4 (50%)
1996	55	31	3 (9.7%)	2 (66.7%)	1 (50%)	3, 14 weeks	5 (9.1%)	3 (60%)

Table 2-3. Reproductive success parameters for Florida's crested caracaras, 1994 - 1996. Nestling survival to fledging (number of fledglings/number of eggs laid), fledgling survival to independence (number of young alive at end of the post-fledging dependency period/number fledged), and egg success (proportion of eggs laid that produced independent young) for eggs from known size clutches.

Year	No. clutches	Clutch size	Eggs Laid	Brood size	No. broods	Percent of clutch size	No. fledged	Nestling Survival	No. survived to end of PFDP	Fledgling Survival	Egg Success
1994	16	2.56 (0.16)	41	2.23 + 0.20	13	87%	27	65.9%	22	81.5%	0.54
1995	41	2.17 (0.08)	89	1.75 + 0.12	32	81%	51	57.3%	34	66.7%	0.38
1996	41	2.17 (0.08)	89	1.75 + 0.12	36	81%	56	62.9%	50	89.3%	0.56
Pooled	98	2.23 (0.05)	219	1.83 + 0.07	81	82%	134	61.2%	106	79.1%	0.48

Table 2-4. Estimates of Mayfield nest success probabilities for breeding pairs of crested caracaras in south-central Florida, 1994 - 1996.

Year	Territories Followed	Nesting Attempts	Incubation period (SD)	Nestling period (SD)	Fledgling period (SD)	Total probability of nest success (SD)
1994	30	33	0.75 (0.06)	0.95 (0.02)	0.93 (0.02)	0.66 (0.09)
1995	48	62	0.87 (0.02)	0.82 (0.02)	0.83 (0.02)	0.59 (0.04)
1996	55	62	0.94 (0.02)	0.92 (0.01)	0.98 (0.01)	0.85 (0.03)
Overall	65	157	0.89 (0.02)	0.88 (0.01)	0.93 (0.01)	0.74 (0.03)

Table 2-5. Measures of annual productivity (mean \pm SE) and Index of Productivity for crested caracaras in south-central Florida, 1994 - 1996. See text for calculation of Index of Productivity. Productivity per successful pair includes young from renesting attempts.

Year	Number of independent		Number of independent		Index of Productivity
	young per attempt	<i>n</i>	young per successful pair	<i>n</i>	
1994	1.33 \pm 0.16	33	1.87 \pm 0.16	23	1.55
1995	0.98 \pm 0.11	62	1.69 \pm 0.10	36	1.32
1996	1.34 \pm 0.10	62	1.69 \pm 0.09	49	1.36

Table 2-6. Variability in reproductive parameters for crested caracaras during 3 years in south-central Florida. CV = coefficient of variation (standard deviation/mean). Productivity/successful pair include young from renesting efforts. $n = 98$ clutches.

Parameter	1994		1995		1996		Total	
	Mean (SD)	CV (%)						
Clutch size	2.56 (0.63)	24.6	2.17 (0.54)	24.9	2.17 (0.50)	23.0	2.23 (0.55)	24.4
Productivity per nesting attempt	1.33 (0.89)	66.9	0.98 (0.90)	91.8	1.34 (0.79)	59.0	1.20 (0.87)	72.5
Productivity per successful pair	1.87 (0.78)	41.7	1.69 (0.62)	36.7	1.69 (0.62)	36.7	1.73 (0.65)	37.6
Nesting success (Mayfield)	0.66 (0.09)	13.6	0.59 (0.04)	6.8	0.85 (0.03)	3.5	0.74 (0.03)	4.0
		n	n	n	n	n	n	n
		16	41	41	41	41	98	98
		33	62	62	62	62	157	157
		23	36	36	36	49	108	108
		33	62	62	62	62	157	157

Table 2-7. Seasonal decline in breeding performance (mean \pm SE) for known size clutches and for all nest attempts of crested caracaras in south-central Florida, 1994 - 1996. Early nests initiated egg-laying before the median week of egg-laying each year, late nests initiated egg-laying after the median week.

	Year				Total	n	
	1994	n	1995	n			1996
Clutch size (n = 98)							
Early	2.75 + 0.16	8	2.29 + 0.11	24	2.24 + 0.09	29	2.33 + 0.07 61 ^a
Late	2.38 + 0.26	8	2.00 + 0.12	17	2.00 + 0.12	12	2.08 + 0.09 37 ^a
Number independent young per attempt (n = 157)							
Early	1.53 + 0.19	19	1.27 + 0.18	26	1.39 + 0.16	31	1.38 + 0.10 76 ^b
Late	1.07 + 0.25	14	0.76 + 0.14	36	1.29 + 0.12	31	1.02 + 0.09 81 ^b
Nest success (n = 157)							
Mayfield estimate (SD)							
Early	0.95 (0.03)	19	0.72 (0.06)	26	0.82 (0.05)	31	0.79 (0.03) 76 ^c
Late	0.55 (0.11)	14	0.50 (0.06)	36	0.88 (0.04)	31	0.64 (0.04) 81 ^c

^a $t = -2.18, P = 0.03$

^b $U = 6687.5, P = 0.02$

^c $Z = -3.05, P < 0.001$

Table 2-8. Fates of eggs from known-size clutches for crested caracara nests in south-central Florida, 1994 - 1996.

Fate	1994	1995	1996
Chick survived to independence	22 (53.7%)	34 (38.2%)	50 (56.2%)
Incubation stage			
Unknown egg/chick ^a	5 (12.2%)	20 (22.5%)	23 (25.8%)
Eggs did not hatch	3 (7.3%)	1 (1.1%)	0
Died during pipping	0	1 (1.1%)	0
Eggs abandoned	0	8 (9.01%)	0
Known predation	3 (7.3%)	2 (2.2%)	0
Nesting stage			
Chick died in nest ^b	0	0	2 (2.2%)
Chick defect/disease ^c	0	2 (2.2%)	0
Chick disappeared, fate unknown	2 (4.9%)	4 (4.4%)	7 (7.9%)
Chick fell out of nest	1 (2.4%)	1 (1.1%)	1 (1.1%)
Fledgling stage			
Killed by vehicle	1 (2.4%)	7 (7.9%)	6 (6.7%)
Fledgling found dead, cause unknown	2 (7.3%)	8 (9.0%)	0
Fledgling disappeared, fate unknown	2 (2.4%)	1 (1.1%)	0
Total eggs	41	89	89

^a Not known whether eggs were lost during incubation or whether they hatched and chicks were lost during early nesting stage.

^b Chick found dead in nest during first two weeks, from unknown causes.

^c Chick died of injury or defect before it fledged.

Table 2-9. Failure of crested caracara nests in south-central Florida, 1994-1996.

	1994	1995	1996
Total nest attempts	32	62	62
Total territories	30	48	55
Failures (% of all nest attempts)	7 (21.9%)	24 (38.7%)	11 (17.7%)
During incubation/hatching	2	9	5
During nesting period	2	7	3
After fledging	3	8	3
Territories that did not produce any young despite nesting attempt	6 (20.0%)	11 (22.9%)	5 (9.1%)

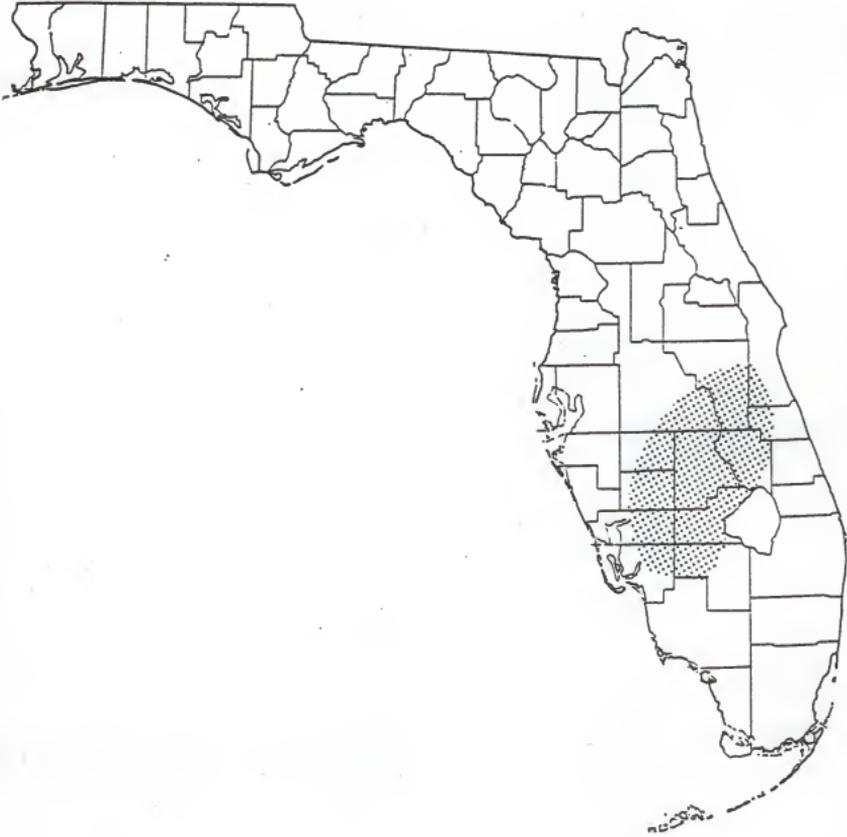


Figure 2-1. Location of study area for crested caracaras in south-central Florida. Study area encompassed much of the species' current known breeding range in Florida.

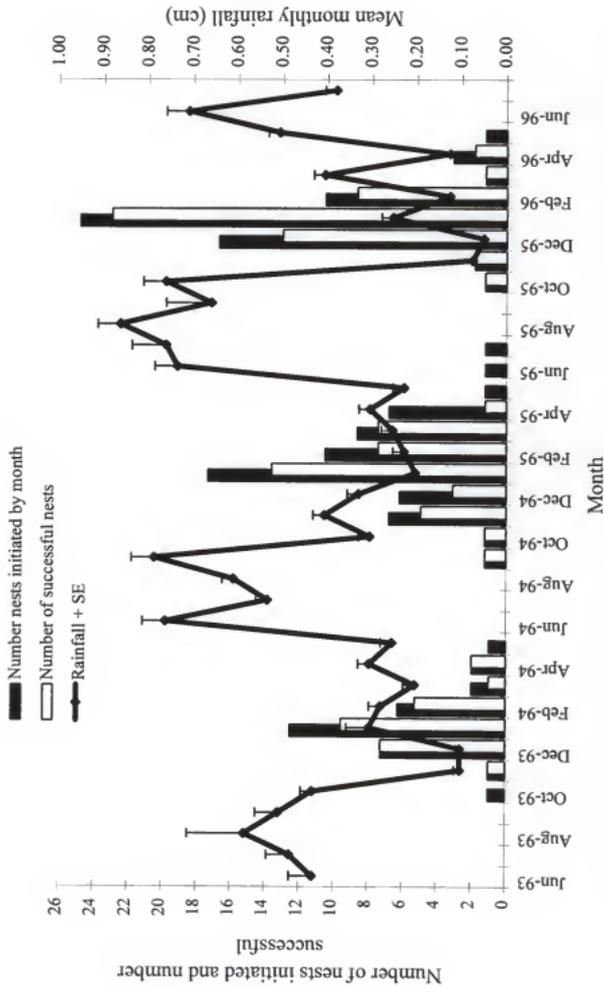


Figure 2-2. Mean monthly rainfall and breeding chronology of crested caracaras during 3 years in south-central Florida. 1994 (n = 33 nest attempts), 1995 (n = 62 attempts), 1996 (n = 62 attempts).

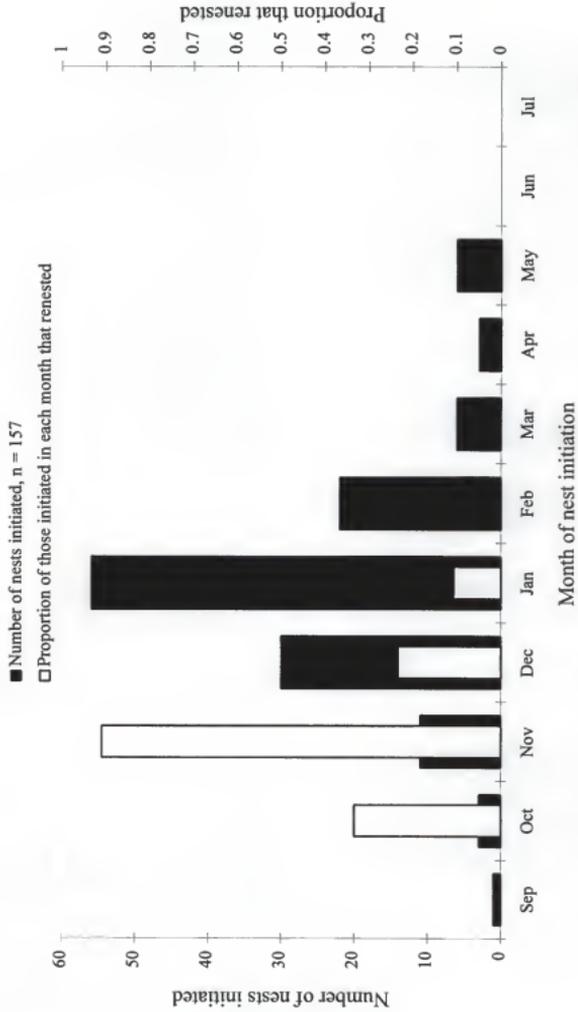


Figure 2-3. Relationship between month of first nest initiation and occurrence of re-nesting by created caracaras following either an early failure or a successful first brood, south-central Florida, 1994 - 1996.

