

EFFECTS OF DOUBLE BROODING ON PRODUCTIVITY OF CRESTED CARACARAS

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ABSTRACT.—During at least one of three nesting seasons, 13 breeding pairs of Crested Caracaras (*Caracara plancus*) in south-central Florida made a second nesting attempt following a successful first attempt. Ten pairs successfully fledged young in both attempts. Only early nesting pairs attempted a second brood. Most double-brooded pairs fledged their first brood before 1 March. The time interval between first and second nesting attempts was positively correlated with the number of young fledged from the first attempt. Clutch size declined between first and second nests of double-brooded pairs, and second nests failed more often, but pairs that attempted two broods in a season fledged significantly more young than did single-brooded pairs. Estimates of survivorship to recruitment were higher for young from first broods than for young from single or second broods. Although the influence of double brooding on annual productivity seems only marginal, this strategy likely persists because of the potential increase in fitness incurred by individuals that successfully fledge two sets of young in a single nesting season. Received 24 February 1997, accepted 19 March 1998.

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

In temperate latitudes, many bird species raise more than one brood per year (Smith and Roff 1980, Westmoreland et al 1986, Boer-Hazewinkel 1987, Guepel and DeSante 1990, Smith and Marquiss 1995). The occurrence of multiple brooding and the 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 parental experience (Perrins 1970; Ricklefs 1984; Askenmo and Unger 1986; Bednarz 1987; Tinbergen and van Balen 1988; Holmes et al. 1991, 1992).

Raising more than one brood per nesting season may increase fitness only if the strategy does not decrease the future fecundity or survival of breeders or first-brood young (Williams 1966, Boer-Hazewinkel 1987, Nur 1988,

Smith and Marquiss 1995, Verhulst and Hut 1996). Multibrooded individuals may 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 offspring recruiting into the breeding population is lower for second-brood young (Smith and Roff 1980, Hochachka 1990). Despite these potential costs, multiple brooding may be maintained in some species because it increases an individual's fitness (Perrins 1970, Boer-Hazewinkel 1987, Newton 1989) and, under certain environmental conditions, the cost of producing additional broods may be small (Ormerod and Tyler 1993, Smith and Marquiss 1995).

Raptors typically raise only one brood per year because of the length of time required for the breeding cycle, which includes an extended postfledging dependency period for many species (Newton 1979). Although many raptors re-nest after losing a clutch (Newton 1979, Wood and Collopy 1993, Forsman et al 1995), true double brooding (individuals attempting a second brood soon after a successful first effort) rarely has been confirmed. Second brood attempts, generally in response to prey abundance, have been reported for smaller species with short breeding cycles such as American Kestrels (*Falco sparverius*; Howell 1932, Stahlecker and Griese

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1977, Toland 1985), Eurasian Kestrels (*F. tinnunculus*; Fargallo et al. 1996), Black-shouldered Kites (*Elanus caeruleus*; Malherbe 1963), Burrowing Owls (*Athene cunicularia*; Millsap and Bear 1990), and Barn Owls (*Tyto alba*; Witmer and Patrick 1987). Multiple brooding occurs in some larger species that live year-round in subtropical and tropical environments where food is abundant for most of the year, such as Harris's Hawks (*Parabuteo unicinctus*; Mader 1975, Bednarz 1987), Pale Chanting-Goshawks (*Melierax poliopterus*; Smeenk and Smeenk-Enserink 1975), and Galapagos Hawks (*Buteo galapagoensis*; DeVries 1975).

I documented double brooding in Crested Caracaras (*Caracara plancus*) during three years in south-central Florida. The Crested Caracara is a medium-sized raptor that occurs in open grasslands and savannas throughout Central and South America, in the southwestern United States, and in Florida (AOU 1983). Circumstantial evidence of double brooding in this species has been reported in Florida (Bent 1938), Texas (Dickinson and Arnold 1996), and Mexico (Rivera-Rodríguez and Rodríguez-Estrella unpubl. data), but few data exist on the prevalence of this phenomenon. Recently, widespread loss of grassland habitats to agriculture and urban development has focused concern on the Florida population (Layne 1996, B. Millsap pers. comm.). This population currently is listed as Threatened by the U.S. Fish and Wildlife Service and the state of Florida. Because successful double brooding may have important consequences for lifetime reproductive success and population productivity, I was interested in evaluating the extent to which double brooding occurs and the factors that may contribute to its occurrence in this population of caracaras. To examine the possible benefits and costs of this strategy, I tested the following hypotheses: (1) no difference exists in productivity between caracara pairs that attempt two broods and those that produce only one brood per nesting season, and (2) first-brood young exhibit lower survivorship owing to reduced parental care.