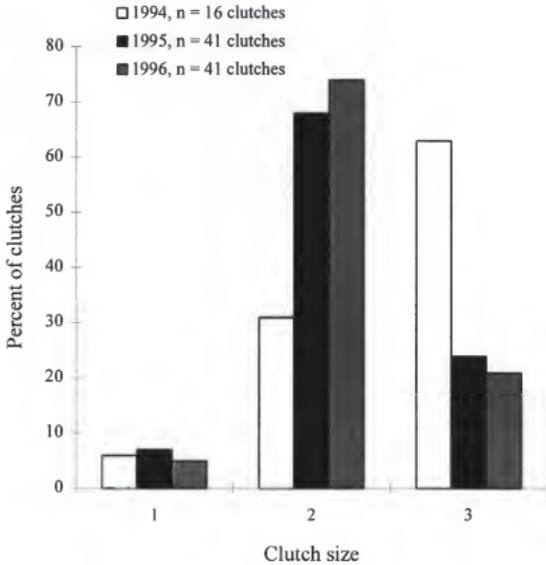


Figure 2-4. Distribution of clutch sizes by year, for crested caracara nests in south-central Florida, 1994 - 1996.

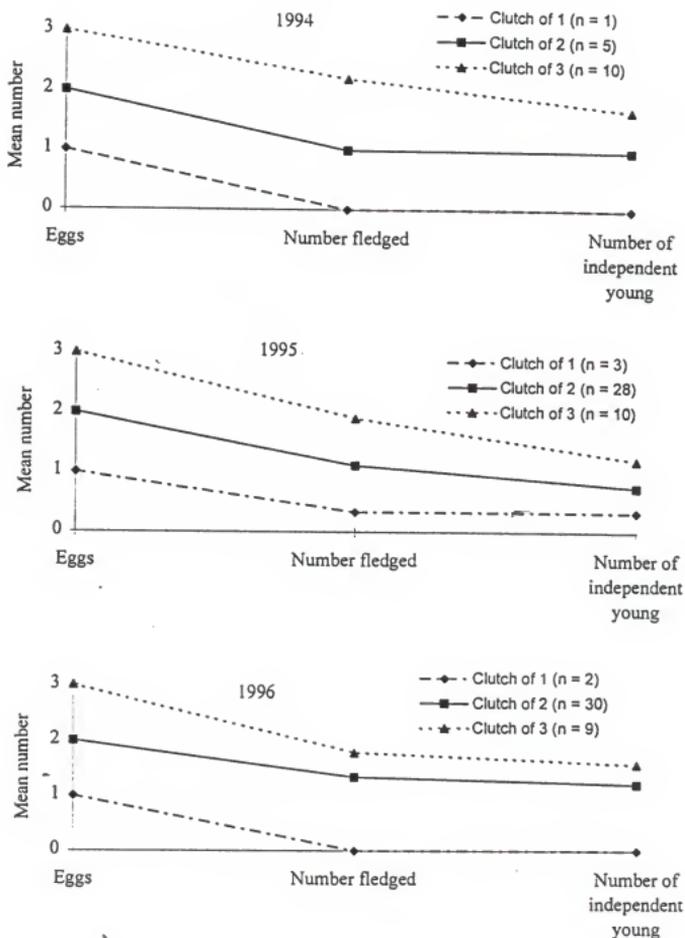


Figure 2-5. Mean number of fledglings and independent young per nest for each clutch size during each year for crested caracaras in south-central Florida, 1994 - 1996. n = indicates number of clutches.

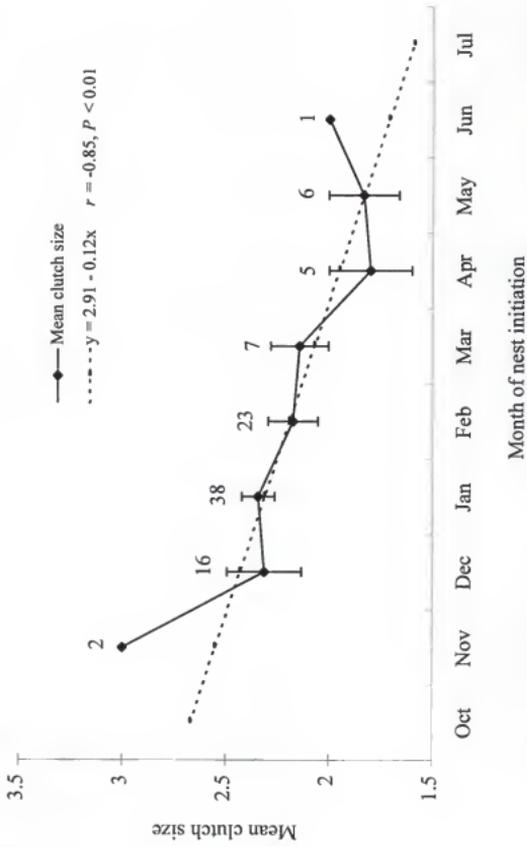


Figure 2-6. Relationship between mean clutch size and month of nest initiation for 98 known-size clutches of crested caracaras in south-central Florida, 1994 - 1996. Number of clutches is shown above each month.

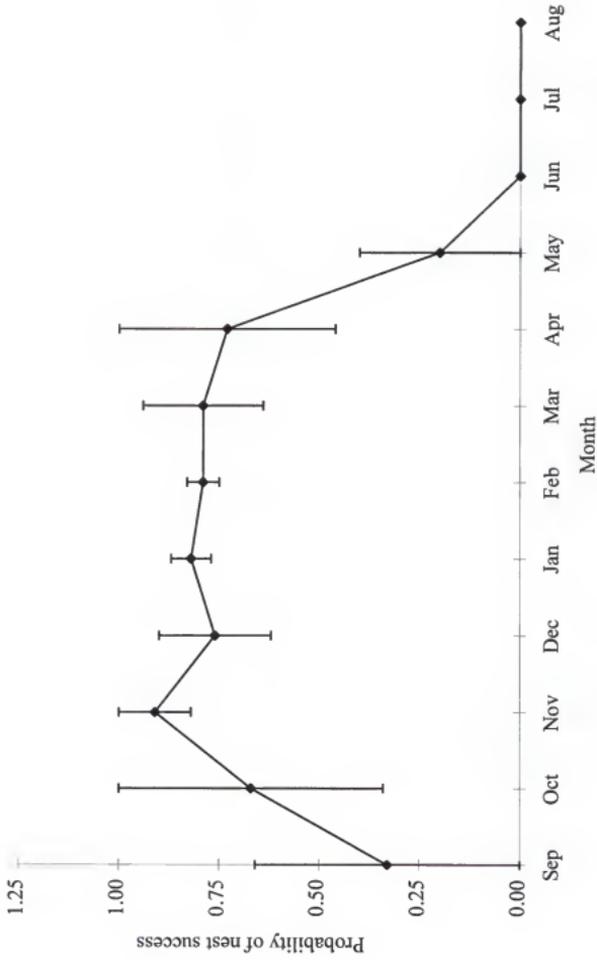


Figure 2-7. Mayfield probability of nest success (\pm SD) by month for crested caracaras in south-central Florida, 1994 - 1996 ($n = 157$ nest attempts).

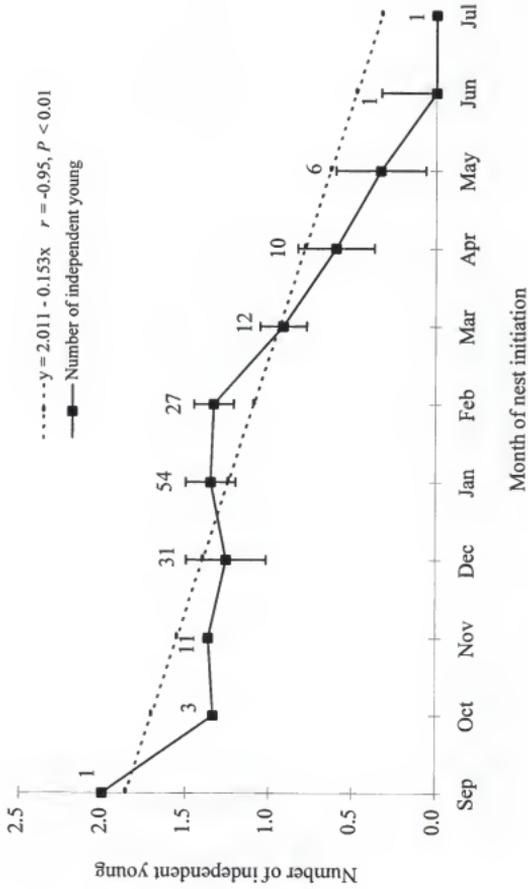


Figure 2-8. Relationship between productivity per nest attempt ($n = 157$ attempts) and month of nest initiation for crested caracaras in Florida, 1994 - 1996. Number of nest attempts is shown above each month.

CHAPTER 3

EFFECTS ON PRODUCTIVITY AND POTENTIAL COSTS OF DOUBLE BROODING IN CRESTED CARACARAS

Introduction

Reproductive success in birds is determined by the number of broods and productivity per brood (Drury 1961, Lack 1966). The number of successful broods produced each breeding season by a breeding pair is an important contribution to an individual's annual and lifetime productivity (Lack 1954, Stearns 1992, Newton 1989). Successful multiple brooding may also be important in the maintenance of populations (Holmes et al. 1992).

In temperate latitudes, many avian species regularly raise more than one brood per year (Smith and Roff 1980, Westmoreland et al 1986, den Boer-Hazewinkel 1987, Guepel and DeSante 1990, Smith and Marquiss 1995). Occurrence of multiple brooding and temporal spacing of broods are influenced by length of the breeding season, food availability, body size, clutch size, development time, amount of parental care, and experience of the parents (Perrins 1970, Ricklefs 1984, Bednarz 1987, Askenmo and Unger 1986, Tinbergen and van Balen 1988, Holmes et al. 1991, 1992).

Successful production of multiple broods in a season may increase fitness only if the strategy does not negatively influence the future fecundity or survival of either breeders or first-brood young (Williams 1966, den Boer-Hazewinkel 1987, Nur 1988, Smith and Marquis 1995, Verhulst and Hut 1996). Multiple-brooded individuals usually fledge significantly more young per season than single-brooded individuals, but reproductive success and offspring quality generally decline between first and second broods, and the probability of independent offspring being recruited into the breeding population is lower for young from second broods (Smith and Roff 1980, Hochachka 1990). Despite these costs, multiple brooding may be maintained in some species

because it increases an individual's lifetime reproductive success (Perrins 1970, den Boer-Hazewinkel 1987, Newton 1989). Under certain environmental conditions, there may be little cost to producing additional broods (Ormerod and Tyler 1993, Smith and Marquiss 1995), so the benefit easily outweighs the cost.

Raptors typically raise only one brood per year because of the length of time required for the complete breeding cycle including, for many species, an extended post-fledging dependency period (Newton 1979). Although many raptors reneest after losing a clutch (Newton 1979, Wood and Collopy 1993, Forsman et al 1995), true double brooding (i.e., individuals attempting to rear a second brood in the same breeding season after a successful first attempt) rarely has been confirmed. Second brood attempts, generally in response to peaks in prey cycles, have been reported for some smaller species with short breeding cycles such as the American Kestrel (*Falco sparverius*; Howell 1932, Stahlecker and Griese 1977, Toland 1985), Eurasian Kestrel (*F. tinnunculus*; Fargallo et al. 1996), Black-shouldered Kite (*Elanus caeruleus*; Malherbe 1963), Burrowing Owl (*Athene cunicularia*; Millsap and Bear 1990), and Barn Owl (*Tyto alba*; Witmer and Patrick 1987). Multiple brooding occurs in some larger raptors that live year-round in subtropical and tropical environments where food is abundant for most of the year, such as the Harris' Hawk (*Parabuteo unicinctus*; Mader 1975, Bednarz 1987), Pale Chanting Goshawk (*Melierax poliopterus*; Smeenk and Smeenk-Enserink 1975), and Galapagos Hawk (*Buteo galapagoensis*; DeVries 1975).

I documented double brooding in crested caracaras (*Caracara plancus*) during three successive years in south-central Florida. The crested caracara is a medium-sized raptor that occurs in open grassland and savanna habitats throughout Central and South America, in the southwestern U.S., and in Florida (del Hoyo et al 1994). Circumstantial evidence of possible double brooding in this species has been reported in Florida (Bent 1937), Texas (Dickinson and Arnold 1996), and Mexico (Rivera-Rodríguez and Rodríguez-Estrella unpubl. data) but the prevalence of this phenomenon remains unknown. Recently, widespread loss of grassland habitats to expanding agriculture and urban development has focused concern on the Florida population (Layne 1996, B.

Millsap pers. comm.), which is currently listed as Threatened by the U.S. Fish and Wildlife Service and by the state of Florida. Because successful double brooding may affect individuals' lifetime reproductive success and annual population productivity, I was interested in evaluating (1) the extent to which double brooding occurs, (2) the contribution of second broods to an individual's annual productivity, (3) potential costs in terms of reduced survivorship of first- or second-brood young, (4) potential costs to double brooded adults in terms of reduced survival or fecundity, or delayed nesting in the following year, and (5) factors that may contribute to the occurrence of double brooding.