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' current 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 of caracaras are monogamous and remain on their territories year-round (Morrison 1996).

Beginning in January 1994, I conducted monthly surveys of known territories to look for signs of nesting activity. Once found, nests were checked weekly until fates were determined. I defined a nesting attempt as the laying of at least one egg in a nest. Clutch size, hatching date, brood size, and chick age were determined with the aid of a mirror attached to an extendible pole. Age was determined by assessing the chicks' size and feather development.

I assigned each nest an initiation week based on known time of egg laying or on backdating from known hatching or fledging dates (assuming an incubation period of approximately 32 days and a nestling period of approximately 8 weeks). Week of initiation was then calculated from the first week of September, which I assigned as the first week of the breeding season based on the earliest known nesting attempts during all three years.

I estimated annual nesting success using the Mayfield method (Mayfield 1961). A successful nest was defined as one that fledged at least one young. Mayfield estimates of nesting success were compared among nest types (e.g. first vs. second nests) using a Z-test (Hensler and Nichols 1981). Annual productivity was measured as the number of young fledged per territorial pair. The classification of "single brood" was assigned to pairs that made only one nesting attempt during a single nesting season. Double-brooded pairs made a second nesting attempt following a successful first effort in the same nesting season. Territories in which pairs produced replacement clutches after nesting failures were not included. Clutch size is reported only for nests with eggs. 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 postfledging care or the survival of first-brood fledglings, I used radio telemetry to determine the timing of departure of first- and second-brood young from their natal territory. Caracaras were color banded and radio tagged (one per nest) while still in the nest at 7 to 8 weeks of age, or just after fledging. Because young continue to beg and be fed by their parents for several months after fledging (Morrison unpubl. data), 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 (Morrison unpubl. data). I defined permanent

TABLE 1. Occurrence and timing of nesting attempts between years by Crested Caracaras in south-central Florida.

Year	No. of territories followed ^a	No. of second nesting attempts ^b	Median initiation of single-brood nests ^c	Median initiation of first of two nesting attempts ^c	Median initiation of second of two nesting attempts ^c
1994	28	3	3rd week Jan (25)	5th week Nov (3)	2nd week Apr (3)
1995	43	8	4th week Jan (35)	4th week Nov (8)	2nd week Apr (8)
1996	48	5	4th week Jan (43)	3rd week Dec (5)	4th week Apr (5)

^a 60 territories total.

^b 16 attempts found on 13 different territories.

^c Number of territories in parentheses.

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 three consecutive weeks of locations more than >3 km from the nest.

Survival data for 61 radio-tagged young through their first year were obtained via weekly aerial radio-tracking 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 individuals (Pollock et al. 1989). Age at first reproduction is not known for this species but is estimated at three to four years of age (Voous 1983, Layne 1996), so I used approximately 1,200 days postfledging 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).

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 and number of fledglings in the first brood influenced the occurrence of double brooding during the same nesting season. For pairs whose reproductive history was known for at least two years, I examined whether the occurrence of double brooding during any year was influenced by: (1) whether the pair had attempted to raise two broods during the previous year, (2) the number of fledglings from the previous year, and (3) the fledging date from the previous year.

I used SigmaStat (Jandel Scientific 1995) for statistical tests. Comparisons of fecundity, timing of nest initiation, and productivity were made using Wilcoxon rank-sum and Kruskal-Wallis nonparametric tests (Sokal and Rohlf 1995).