Study Area and Methods

The study area in south-central Florida included all or parts of Highlands, Glades, Okeechobee, Osceola, DeSoto, Polk, Hendry, and Indian River counties and was centered on the MacArthur Agro-Ecology Research Center (27°10'N, 81°12'W), Highlands County. This area encompasses much of the species' currently known breeding range in Florida. Breeding pairs of crested caracaras occupy open grassland and pasture habitats containing single or small clumps of live oaks (*Quercus virginiana*), cypress (*Taxodium sp.*), and cabbage palms (*Sabal palmetto*). Breeding pairs are monogamous and remain on territories year-round (Morrison 1996).

Beginning in January 1994, I conducted monthly surveys in known territories to look for signs of nesting activity. Once found, nests were checked weekly until fates were determined. I considered a nesting attempt to be actual egg-laying, not just nest construction. I determined clutch size, hatching date, brood size, and chick age at each nest using a mirror attached to an extendible pole. Age was determined by assessing the chicks' size and feather development.

I assigned each nest a week of initiation based either on known time of egg-laying or on back-dating from known hatching or fledging dates (assuming an incubation period of approximately 32 days and a nestling period of approximately 8 weeks). I then calculated week of initiation from the first week of September, which I assigned as the

first week of the breeding season based on the earliest known egg-laying during all three years.

I estimated annual nesting success using Mayfield's method (Mayfield 1961). I defined a successful nest as one that fledged at least one young. I compared Mayfield estimates of nest success among nest types using a Z-test (Hensler and Nichols 1981).

I measured annual productivity as the number of young fledged per successful pair. I assigned the classification of "single brood" to pairs that made only one nesting attempt during an annual breeding season. Double brooded pairs were defined as those that made a second nesting attempt following a successful first effort, in the same breeding season. Territories in which pairs produced replacement clutches after nest failures were not included. Clutch size is reported only for known-size clutches. I defined interbrood interval as the number of weeks between fledging of the first brood and initiation of egg-laying in the second nest.

To evaluate whether laying a second clutch affected the duration of post-fledging care or survival of first-brood fledglings, I used radiotelemetry to determine times of departure of first and second-brood young from their natal territory and survival past independence. Nestling caracaras were color banded and radiotagged (one per nest) while still in the nest at 7-8 weeks of age or just after fledging, when they could be captured easily on the ground. Young continue to beg and be fed by their parents for several months after fledging (Morrison unpubl. data), so I measured the duration of parental care as the period during which young remained in their natal territory. The natal territory was defined as the area within a radius of 3 km from the nest, which approximates a breeding pair's home range (see Chapter 4). I defined permanent departure from the natal territory as the first time a juvenile was located more than 3 km from the nest followed by a minimum of 3 consecutive weeks at distances > 3 km from the nest.

I obtained survival data for 61 radiotagged young through their first year via weekly aerial radiotracking surveys. I estimated probabilities of survival to recruitment for young from single, first, and second nests using these survival data along with the

Kaplan-Meier procedure modified for staggered entry of animals (Pollock et al. 1989). Age at first reproduction is not known for this species but is estimated to be 3 to 4 years (Voous 1983, Layne 1996), so I used 1200 days post fledging as an estimate of recruitment age. I compared survival probability functions between groups using the log-rank test (Cox and Oakes 1984, Pollock et al. 1989).

To evaluate potential costs to double brooded adults, I followed the fate of color-banded individuals. I used the likelihood ratio test in PROC LIFETEST in SAS (SAS Institute 1985) to compare predicted survival estimates for 16 known double-brooded and 38 known single-brooded adults. Survival through at least 2 years was known for 11 double-brooded and 27 single-brooded adults. Survival was defined as remaining and breeding on the same territory in subsequent breeding seasons. To assess the potential cost of reduced fecundity in the year following a double brood event, for 1995 and 1996, I compared clutch sizes between the group of known adults that had double brooded the previous year and the group of known adults that produced only one brood. I also examined whether double brooding had any influence on timing of the first nest attempt of these pairs in the following year. For 1995 and 1996, I compared timing of first nest initiation between pairs that had double brooded the previous year and pairs that produced only one brood.

I evaluated potential effects of double brooding on population growth rates and likelihood of persistence. For this analysis, I used values previously calculated for survival of single- and double-brooded adults through 2 years, survival of first-, second-, and single-brood young to 2 years post-fledging, and mean numbers of young fledged for single- and double-brooded pairs. I calculated population size and population growth rate during 3 consecutive years for two hypothetical populations, one in which double brooding occurred in approximately 10% of the population each year, and one with no double brooding. I assumed each initial population size to be 100 breeding pairs (50 females) and age of first breeding to be 4 years.

I used logistic regression to evaluate the effects of several factors on the occurrence of double brooding in this population. I examined whether initiation date of

the first clutch (INITWK) and numbers of fledglings in the first brood (NUMFRST) influenced the occurrence of double brooding during the same year. For pairs whose reproductive history was known for at least 2 years, I examined whether the occurrence of double brooding during any year was influenced by whether or not the pair had double brooded during the previous year (DBPREV), the number of fledglings from the previous year (NUMPREV), and the fledging date from the previous year (WKPREV).

Statistical tests were conducted using SigmaStat (Jandel Scientific 1995). Significance for all tests was assumed at the $\alpha = 0.05$ level. Comparisons of fecundity, timing of nest initiation, and productivity were made using Wilcoxon rank sum and Kruskal-Wallis nonparametric tests (Sokal and Rohlf 1995). Post-hoc power estimates for two-sided Wilcoxon tests were obtained using the program Resampling Stats (Resampling Stats Inc. 1995). I first simulated 10,000 values of the rank sum statistic under the null hypothesis of no differences between nest types. The 95th percentile of these values was used as the critical value for determining significance of the difference between nest types, given the two corresponding sample sizes. Real data values were resampled to approximate the alternate distribution of the rank sum statistic as suggested by the data. The power of the Wilcoxon test at the 0.05 level was then estimated as the proportion of times out of 10,000 iterations that the resampled test statistic was at least as large as the critical value.

Results

Extent of Occurrence of Double Brooding

I monitored breeding activity on 60 different territories throughout the study, although only a subset of those each year (Table 3-1). A second brood attempt was made on 13 territories (21.7%, Table 3-1). In three territories, the pair initiated a second nesting attempt during two consecutive years, although none of these pairs successfully fledged two broods in more than one year. Both adults were color banded in one territory where double brooding occurred. In all other territories where double brooding occurred, one adult was banded and participated in both nesting efforts.

Timing of Broods

Pairs that attempted a second brood initiated their first nests significantly earlier ($U = 1504.5$, $P = 0.00$, $n = 16$) than single-brooded pairs ($n = 103$) (Table 3-1). Second nests of double-brooded pairs were initiated 9 - 13 weeks later ($U = 26.5$, $P = 0.00$, $n = 16$) than nests of single-brooded pairs. Median week of nest initiation did not differ among years for each nest type (single brood, $H = 0.79$, $P = 0.67$, $n = 103$; first of two, $H = 1.88$, $P = 0.39$, $n = 16$; second of two, $H = 0.65$, $P = 0.72$, $n = 16$, Table 3-1).

Only early breeders attempted to double brood. The number of pairs that attempted second broods decreased with increasing laying date (Figure 3-1). Of pairs that attempted a second brood ($n = 16$), 72% fledged young from their first brood before 1 March, 94% before 1 April. Of all pairs that fledged a brood before 1 March ($n = 16$), 69% made a second nesting attempt. The mean interbrood interval was 7.6 weeks (range 2 - 13 weeks, $n = 16$), and interval length was positively correlated with the number of young fledged from the first nest ($r = 0.50$, $P < 0.05$, Figure 3-2).

Productivity and Nesting Success

Mean clutch size declined between the first and second nests of double-brooded pairs (Table 3-2). Laying times of second clutches and the first clutches of late breeders overlapped during March and early April (Figure 3-1). Mayfield success estimates for second nests were significantly lower than those for first nests or nests of single-brooded pairs (Table 3-2). Of the pairs that attempted two broods, those that had an early first nest produced the earliest second broods; these early second broods had the highest probability of success (Figure 3-3). Taking into account all nesting attempts, double brooded pairs did not necessarily fledge more young than single-brooded pairs ($T = 1697.50$, $P = 0.21$, Figure 3-4), primarily owing to high failure rates of late second broods. Pairs that nested earliest however, had the highest chance of successfully fledging both broods (Figure 3-3), thus also had the highest chance of fledging more young each year than single brooded pairs.

Parental Care and Post-fledging Survival

First-brood young incurred shorter periods of post-fledging parental care. Mean time to departure from the natal territory of first-brood fledglings ($11 \text{ wk} \pm 2.56 \text{ SE}$, $n=14$ broods) was significantly shorter ($U=290.5$, $P=0.00$) than that of fledglings from single-brood pairs ($33 \text{ wk} \pm 1.61 \text{ SE}$, $n=32$ broods) or of second-brood fledglings ($29.7 \text{ wk} \pm 1.73 \text{ SE}$, $n=6$ broods, $U=33.0$, $P=0.01$). Post-fledging care of first-brood young overlapped incubation of the second clutch in all cases. Young from first broods typically left the natal territory during the early nestling stage of the second brood, but whether the parents enforced this departure is not known. The period of post-fledging parental care for fledglings from single-brood pairs and second-brood fledglings did not differ ($U=54.4$, $P=0.40$). In many cases, single- and second-brood fledglings remained in the natal territory until the parents began breeding the following year.

Estimates of survival probability to recruitment differed between young from first and second broods (Kaplan-Meier survival function, $X^2=8.51$, $P=0.004$, Figure 3-5). Survival estimates for young from first broods were also higher than estimates for young from single broods ($X^2=75.95$, $P=0.00$, Figure 3-5).

Potential Costs to Adults

Survival estimates to subsequent breeding seasons did not differ ($X^2=0.01$, $P=0.92$) between known double brooded ($n=16$) and single-brooded ($n=38$) adults (Table 3-3). Clutch sizes did not differ ($U=95.0$, $P=1.0$) between known adults that had successfully double brooded in the previous year (2.67 ± 0.33 , $n=10$) and known adults that produced only one brood (2.22 ± 0.22 , $n=19$), but power of this test was low ($1-\beta=0.05$) because of small sample sizes each year. I did not detect a delay in nesting by double brooded adults in the year following a double brood event. The median week of egg-laying did not differ between pairs that had successfully double-brooded the previous year and pairs that fledged only one brood in either 1995 ($U=80.0$, $P=0.13$; median week = 19, $n=3$ double brooded pairs; median week = 22, $n=35$ single-brooded pairs) or 1996 ($U=105.0$, $P=0.46$; median week = 20, $n=4$ double brooded pairs;

median week = 22, $n = 43$ single-brooded pairs). Power of these tests was low, however, at 0.23 and 0.12, respectively.

Effects on Population Growth and Persistence

The hypothetical population that included double brooding by approximately 10% of pairs annually grew at a slightly faster rate than the population comprised of only single-brooded pairs. After 3 years, differences in size were negligible between the two populations, however (Table 3-4).

Influence of Factors

Timing of initiation of the first brood (INITWK) was the only factor important in predicting the occurrence of double brooding that same year by caracara pairs (Table 3-5). For pairs whose reproductive status was known for the previous year ($n = 45$), the occurrence of double brooding in any year was not influenced by double brooding the previous year, the number fledged during the previous year, or the date of fledging the previous year (Table 3-6).

Discussion

Life history theory predicts that a breeding attempt will occur when the likely benefits to lifetime reproductive success exceed expected costs (Williams 1966, Stearns 1992). In Florida's crested caracara population, only a small percentage of pairs attempt a second brood in any year. This strategy may be maintained, however, because double brooded individuals may incur higher lifetime reproductive success (Perrins 1970, den Boer-Hazewinkel 1987). Few second nests are successful and the probability of recruitment is lower for second-brood young. Individuals that successfully fledge two broods in a season are more productive, however, so they potentially have more young recruited into the breeding population. In addition, costs of double brooding to adults and young seem minimal.

Second clutches may reduce the reproductive value of the first brood because of reduced post-fledging care of first-brood fledglings (Verhulst and Hut 1996). I found no evidence that first-brood young incurred reduced post-fledging survival despite

substantially reduced post-fledging parental care. Indeed, first-brood fledglings actually had the highest probability of survival to recruitment. This suggests that juvenile caracaras can become independent foragers in a period as short as 7-8 weeks.

I found little evidence of costs to double brooded adults, though these conclusions are preliminary because of the short time frame of the study, small sample sizes, and low power of statistical tests. Caracaras are long-lived (Klimkiewicz and Fletcher 1989, Morrison 1996), so true costs may not be evident in the short term. Additional years of tracking the survival and reproductive efforts of known adults would be needed to properly evaluate these potential costs.

The occurrence of double brooding in Florida's crested caracara population may be related to both length of the breeding season and to food availability, two factors that determine the number and the timing of broods produced by a breeding pair (Perrins 1970, Newton 1979, Tinbergen and van Balen 1988). Crested caracaras in Florida exhibit a long breeding season, generally beginning in September and continuing throughout the winter and into June or early July (Morrison 1996). Pairs that nest early may have sufficient time to raise two broods.

Food supply is known to influence the occurrence and timing of breeding in raptors (Cavé 1968, Dijkstra et al. 1982, Newton and Marquiss 1984). Food supply has been shown to influence the number of young fledged annually by a breeding pair primarily by influencing the occurrence of multiple brooding (Malherbe 1963, Bednarz 1987). The crested caracara has a varied diet and feeds on live vertebrate and invertebrate prey as well as carrion (Richmond 1976, Ellis et al. 1988, Morrison 1996), therefore breeding need not be synchronized with availability of particular foods. The caracara typically inhabits areas associated with human activity such as cattle ranches, agricultural lands, and urban dumps (Rodríguez-Estrella 1996, pers. obs.). These habitats may provide a diversity of predictable food resources, perhaps owing to regular schedules of management activities. The combination of a relatively mild climate and the perpetual availability of a variety of food resources apparently allows early initiation of breeding and occasionally, double brooding by some pairs. Whether individuals actually attempt a

second brood or even attempt to nest early in the season may depend on the age and quality of individuals, experience of pairs, and territory quality. The occurrence of double-brooding in any year was not influenced by the previous year's reproductive effort, suggesting that double brooded individuals may be the most fit.

Year-round residency and persistence of the pair bond between nesting seasons may facilitate double brooding in crested caracaras because of individuals' familiarity with habitats and resources. Males and females have similar parental roles, so pairs may have little difficulty feeding first-brood fledglings and incubating a second clutch. Caracaras also frequently reuse old nests for first and second breeding attempts. Reuse of old nests reduces the time required for nest-building (Mader 1975, Toland 1985, Westmoreland et al. 1986).

Double brooding appears to be a regular but uncommon occurrence in Florida's population of crested caracaras and may occur in other populations (Dickinson and Arnold 1996, Rodríguez-Estrella and Rivera-Rodríguez, unpubl. data). An extended breeding season and post-fledging dependency period may have contributed to a previous lack of its confirmation. Some juveniles remain on their natal territory for several months after fledging (Morrison 1996). Therefore, determining whether juveniles seen with adults during any month of the year are from a single or second brood is not possible, unless individual birds are marked and have a known history.

The ultimate value of double brooding must be that double-brooded individuals produce more young with some probability of establishing themselves in the breeding population. Whether or not double-brooding contributes to overall population growth rates is of lesser importance; the overriding goal for individuals is to leave more offspring than the average member of the population. Combined with an extended breeding season, environmental and food conditions during some years may be favorable for some caracara pairs to attempt a second nest. In addition, costs may be small, at worst. Of greater interest is why more individuals do not attempt second broods. For many avian species, the occurrence and timing of a breeding effort is influenced by age and experience of the parents or energetic constraints related to territory or individual quality

(e.g., Smith and Roff 1980, Evans Ogden and Stutchbury 1996). The absence of double brooding in some early nesting pairs of crested caracaras and the lack of earlier nesting by many single-brooded pairs may be related to these factors. Further studies of conditions that influence the occurrence and timing of breeding by individuals and a more accurate assessment of recruitment rates of first and second-brood young are needed to better understand the contribution of double brooding to individuals' lifetime reproductive success and to the overall dynamics of Florida's crested caracara population.

Table 3-1. Occurrence and timing of nesting attempts between years for crested caracaras in south-central Florida. NA = not applicable for that year.

Year	Total territories examined/new territories added	No. of 2nd nest attempts found (%) / Different from previous year	Median week of initiation of single brood nests	n	Median week of initiation of first of two nest attempts	n	Median week of initiation of second of two nest attempts	n
1994	28/28	3 (10.7)/NA	21 (3rd wk Jan)	25	14 (5th wk Nov)	3	32 (2nd wk Apr)	3
1995	43/17	8 (18.6)/7	22 (4th wk Jan)	35	12 (4th wk Nov)	8	32 (2nd wk Apr)	8
1996	48/15	5 (10.4)/3	22 (4th wk Jan)	43	16 (3rd wk Dec)	5	35 (4th wk Apr)	5
Overall	60 territories	16 attempts/13 territories		103		16		16

Table 3-2. Clutch size (mean \pm SE) and nesting success (SD in parentheses) between nest types for crested caracaras in south-central Florida, 1994-1996. The same letter indicates significant differences between nest types. ND = no data on clutch sizes of first or second nests in 1994 because these nests were found after hatching.

Nest type	Year	Clutch size	<i>n</i>	Mayfield nest success	<i>n</i>
Single broods	1994	2.60 + 0.16	15	0.67 (0.09)	25
	1995	2.28 + 0.11	25	0.72 (0.05)	35
	1996	2.22 + 0.09	32	0.92 (0.03)	43
Pooled		2.32 + 0.07	72	0.81 (0.03) ^a	103
First of two	1994	ND		1.00 (0.00)	3
	1995	2.66 + 0.32	3	1.00 (0.00)	8
	1996	2.33 + 0.33	3	1.00 (0.00)	5
Pooled		2.50 \pm 0.22 ^b	6	1.00 (0.00) ^c	16
Second of two	1994	ND		1.00 (0.00)	3
	1995	1.80 + 0.02	5	0.35 (0.15)	8
	1996	2.00 + 0.00	2	0.25 (0.20)	5
Pooled		1.86 \pm 0.14 ^b	7	0.35 (0.12) ^{ac}	16

^a $Z = 3.72, P < 0.0002$

^b $U = 33.0, P = 0.03$

^c $Z = 4.19, P < 0.0001$

Table 3-3. Estimated parameters for evaluating contribution of double brooding to population growth for Florida's crested caracaras. Parameters estimated from data collected during 1994 - 1996.

Parameter	Mean number fledged per year	Probability of adult survival to subsequent year	Probability of fledgling survival to subsequent year
Year 1			
Single	1.80	0.82	0.71
Double	3.00	0.88	0.75 ^a
Year 2			
Single	1.60	0.70	0.46
Double	1.19	0.78	0.43
Year 3			
Single	1.53	0.70	0.43
Double	1.30	0.78	0.36

^a Survival estimates were calculated separately for young from first and second broods. I assumed half of all young produced by double-brooded adults were from single broods and half were from second broods.

Year 1 ($0.5 \cdot 1.00 + 0.5 \cdot 0.50$)

Year 2 ($0.5 \cdot 0.73 + 0.5 \cdot 0.13$)

Year 3 ($0.5 \cdot 0.58 + 0.5 \cdot 0.13$)

Table 3-4. Estimation of population size and annual growth rate for two hypothetical populations of crested caracaras in south-central Florida, one in which all pairs only produce a single brood each year, and one in which approximately 10% of pairs successfully produce two broods each year.

Single broods only

Year	Adults	Total number young fledged	Total number 1 year olds	Total number 2 year olds	Total N	λ
1	50.00	90.00			140.00	2.80
2	41.00	65.60	63.90		170.50	1.22
3	28.70	43.91	46.58	29.39	148.58	0.87
Mean						1.63

Single and double broods

Year	Adults	Total number young fledged	Total number 1 year olds	Total number 2 year olds	Total N	λ
1						
single	45.00	81.00			126.00	2.92
double	5.00	15.00			20.00	
2						
single	37.17	59.47	57.51		154.15	1.14
double	4.13	4.91	3.69		12.73	
3						
single	26.32	40.26	42.23	26.45	135.26	0.88
double	2.92	3.80	2.85	1.23	10.80	
Mean						1.65

Table 3-5. Statistics for logistic regression analysis of the influence of timing of initiation of the first brood (INITWK) and the number fledged in the first brood (NUMFRST) on the occurrence of double brooding in crested caracaras in south-central Florida, 1994 - 1996.

n = 16 double-brooded pairs, 103 single-brooded pairs.

Variable	Coefficient	SE	<i>P</i>
Constant	7.50	2.22	0.001
INITWK	-0.52	0.12	<0.001
NUMFRST	0.01	0.43	0.97

Table 3-6. Statistics for logistic regression analysis of the influence of double brooding the previous year (DBPREV), fledging date (WKPREV) and number fledged the previous year (NUMPREV) on the occurrence of double brooding in crested caracaras in south-central Florida, 1994 - 1996. $n = 11$ double-brooded pairs, 34 single-brooded pairs.

Variable	Coefficient	SE	<i>P</i>
Constant	2.40	0.28	0.39
DBPREV	0.72	0.92	0.44
WKPREV	-0.12	0.86	0.15
NUMPREV	0.27	0.55	0.63

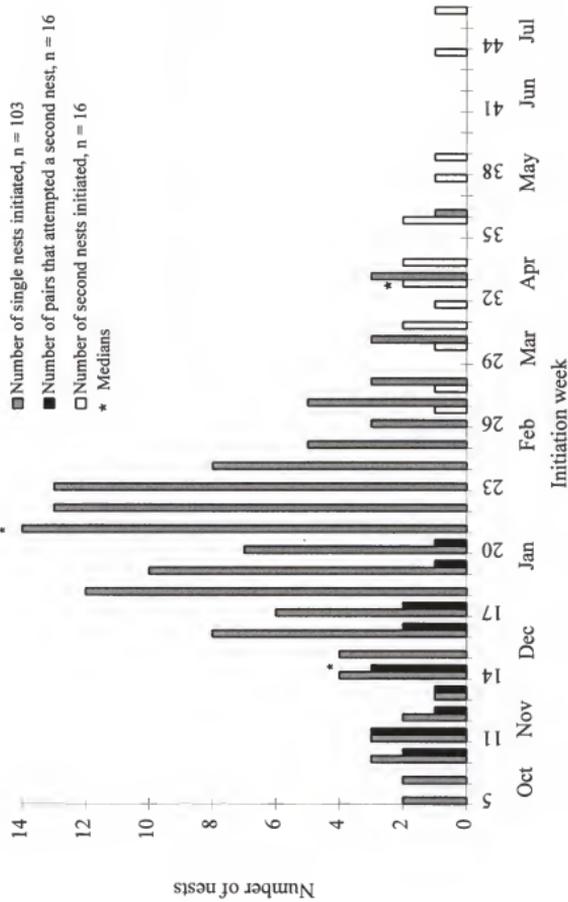


Figure 3-1. Timing of nest initiation throughout the breeding season for crested caracaras in south-central Florida, 1994 - 1996.

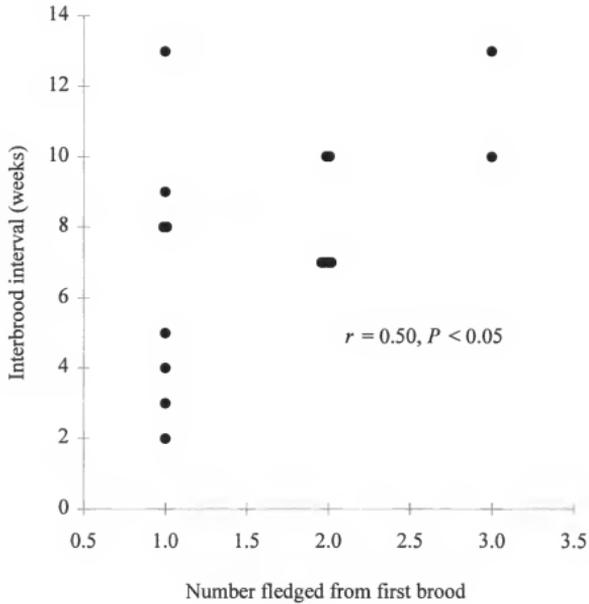


Figure 3-2. Length of the interbrood interval in relation to number fledged from the first nesting attempt for double brooded crested caracaras in south-central Florida, 1994 - 1996. $n = 16$ pairs.

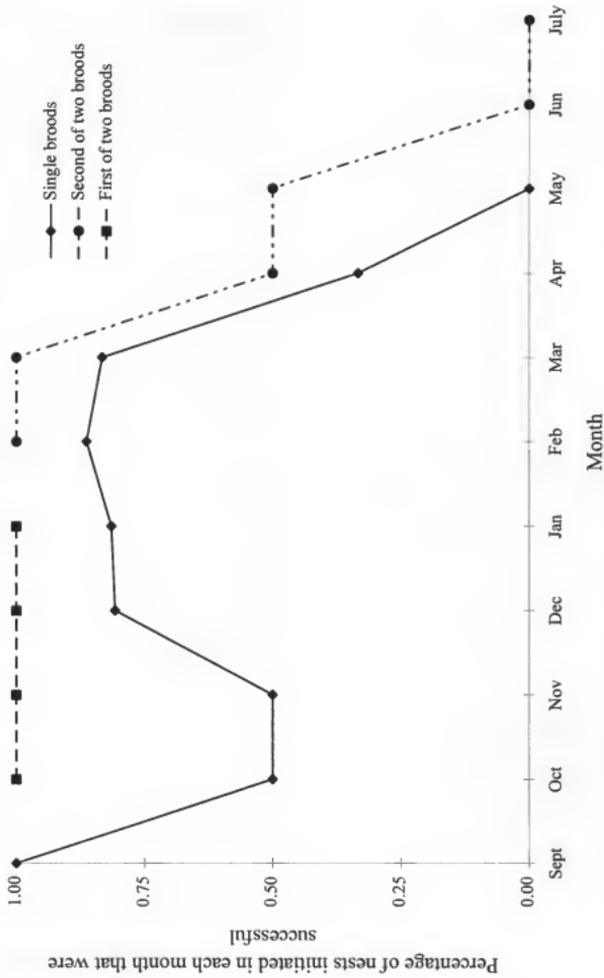


Figure 3-3. Proportion of nests initiated in each month that were successful, for crested caracaras in south central Florida, 1994 - 1996.

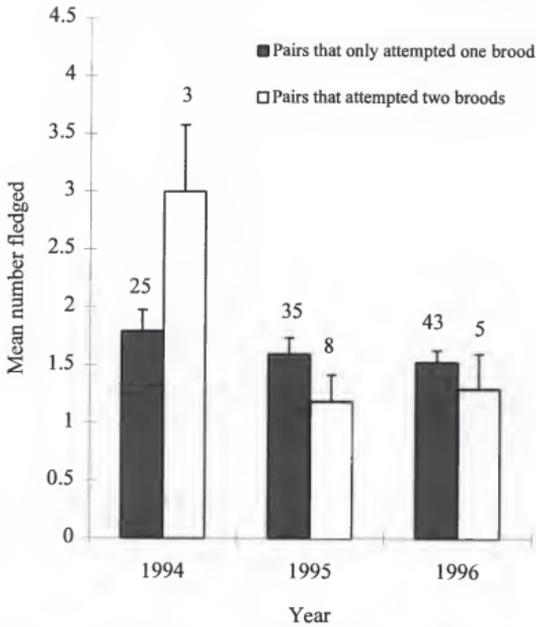


Figure 3-4. Mean number of young fledged per pair for pairs of crested caracaras nesting in south-central Florida, 1994 -1996. Number of pairs is shown above each column.

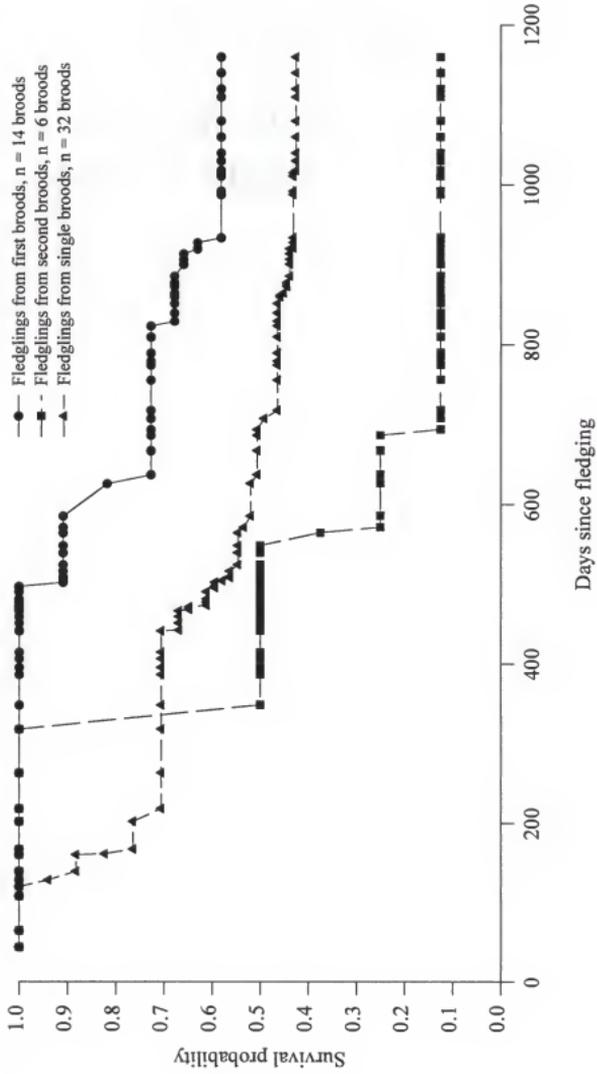


Figure 3-5. Kaplan-Meier survival functions estimated for juvenile crested caracaras from first, second, and single broods in south-central Florida, 1994 - 1996.

CHAPTER 4

HABITAT ASSOCIATIONS AND PRODUCTIVITY OF CARACARAS ON CATTLE RANCHES

Introduction

Wildlife managers face the increasingly difficult task of providing suitable areas and habitats for wildlife in landscapes that are continually changing due to a complex array of human-induced processes. Management of wide-ranging species can be particularly challenging because individuals' activity areas may cross socio-political or landownership boundaries.

The crested caracara is a gregarious raptor with a limited distribution in North America. In Florida, a small population occurs in the south-central peninsula, a region historically dominated by native prairie. Much of this ecosystem, in which the caracara historically occurred (Phelps 1912, Nicholson 1929, 1930, Howell 1932), has been replaced by large acreages of privately-owned cattle ranches. Although these ranches consist of open grasslands with scattered trees, vegetation cover types and land management practices differ considerably from those occurring on native prairies. Most ranches include large areas of improved pasture, grasslands dominated by non-native vegetation species that are intensively managed to produce forage for cattle. The natural hydrologic regime in improved pastures also has been altered by extensive ditching and draining of wetlands.

The current landscape in south-central Florida reflects complex patterns of land ownership and land uses. Within recent decades, urban and agricultural development has escalated in this region. On private lands, remnant prairie and, increasingly, pasture habitats are being converted to citrus and sugar cane. The crested caracara is likely to be affected by these land use changes. This raptor is now often found on the cattle ranches (Layne 1978, Millsap 1989), but the degree of dependence on ranch habitats is not well

understood. Because the spatial and habitat requirements of the crested caracara and land management practices compatible with its survival remain poorly known, consequences of land use changes on this Threatened population are difficult to predict.

Understanding relationships between caracaras and land uses is critical to conservation planning for Florida's population. The objective of this study was to examine these relationships by considering habitat and spatial use of breeding adults and productivity of pairs nesting on the cattle ranches. Specifically, I identify patterns of land ownership and land use associated with active nest sites, examine home ranges of breeding adults and spatial relationships among neighboring pairs, evaluate landscape-level habitat selection by breeding pairs, and examine productivity by pairs in relation to habitat variables characteristic of cattle ranches.

Study Area

The study area encompassed approximately 21,000 km² and included all or parts of Highlands, Glades, Okeechobee, DeSoto, Osceola, Polk, Hendry, and Indian River Counties (Figure 4-1). The landscape is a mosaic of habitats, primarily grasslands and pastures interspersed with cropland, citrus groves, dairies, pine flatwoods, freshwater marshes and lakes, oak scrub, hardwood hammocks, and urban developments. Over half of this area is in private ownership. Principal land uses are cattle ranching, citrus production, and other agricultural crops. The land in public ownership is managed for a variety of uses including recreation, military training, hunting, natural areas, and river floodplain management.

Methods

Land Ownership/Land Use

I located active caracara nests by visiting known historic territories (B. Millsap pers. comm., J. Layne pers. comm.) and areas where caracaras had been observed within the past 5 years, and by searching other areas of potentially suitable habitat on both public and private lands. The searching methodology involved conducting observations near potential nest sites. I also covered entire areas on foot to look into individual cabbage

palm (*Sabal palmetto*) and live oak (*Quercus virginiana*) trees. When caracaras were observed on private land, the landowner was contacted for access permission. For each territory located, I classified landownership as private or public and primary land use in the vicinity of the nest tree as ranching, other (including urban or other agriculture), or natural.

To evaluate whether occupancy and breeding rates in caracara territories were related to patterns of land use and land ownership, I used a set of 37 territories that were monitored during all 3 years. For each year, I recorded whether or not each territory was occupied and if so, whether or not the pair made a breeding attempt. Using a Z-test with Yates' correction (Sokal and Rohlf 1995), I tested the null hypothesis of no differences in the proportions of territories that were occupied or where the pair made a breeding attempt during all 3 years, between territories on privately owned ($n = 30$) and publicly-owned lands ($n = 7$).

Home Range Estimation and Spatial Dispersion of Territories

I trapped and radiotagged 39 (16 females, 23 males) breeding adult caracaras during the nesting seasons in 1994 through 1996 (Morrison and McGehee 1996). Each captured adult was banded with a standard U.S. Fish and Wildlife Service aluminum leg band and a colored aluminum band with a unique alphanumeric character that permitted identification of individuals. Radiotransmitters (Holohil, Ltd.) were attached using a standard backpack harness constructed of Teflon ribbon and secured at the bird's chest. Because caracaras are monomorphic, gender of captured adults was determined using DNA from blood samples collected in the field (Morrison and Maltbie *in review*).

I monitored radiotagged adult caracaras throughout the year. I located all radiotagged adults (Mech 1983) and obtained GPS coordinates of their locations during weekly aerial surveys from a fixed-wing Cessna 172 aircraft. I ascertained additional locations for adult caracaras by triangulation (White and Garrott 1990). Determining ground locations was facilitated by access to ranch interiors granted by local ranchers. Most locations were taken from a distance of < 500m. I also recorded visual observations

of radiotagged adults during scheduled visits to territories. Triangulation and visual locations used for home range estimation comprised approximately 18% and 15%, respectively, of all locations for adults.

The 95% confidence circle around aerial location estimates (Marzluff et al. 1994) was approximately 42 ha. Error polygons around triangulated locations (White and Garrott 1990, Kennedy et al. 1994) were all < 50 ha; most were < 20 ha. Because all locations used for home range estimation were taken at least 24 hours apart, I did not conduct tests for independence of observations (Swihart and Slade 1985).

I delineated home ranges using kernel methods (Worton 1989, 1995, Seamen and Powell 1996) and the software RANGESV (Kenward and Hodder 1995). The boundary of each caracara's home range was defined as the 99% contour estimated with the fixed kernel method and a 0.85 smoothing factor (Kenward and Hodder 1995, Seamen and Powell 1996). Core areas (Wray et al. 1992) were identified as the 60% kernel contour using cluster analysis in RANGESV.

I compared home range estimates between males and females and between breeding and non-breeding seasons using a two-tailed Mann-Whitney test (Sokal and Rolf 1995). The breeding season was defined as the period from the beginning of incubation to the end of the post-fledging dependency period, 8 weeks after the young fledged from the nest. After this time, young were considered independent, and parents and young were together less often as a family unit.

To evaluate nesting density and spatial relationships among territories, I calculated distances between adjacent caracara nests. Using RANGESV, I evaluated overlap of 99% contours and core areas among 9 neighboring, successfully breeding pairs of caracaras inhabiting the MacArthur Agro-Ecology Research Center (MAERC) and an adjoining ranch, and among 4 neighboring, successfully breeding pairs at a site along the Kissimmee River.

Landscape-level Habitat Selection by Breeding Pairs

Habitat data

Data on vegetation cover types throughout the study area were obtained from the Florida GAP Analysis project at the University of Florida. Analyses were performed in ArcINFO GRID (Environmental Sciences Research Institute 1996). The study area map, initially classified from 1994 LANDSAT satellite imagery, was imported into the GIS in grid-cell (raster) format. The map was 1909 X 1571 cells at a grid cell resolution of 90m. I recognized 13 natural and semi-natural vegetation cover types (Table 4-1). Other cover types reflected land use conversion by humans such as citrus, croplands, sod fields, quarries, and urban areas.

Model development

I used resource selection techniques (Thomas and Taylor 1990, Manly et al. 1993) to identify habitats and landscape features that distinguished between known caracara home ranges and potentially "available" home ranges throughout the study area. These "available" units were 1296 ha in size, comparable to the average caracara's home range, and were sampled across the entire study area using a sliding window technique and the GIS. Because of the finite 90m grid cell size, square units 40 cells (3600m) on a side were used.

Resource categories used for model development consisted of variables describing proportions of the 13 natural and semi-natural vegetation cover types (Table 4-1). Cover types that reflected habitat conversion, such as citrus groves, row crops, and urban development were not included, although some caracara home ranges contained them. I assumed that conversion occurred after a caracara pair had selected the territory, so these cover types were associated by default with cover types actually selected by caracaras. Other variables included (1) total proportion vegetated, (2) total proportion of open habitat, (3) total proportion of shrubs, (4) total amount of improved pasture habitat, and (5) largest contiguous patch of improved pasture habitat (Table 4-1).

Using the GIS, I determined that caracara home ranges were at least 53% vegetated with natural or semi-natural vegetation. For model development, I only used available units that contained more than 53% natural or semi-natural vegetation ($n = 925$) and the 25 known caracara home ranges. I used the GIS to calculate values for all variables for all home ranges and available units.

I used logistic regression procedures in SAS (SAS Institute 1995) to calculate coefficients and standard errors for all variables (Manly et al. 1993). These procedures fit linear logistic regression models for binary data by the method of maximum likelihood (Menard 1995). The response probability produced by the models was the probability of a sample unit being a territory, or “used.” I assumed that variables that distinguished between the home ranges and the available units indicated selection by caracaras. Significance of variables was assumed at the $\alpha = 0.10$ level.

Because use of multiple variables results in many alternative models, selection of the “best” or “correct” model is an important step in data analysis (Burnham and Anderson 1992). To choose among the models produced in SAS, I used AIC (Akaike 1985, Burnham and Anderson 1992) and Goodman’s criterion (Goodman 1984), both of which consider the principle of parsimony in model selection. To evaluate model fit, I conducted Hosmer and Lemeshow’s goodness of fit test (Hosmer and Lemeshow 1989), which tests the null hypothesis that there are no differences between the observed and expected number of observations in each of several groups based on the percentiles of the estimated probabilities.

Model validation

A model used to make inferences about important habitats for a species is only as good as its ability to make correct predictions about new observations. I tested the ability of the “best” logistic regression model to predict use of 29 other known caracara home ranges. Because I did not have telemetry data for these test ranges, they were delineated using the GIS. For each test range, I created an area 1296 ha in size (square units 3600m

on a side) centered on the nest. I then applied the model to each test range to calculate probability of use.

Caracaras and Cattle Ranches

To evaluate the caracara's use of cattle ranches, I investigated relationships between home range size, productivity, and the proportion of improved pasture in each home range. I defined productivity as the total number of young produced during all 3 years of the study by each pair. For this analysis, I only used home ranges for which I had these data ($n = 18$). Statistical tests were conducted using SigmaStat (Jandel Scientific 1995).

Results

Land Ownership/Land Use

Land ownership and land use patterns were determined for 65 active caracara territories. Most territories found were on privately-owned land (Table 4-2). The major land use in the vicinity of caracara nests at all sites was cattle ranching (Table 4-2). Lands under public ownership where I found caracara territories were primarily managed for native habitats, including prairie, although moderate grazing occurred in some areas. The proportions of the 37 preselected territories that were occupied and where adults attempted breeding during all 3 years were higher ($z = 2.64$, $P = 0.008$, $1-\beta = 0.71$ and $z = 2.02$, $P = 0.04$, $1-\beta = 0.52$, respectively) for territories on privately-owned lands (Figure 4-2).

Home Ranges and Spatial Dispersion of Territories

Breeding adult caracaras remained on territory throughout the year. I obtained usable data for home range estimation from 25 individuals (16 males and 9 females). Home range sizes varied from approximately 551 to 2778 ha (Table 4-3). Most home ranges were more than 80% vegetated with natural or semi-natural vegetation. All ranges contained improved pasture, ranging from approximately 11% to 94% of the naturally vegetated area (Table 4-3).

Approximately 90% of locations for all adults were within 2.5 km of the nest (Figure 4-3). Home range sizes did not differ between males and females ($t = 1.13$, $P = 0.27$, $df = 23$), although power of this test was low ($1-\beta = 0.10$). Adult caracaras ranged farther from the nest, on average, during the non-breeding season ($X^2 = 56.17$, $P < 0.001$, $df = 7$, Figure 4-4). For 11 adult caracaras (7M, 4F) having approximately equal numbers of radiolocations for each season, breeding season home ranges were smaller than non-breeding season home ranges (paired t -tests, $t = -3.45$, $P = 0.006$, $df = 10$, $1-\beta = 0.86$).

Inter-nest distances for neighboring successfully breeding pairs averaged 3.08 km \pm 0.18 SE (range 1.01 - 5.08 km, $n = 30$ pairs, Figure 4-5). Core areas rarely overlapped (Table 4-4), although 99% contours overlapped on average $14.7\% \pm 2.82$ SE at MAERC and $10.08\% \pm 5.39$ SE at the Kissimmee River site (Table 4-5). At MAERC, 6 caracara home ranges overlapped home ranges of at least 2 other pairs of caracaras.

Landscape-level Habitat Selection by Breeding Pairs

The model that best distinguished between known caracara home ranges and available units throughout the study area indicated a negative association of caracara home ranges with the variables pine forest, mixed forest, and woodland, and a positive association with the variables improved pasture, and contiguous pasture. All variables were significant at the 0.10 level (Table 4-6). Hosmer and Lemeshow's test indicated good fit of this model ($G = 10.16$, $P = 0.25$).

Since caracaras are known to be associated with open rather than forested habitats, I reran logistic regression analysis with the forest and woodland variables omitted. Results of this analysis indicated a positive association between caracara home ranges and improved pasture, native grassland/prairie, and wax myrtle, a shrub commonly associated with grassland habitats. Again, all variables were significant at the 0.10 level (Table 4-7). Hosmer and Lemeshow's goodness of fit test indicated a poorer fit of this model, however ($G = 22.86$, $P = 0.003$).

Although these 2 models were biologically meaningful and statistically fit the data, their predictive capability was poor. For the model that included the forest and woodland variables, the mean predicted probability of use for the 29 test ranges was 0.10 (range = 0.00 to 0.31, Table 4-8). The model that did not contain the forest variables was only slightly better at predicting probability of use for the test ranges (mean = 0.13, range 0.00 to 0.42, Table 4-8).

Caracaras and Cattle Ranches

I found a strong inverse relationship between the proportion of improved pasture and home range size ($r = -0.57$, $P = 0.003$, $df = 23$, $n = 25$, Figure 4-6). For pairs for which I had telemetry data and reproductive information for all 3 years ($n = 18$), the total number of young fledged during all 3 years was positively but not significantly correlated with the proportion of improved pasture in the home range ($r = 0.20$, $P = 0.42$, $df = 16$, Figure 4-7). Home ranges on the study area landscape are shown in Figure 4-8.

Discussion

In south-central Florida, breeding pairs of crested caracaras are distributed across the landscape in well-defined, year-round territories. Caracara home ranges are strongly associated with improved pasture habitats on cattle ranches. Little overlap of core areas among neighboring pairs suggests that breeding pairs are highly territorial near the nest. Food resources may be shared in areas distant from the nest, however, as indicated by overlapping 99% contours among neighboring pairs. This territorial dispersion pattern is typical of raptors. Many species are highly territorial around the nest site. In habitats containing adequate food resources, nests may occur close together and feeding areas may overlap (Schoener 1968, Newton 1979, Village 1982).

Estimates of home range size varied considerably among breeding individuals. Despite this variation, results indicate substantial differences in overall estimates of home range size and nesting density from those reported by Layne (1996). Layne (1996) estimated home ranges of 1800-7400 ha based on maximum observed distances of 4.8 km to 9.7 km between sightings of unmarked individuals presumed to be members of the

same pair. He also recorded maximum local density of 1 pair/1400 ha, but suggested that average density was much less. In this study, home ranges varied from approximately 500 to 2800 ha. Local density was 9 successfully breeding pairs within about 5000 ha, or approximately 1 pair/555 ha on MAERC and an adjacent ranch in Highlands County. This density is more than twice the maximum local density estimated by Layne (1996). The availability of food and nest sites generally limits breeding density (Village 1982, 1983). Typically, large raptors breed at lower densities than small raptors, which utilize a wider variety of prey species (Newton 1979). High local density of crested caracaras on MAERC may reflect habitat quality (availability of both food and nest sites) in that area. Although the density of caracaras at MAERC may not occur throughout the population's entire Florida range, results of this study suggest that at least in some areas, nesting densities may be substantially higher than previously thought for this population.

A positive association between caracaras and improved pastures suggests that caracaras may benefit from land management activities routinely conducted on cattle ranches such as grazing, burning, mowing, and disking. Territory occupancy, reproductive activity, and nesting success were more consistent at territories on ranches. Pairs nesting on cattle ranches apparently produce more fledglings than pairs nesting on lands managed as natural areas. In general, however, comparisons between territories associated with different land uses were difficult because I had trouble locating caracaras on lands other than cattle ranches. Despite regular searching on public lands or other lands managed as natural areas, few territories on entirely native habitat were found.

Movement patterns of crested caracaras reflects breeding commitments and temporal and spatial variation in food availability, particularly the amount and configuration of suitable foraging habitat within each home range. The availability of nest sites also influences the size and shape of the home range. In this study, few caracara ranges were circular or centered on the nest. On most cattle ranches, suitable nest trees typically are few in number and occur in clumps. Home range size and shape primarily reflected the relationship between the nest site and improved pasture habitat (see map).

Caracaras exhibit strong fidelity to a nest site and year-round home range. Management recommendations for raptors typically focus on protecting the nest site and a circular buffer around the nest in which development or management activities are limited (U.S. Fish and Wildlife Service 1987b). Suitable caracara nest trees are often clumped and associated with hammocks that do not constitute suitable foraging habitat. A circular buffer around a nest may not encompass areas required for all activities associated with reproduction and year-round survival of a breeding pair of caracaras. Management plans for this species must consider the arrangement as well as the amount of both nest sites and suitable foraging habitat.

A landscape approach to identifying important habitats and assessing a species' distribution is particularly appropriate for raptors (Austin et al. 1996, Johansson et al. 1994, Carey et al. 1992). Many species require large areas of land to support viable populations and are particularly sensitive to changes in land use (Marquiss et al. 1985, Carey et al. 1992). Conservation of such species requires consideration of land uses and management practices throughout entire regions. Landscape-level models that evaluate resource selection by animals can provide information about important habitats and about land uses compatible with species' survival. These models ultimately can be used to evaluate a species' distribution, delineate key protection areas, predict effects of future land use changes, and identify potential areas for habitat improvement or restoration.

The models developed here represent an important first step in identifying habitat and landscape features important to crested caracaras in Florida. These models corroborate the observed association between breeding crested caracaras and improved pasture on cattle ranches. These models must be used with caution, however. While they showed a good fit statistically, their biological usefulness for management is currently limited, as indicated by the poor ability of the statistically "best" models to predict use of the 29 test ranges.

Future model development would benefit from consideration of two current constraints. First, agricultural and grassland habitats were poorly classified on the study area map obtained from the Florida GAP Analysis Project. The resolution of the

available GIS data did not permit detailed differentiation among these cover types or delineation of habitats within them such as patches of hammocks, wetlands, and ditches, which might be important to caracaras in selection of a territory. Second, these models did not consider context of habitats either within or around caracara home ranges. Habitat quality is determined not only by content but by the context of suitable habitats (Kushlan 1981, Janzen 1986, Fahrig and Merriam 1994, Harris et al 1996). Further research directed towards understanding relationships between caracaras and habitats should focus on refining cover types that represent open habitats and on considering habitat context both within the home range and at a larger scale.

Table 4-1. Variables included in development of the logistic regression model describing caracara home ranges. Unless noted, all variables are expressed as proportions of the total area of the home range that was vegetated with natural or semi-natural* vegetation.

Variable	Symbol
oak forest	OAKFOR
pine forest	PINEFOR
cypress	CYPRESS
mixed forest	MIXFOR
saw palmetto	SAWP
oak shrub	OAKSHRB
hypericum shrub	HYPSHRB
woodland	WOODL
willow	WILL
wax myrtle	WAXMYRT
seasonally flooded native grassland or prairie	GRASSL
marsh	MARSH
improved pasture*	IMPPAST
proportion vegetated with natural or semi-natural vegetation	PROPVEG
proportion of open habitat (pasture + grassland)	OPEN
proportion of vegetated area in shrubs	ALLSHRB
total area of improved pasture*	AMTP
area of largest patch of contiguous improved pasture*	CONTIGP

Table 4-2. Landownership and major land use for crested caracara territories in south-central Florida, 1994 - 1996. $n = 65$ territories.

Landownership	Major land use			Total
	Ranching	Other	Natural	
Private	56 (98.0%)	1 (2%)	0	57 (87.7%)
Public	3 (37.5%)	2 (2.5)	3 (37.5%)	8 (12.3%)
Total	59 (90.8%)	3 (4.6%)	3 (4.6%)	65

Table 4-3. Size and vegetation composition of crested caracara home ranges. Home ranges are defined as the 99% kernel contour estimated using a 0.85 smoothing factor. N = number of radiolocations used to estimate home range size.

Bird ID	Sex	N	Home range size (ha)	% of total home range in natural or semi-natural vegetation	proportion of vegetated area in improved pasture	largest area of contiguous pasture (ha)
120	F	48	1265.273	0.858	0.597	492.342
121	M	26	2190.443	0.933	0.493	373.879
200	M	28	1251.969	0.973	0.406	350.991
280	M	68	551.039	0.531	0.831	227.695
360	F	68	1363.798	0.979	0.732	653.605
458	M	96	1879.477	0.836	0.663	722.800
479	M	43	2777.219	0.976	0.109	53.460
498	M	91	848.295	0.905	0.535	188.930
518	F	27	571.288	0.899	0.849	410.240
538	F	27	1014.189	0.917	0.287	125.636
609	F	67	994.957	0.843	0.741	596.455
689	F	37	736.403	0.986	0.759	526.300
969	M	72	1609.962	0.960	0.690	919.980
1110	M	81	1176.541	0.958	0.581	498.884
1379	F	25	1301.698	0.900	0.571	323.155
1469	M	71	1454.535	0.990	0.642	578.182
1490	M	42	659.221	0.989	0.765	400.091
1558	M	39	1129.249	0.937	0.632	522.410
1568	M	30	1083.789	0.942	0.522	213.750
1589	M	97	1604.085	0.924	0.577	323.356
1600	F	25	1685.152	0.865	0.717	803.179
1608	M	45	681.562	0.790	0.707	325.852
1711	M	38	859.928	0.720	0.691	279.356
1969	F	77	1072.958	0.946	0.937	788.290
1989	M	33	1537.786	0.821	0.709	817.595

Table 4-4a. Matrix of percent overlap of 60% contours (core areas) for 9 adjacent pairs of breeding crested caracaras on MacArthur Agro-Ecology Research Center, Highlands County, south-central Florida. Birds in rows are overlapped by birds in columns.

Bird ID	360	689	969	1469	1490	1558	1600	1608	1711
360	-	0	2.6	0	0	0	0	0	0
689	0	-	0	0	0	4.4	0	0	0
969	2.9	0	-	18.8	0	0	0	0	0
1469	0	0	21.9	-	0	0	0	0	0
1490	0	0	0	0	-	2.8	0	0	0
1558	0	3.7	0	0	1.5	-	0	0	0
1600	0	0	0	0	0	0	-	0	0
1608	0	0	0	0	0	0	0	-	0
1711	0	0	0	0	0	0	0	0	-

Table 4-4b. Matrix of percent overlap of 60% contours (core areas) for 4 adjacent pairs of breeding crested caracaras along the Kissimmee River, Highlands and Okeechobee counties, south-central Florida. Birds in rows are overlapped by birds in columns.

Bird	498	120	1379	1568
498	-	0	0	0
120	0	-	0	0
1379	0	0	-	8.5
1568	0	0	7.5	-

Table 4-5a. Matrix of percent overlap of 99% contours for 9 adjacent pairs of breeding crested caracaras on MacArthur Agro-Ecology Research Center, Highlands County, south-central Florida. Birds in rows are overlapped by birds in columns.

Bird	360	689	969	1469	1490	1558	1600	1608	1711
360	-	0	33.1	12.4	6.2	0	9.7	0	0
689	0	-	0	0	25.9	21.4	3.1	1.9	14.6
969	27.2	0	-	38.8	7.6	4.1	0	0	0
1469	11.0	0	41.7	-	0	0	0	0	0
1490	13.6	31.5	19.8	0	-	24.8	23.0	0	0
1558	0	14.1	5.9	0	13.4	-	0	0	0
1600	7.7	1.4	0	0	8.3	0	-	0	1.5
1608	0	2.4	0	0	0	0	0	-	32.9
1711	0	12.6	0	0	0	0	2.9	22.7	-

Table 4-5b. Matrix of percent overlap of 99% contours for 4 adjacent pairs of breeding crested caracaras along the Kissimmee River, Highlands and Okeechobee counties, south-central Florida. Birds in rows are overlapped by birds in columns.

Bird	498	120	1379	1568
498	-	3.9	11.2	5.7
120	2.7	-	0	0
1379	7.3	0	-	22.4
1568	4.3	0	26.0	-

Table 4-6. Parameter estimates for model produced using logistic regression analysis that best distinguished between known caracara home ranges and available units throughout the study area. Variables include pine forest (PINEFOR), mixed forest (MIXFOR), wax myrtle (WAXMYRT), woodland (WOODL), and contiguous pasture (CONTIGP).

Parameter	DF	Coefficient	Std. Err.	<i>P</i>
Constant	1	-3.04	0.69	0.000
PINEFOR	1	-0.06	0.04	0.087
MIXFOR	1	-0.22	0.12	0.062
WAXMYRT	1	0.10	0.05	0.053
WOODL	1	-0.17	0.07	0.012
CONTIGP	1	0.003	0.001	0.003

Table 4-7. Parameter estimates for model that best distinguished between known caracara home ranges and available units throughout the study area and that did not include forest variables. Variables include native grassland/prairie (GRASSL), wax myrtle (WAXMYRT), improved pasture (IMPPAST), and contiguous pasture (CONTIGP).

Parameter	DF	Coefficient	Std. Err.	P
Constant	1	-9.18	1.31	0.000
GRASSL	1	0.04	0.02	0.069
WAXMYRT	1	0.19	0.06	0.000
IMPPAST	1	0.08	0.02	0.000
CONTIGP	1	0.002	0.001	0.090

Table 4-8. Predicted probabilities of use for test caracara home ranges calculated using logistic regression models that best distinguished between caracara home ranges and available units throughout the study area.

Nest No.	Model that included forest and woodland variables	Model with forest and woodland variables omitted
1	0.000	0.019
2	0.021	0.010
3	0.047	0.052
4	0.256	0.349
5	0.211	0.391
6	0.189	0.172
7	0.096	0.061
8	0.270	0.356
9	0.132	0.351
10	0.015	0.019
11	0.049	0.067
12	0.006	0.001
13	0.151	0.116
14	0.161	0.142
15	0.017	0.013
16	0.042	0.015
17	0.194	0.292
18	0.314	0.418
19	0.056	0.128
20	0.113	0.125
21	0.009	0.033
22	0.000	0.001
23	0.011	0.001
24	0.175	0.154
25	0.122	0.130
26	0.068	0.123
27	0.021	0.021
28	0.045	0.087
29	0.036	0.243
Mean	0.098	0.134



Figure 4-1. Study area for evaluating landscape-level habitat selection by breeding pairs of crested caracaras in Florida, 1994 -1996.

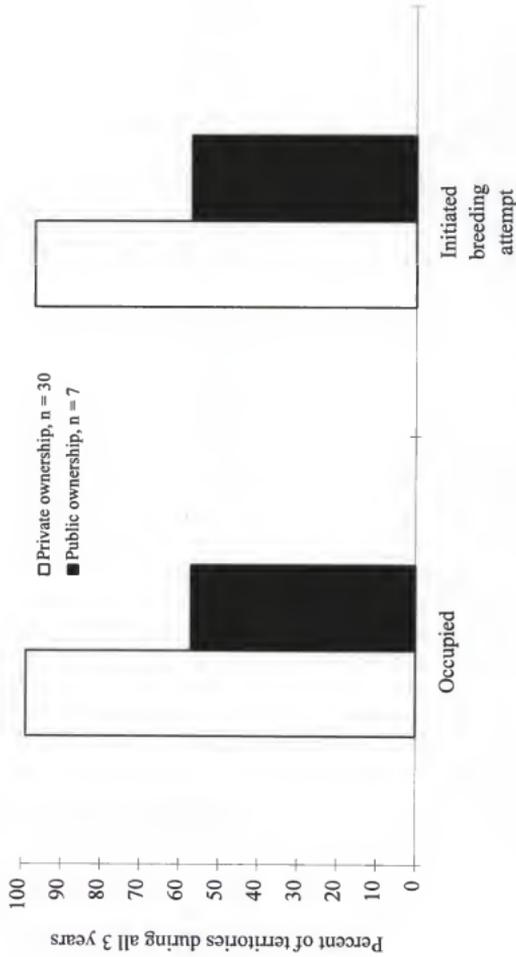


Figure 4-2. Relationship between occupancy, initiation of breeding attempts, and land ownership for 37 crested caracara territories in south-central Florida, 1994 - 1996.

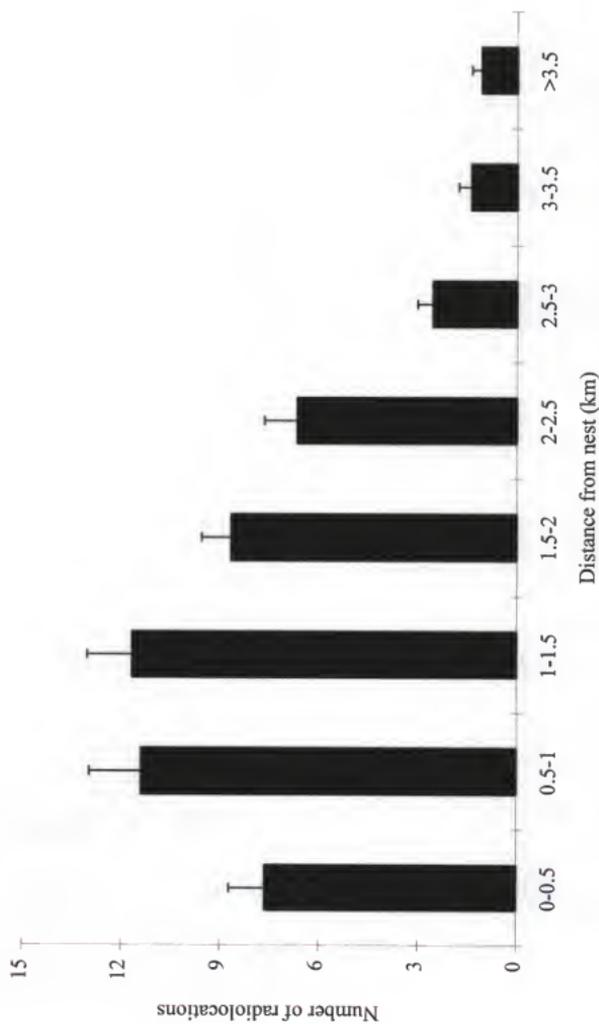


Figure 4-3. Mean (\pm SE) number of radiolocations for 25 breeding adult crested caracaras in relation to distance from the nest. $n = 1283$ total radiolocations.

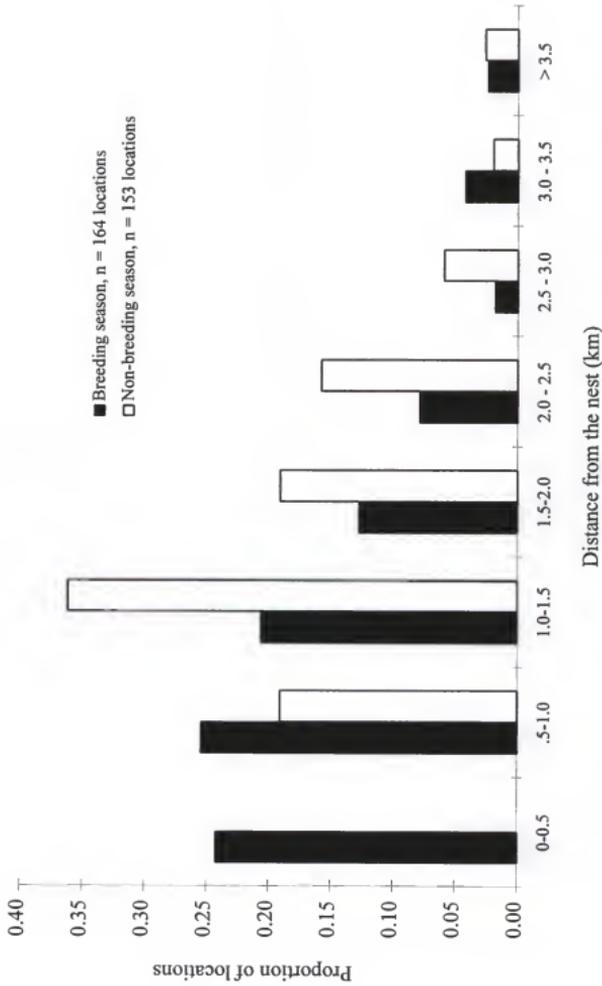


Figure 4-4. Distributions of radiolocations of 25 breeding adult crested caracaras in relation to distance from the nest during the breeding and non-breeding seasons in south-central Florida, 1994 - 1996.

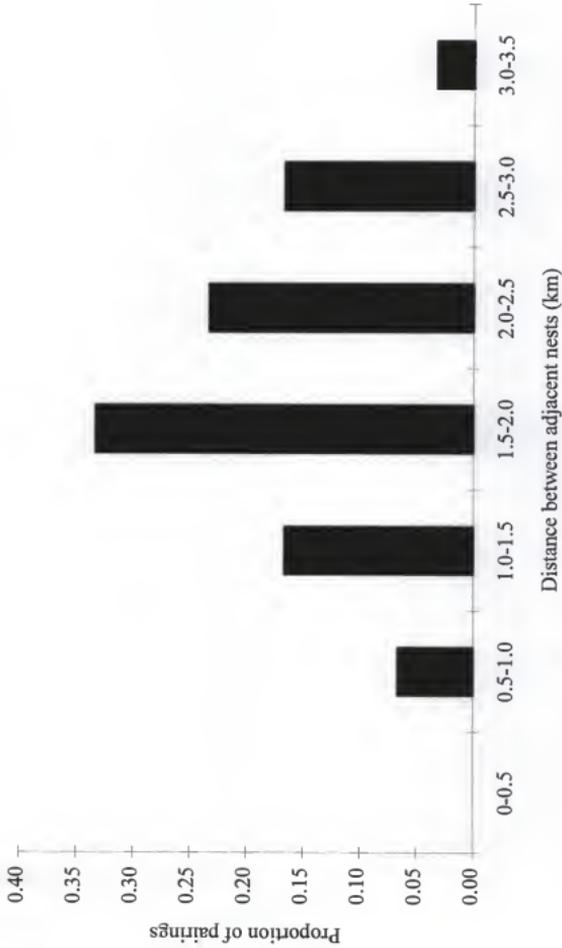


Figure 4-5. Distribution of distances between nests of neighboring pairs of successfully breeding crested caracaras in south-central Florida, 1994-1996. $n = 30$ pairings.

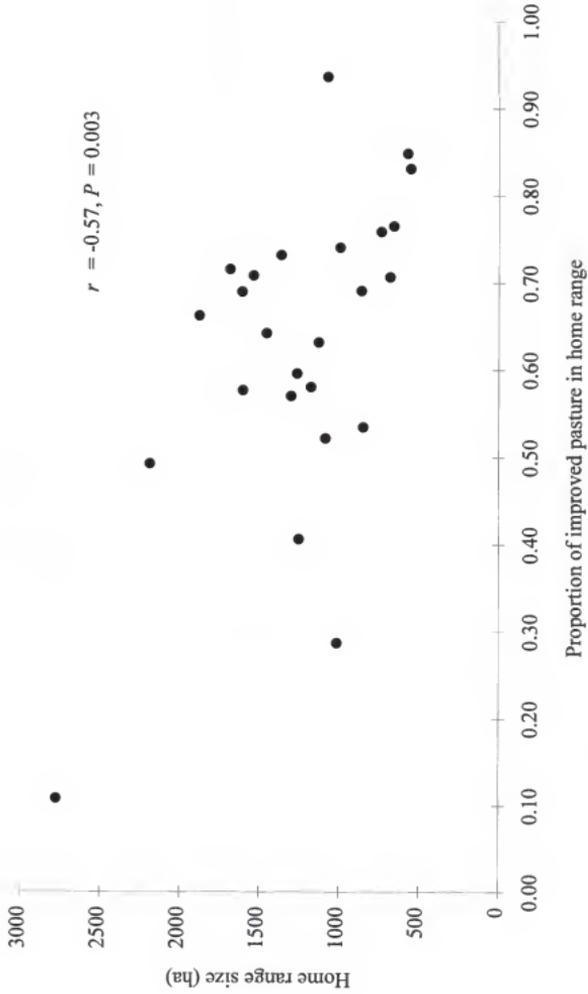


Figure 4-6. Relationship between proportion of improved pasture in home range and home range size for 25 crested caracara home ranges in south-central Florida, 1994-1996.

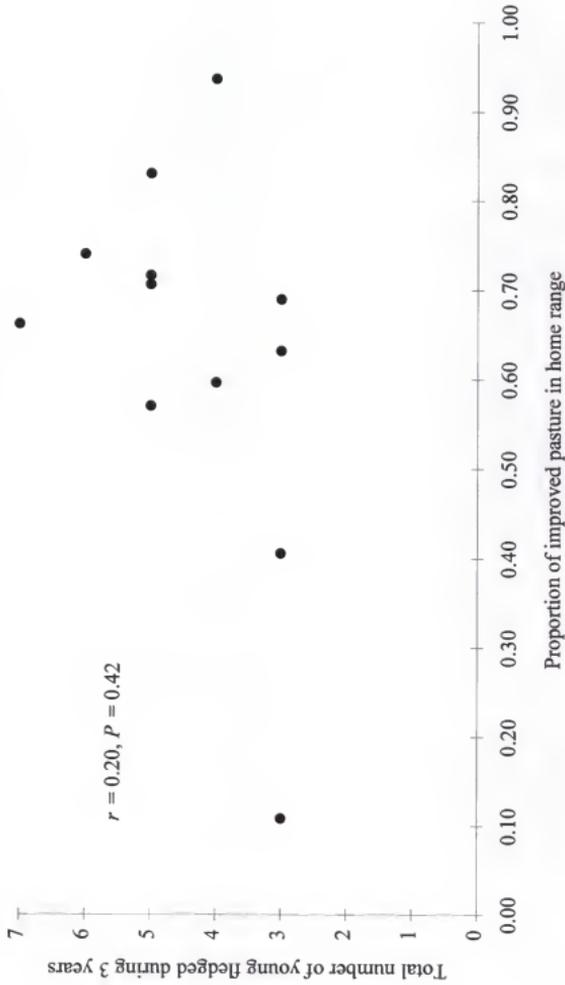


Figure 4-7. Relationship between amount of improved pasture in the home range and total number of young fledged during 1994-1996, for crested caracaras in south-central Florida.

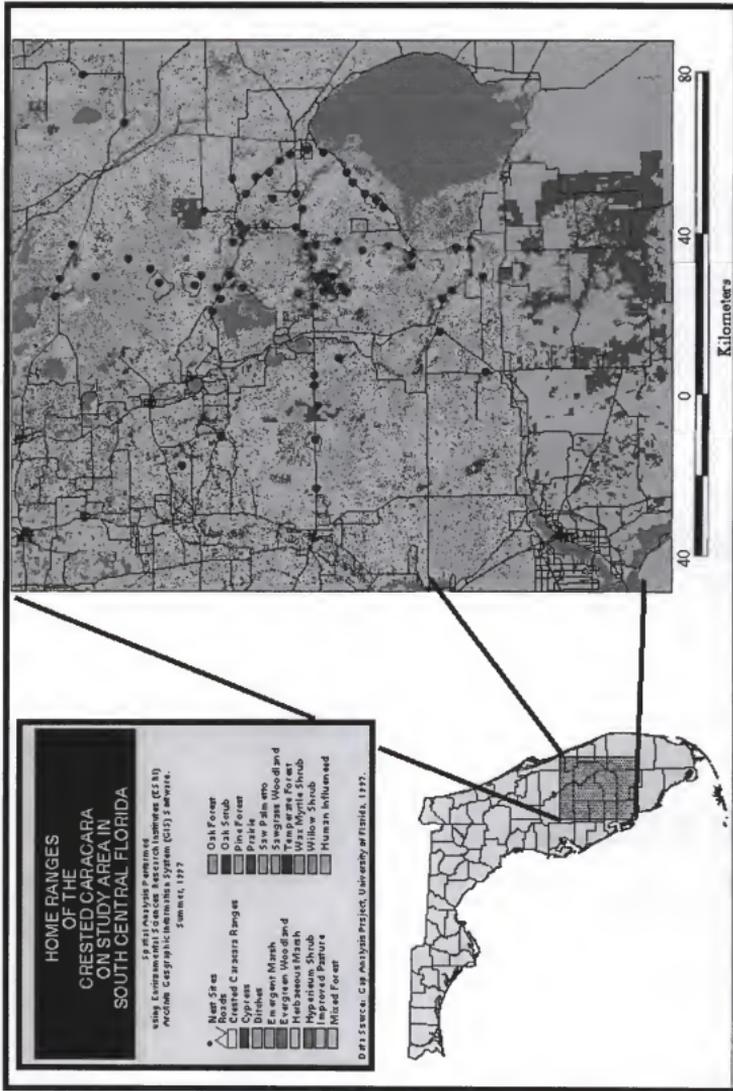


Figure 4-8. Home ranges of the crested caracara on study area in south-central Florida.

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

The Florida population of the crested caracara is isolated and remote from other caracara populations. Because it is relatively small (estimated at 400 - 500 individuals) and yet is a characteristic element of the Florida prairie ecosystem, the species is of both conservation and evolutionary interest. Conversion of grassland and pasture habitats is occurring rapidly throughout the region of Florida that constitutes much of the species' current breeding range in that state. Florida's caracara population is listed as Threatened by the U.S. Fish and Wildlife Service and the Florida Game and Fresh Water Fish Commission. Currently, no habitat protection guidelines or management activities focus on conservation of this population. This is largely due to the paucity of ecological information on the species in Florida or elsewhere.

I undertook this research with the intent of expanding the basic biological knowledge of this raptor and evaluating the status of the Florida population. This study constitutes the first in-depth examination of the ecology of the crested caracara in Florida, or anywhere throughout its geographic range. I examined various aspects of the caracara's biology that might be pertinent to management of Florida's population and attempted to understand relationships between caracaras and privately-owned cattle ranches, where they now mostly persist.

I found that Florida's crested caracaras differ markedly from other, better studied raptors. Crested caracaras in Florida have relatively high nest success and productivity, both compared to most large raptors and in contrast to previously reported estimates for this population. The reproductive strategy of Florida's crested caracaras is typical of other sedentary tropical bird populations. The breeding cycle is closely tied to the annual precipitation cycle. A fairly stable climate, the absence of migration, and, perhaps, an abundance of food in human-influenced habitats facilitate a long breeding season. Spatial

and temporal variability in breeding activity exhibited by individual pairs may be a response to variable environmental conditions both within and between breeding seasons. High nest success and productivity is indicated by high territorial occupancy and breeding rates coupled with the ability of certain pairs to make multi-nesting attempts. Pairs that successfully fledge two broods in one breeding season may realize higher lifetime reproductive success than single-brooded pairs.

Although little historic information is available, reproductive rates for the sample population seem adequate for long-term population maintenance. Florida's caracara population appears to be stable at present. Caution is warranted in evaluating trends, however. Difficulties with access to many areas of suitable habitat, particularly away from major roads, preclude a completely systematic search of the species' Florida range. Counts are hampered by the effects of the birds' terrestrial behavior on their detectability. Because caracaras are long-lived and site-faithful, a significant time lag could occur before any decline is detected.

Results of my research indicate a strong association between breeding pairs of crested caracaras and cattle ranches. The crested caracara is a generalist predator that seems to be tolerant of some human activity and moderate habitat changes as long as they are not harassed and the nest site is left intact. Certain pairs are quite tolerant of small-scale burning, clearing, removal of sod, building construction, and general human activity, even during the nesting season. Normal levels of ranching activities are well-tolerated. Indeed, these activities may have aided in maintaining suitable caracara habitat on private ranchlands. Pasture management programs include controlled fires set during winter and spring. Fires often sweep through active nest stands with little effect.

Estimates of spatial requirements and nesting density for Florida's crested caracaras differed considerably from previously published estimates. I found caracaras nesting as close together as 0.5 km on the cattle ranches. Local nesting density on a cattle ranch in Highlands County was over twice that reported by Layne (1996). These results support the hypothesis that cattle ranches provide good quality habitat for caracaras. Similar densities of breeding pairs may occur on other large ranches where I did not

survey for territories. These findings suggest that (1) it is unlikely that the Florida population was reduced to < 100 birds between 1967 and 1970 (Heinzmann 1970); (2) breeding densities of Florida's crested caracaras may be higher than previously suspected in some areas of their current breeding range; and (3) total population numbers may be higher than published estimates.

Caracara territories were not randomly distributed throughout the study area. Logistic regression analysis revealed a strong association between nesting territories and improved pasture and particularly, with large areas of contiguous pasture. Management activities on ranches such as grazing, burning, plowing, and mowing influence vegetation structure. The short ground cover vegetation on these ranches may provide suitable conditions for this mainly terrestrial forager. Development of a reliable predictive model for suitable caracara habitat was constrained by the resolution of the available GIS data, however, particularly by the inability to identify ditches and wetland habitats within the pastures. Future model development should consider improving differentiation among open grassland habitats as well as habitat context both within caracara home ranges and at a larger, landscape scale.

My research indicates that Florida's caracaras may be doing better than previously believed, especially on privately-owned cattle ranches. If the population is in a long-term decline, factors other than reproduction are likely involved. The greatest threat continues to be loss and degradation of nesting habitat. Observations made during this study suggest that most suitable habitat may be occupied. I found caracara pairs in most areas where I looked for them, particularly on private ranches. Urban development continues to expand inland from the coast and off Florida's central ridge. The accelerating economic value of citrus and sugar cane favors conversion of remaining prairies and grasslands and these pressures are expected to continue. On some ranches, removal of palms has precluded the use of these areas as nesting sites. Although the short-term outlook for Florida's caracaras appears positive, the long-term outlook is less clear. A decline seems inevitable if habitat conversion continues at the present rate throughout the caracara's limited range.

A conservation strategy for this population should be based on protecting known nest sites and large areas of open grassland habitats, particularly pasture. Such a strategy should focus at a regional scale, and include nesting sites on both public and private lands. Because of the variation in context and levels of human disturbance among caracara nest sites, each site may have to be treated separately in management planning. Private ownership of most suitable habitat will complicate conservation efforts. Because caracaras seem to be doing well on cattle ranches, efforts being made in some areas to restore native prairies may target species that require these native habitats. While beneficial for prairie-dependent species, these decisions may preclude management for caracaras on public lands. Habitat conservation must incorporate cooperative efforts among land management agencies and private landowners. Developing means to preserve the large cattle ranches that now apparently support the bulk of this population is critical to conservation of Florida's crested caracaras. These efforts will of necessity include creative alternatives to direct land purchase.

A regional focus to conservation mandates obtaining better information about the distribution of nesting territories throughout the region. Future research should focus on development of better predictive models of the species' distribution and improving the understanding of relationships between caracaras and cattle ranches. Management efforts must also incorporate a strong education component, to reduce the widespread negative impression of scavengers and to stress the value of the crested caracara as an example of the potential for coexistence of sustainable economic activities and native wildlife.

This study represents an important beginning towards understanding the population dynamics, demographics, and habitat ecology of Florida's crested caracara population. As with any species that is long-lived and ranges widely across habitats, however, additional study is required to fully understand the role of the caracara in the Florida landscape.

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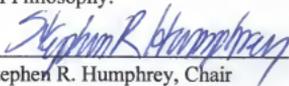
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BIOGRAPHICAL SKETCH

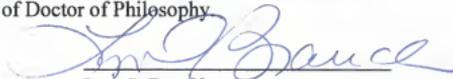
Joan L. Morrison received a Bachelor of Arts degree in biology from the College of Wooster, Wooster, Ohio, in 1975. After working for a year in a research laboratory at the University of Michigan, she attended the School of Natural Resources at the University of Michigan to study the development and pathogenicity of a blood parasite in Canada geese. Subsequent to receiving a Master of Science degree in resource ecology from the University of Michigan in 1979, Joan worked as a biologist for the U.S. Fish and Wildlife Service in Michigan and Colorado and for the U.S. Forest Service in Washington, Alaska, and New Mexico. Beginning in 1985, Joan began working as a contract research biologist for the New Mexico Department of Game and Fish. She studied the life history and distribution of the southwestern subspecies of the meadow jumping mouse (*Zapus hudsonius luteus*) and collaborated on studies of the reproductive and foraging ecology of Accipiter hawks in the mountains of New Mexico. In 1991, Joan entered the doctoral program at the University of Florida. She studied the reproductive ecology, population biology, and habitat associations of the crested caracara, a Threatened bird of prey in Florida. Joan completed her Ph.D. in fall 1997. Currently, she is continuing research on Florida's caracaras and has expanded her research program to include studies of seasonal movements of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) in Everglades National Park and the nesting and foraging ecology of the chimango caracara (*Milvago chimango*) in Chile.

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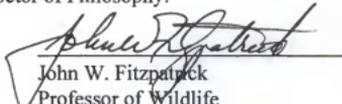
Stephen R. Humphrey, Chair
Professor of Wildlife
Ecology and Conservation

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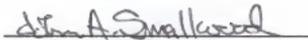
Lyn C. Branch
Associate Professor of Wildlife
Ecology and Conservation

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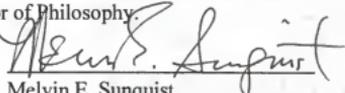
John W. Fitzpatrick
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Ecology and Conservation

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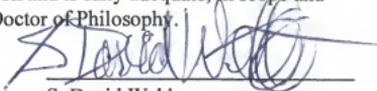
John A. Smallwood
Affiliate Professor of Wildlife
Ecology and Conservation

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Melvin E. Sunquist
Associate Professor of Wildlife
Ecology and Conservation

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S. David Webb
Distinguished Research Professor
of Geology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1997



Dean, College of Agriculture

Dean, Graduate School