RESULTS

Extent of occurrence of double brooding.—I monitored breeding activity on 60 different territories throughout the study, although only a subset was monitored each year (Table 1). A second nesting attempt was made following a

successful first effort on 13 territories (21.7%; Table 1). On three other territories, pairs initiated a second nesting attempt during two consecutive years, although none of these pairs successfully fledged two broods in more than one nesting season. 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 ($U = 1,504$, $P < 0.001$, $n = 16$) than single-brooded pairs ($n = 103$; Table 1). Second nests of double-brooded pairs were initiated 9 to 13 weeks later ($U = 26.5$, $P < 0.001$, $n = 16$) 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 brood of two, $H = 1.88$, $P = 0.39$, $n = 16$; second brood of two, $H = 0.65$, $P = 0.72$, $n = 16$; Table 1).

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

Productivity and nesting success.—The mean clutch size declined between the first and second nests of double-brooded pairs (Table 2). Laying times of second clutches and the first

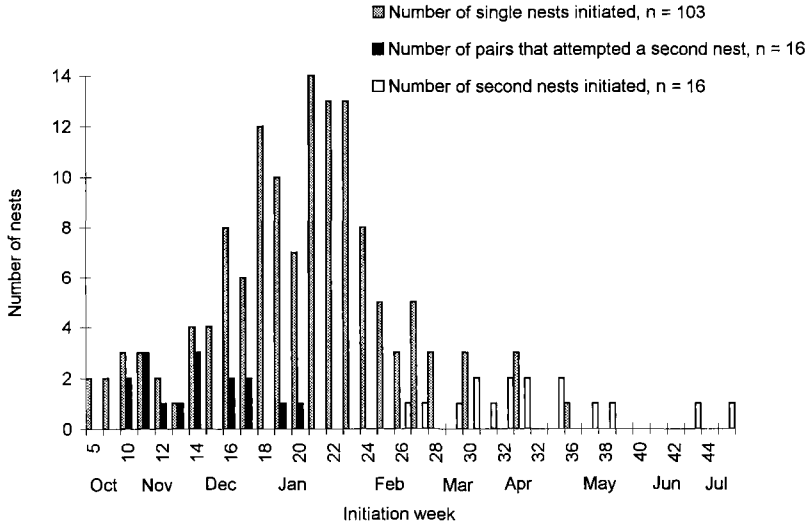


FIG. 1. Timing of nest initiation throughout the breeding season for Crested Caracaras in south-central Florida, 1994 to 1996.

clutches of late breeders overlapped during March and early April (Fig. 1). Mayfield success estimates for second nests were significantly lower than those for first nests and for nests of single-brooded pairs (Table 2). Despite higher failure rates of second nests, pairs that attempted a second brood fledged significantly more young ($U = 1,367, P = 0.002, n = 16$) than

pairs that attempted only a single brood each year ($n = 103$; Fig. 3).

Parental care and postfledging survival.—First-brood young incurred shorter periods of postfledging care. The mean time to departure from

TABLE 2. Clutch size ($\bar{x} \pm SE$) and nesting success (Mayfield estimate $\pm SD$) of Crested Caracaras in south-central Florida, 1994 to 1996. Nesting circumstance centered in bold; n denotes number of territories.

Year	Clutch size	n	Nesting success	n
Single-brood nests				
1994	2.60 \pm 0.16	15	0.67 \pm 0.09	25
1995	2.28 \pm 0.11	25	0.72 \pm 0.05	35
1996	2.22 \pm 0.09	32	0.92 \pm 0.03	43
Total	2.32 \pm 0.07	72	0.81 \pm 0.03 ^a	103
First of two nests				
1994	—	—	1.00 \pm 0.00	3
1995	2.66 \pm 0.32	3	1.00 \pm 0.00	8
1996	2.33 \pm 0.33	3	1.00 \pm 0.00	5
Total	2.50 \pm 0.22 ^b	6	1.00 \pm 0.00 ^c	16
Second of two nests				
1994	—	—	1.00 \pm 0.00	3
1995	1.80 \pm 0.02	5	0.35 \pm 0.15	8
1996	2.00 \pm 0.00	2	0.25 \pm 0.20	5
Total	1.86 \pm 0.14 ^b	7	0.35 \pm 0.12 ^{a,c}	16

^a Success higher for single broods than for second of two broods ($Z = 3.72, P < 0.0002$).

^b Clutch size higher for first of two clutches than for second of two clutches ($U = 33.0, P = 0.03$).

^c Success higher for first of two broods than for second of two broods ($Z = 4.19, P < 0.0001$).

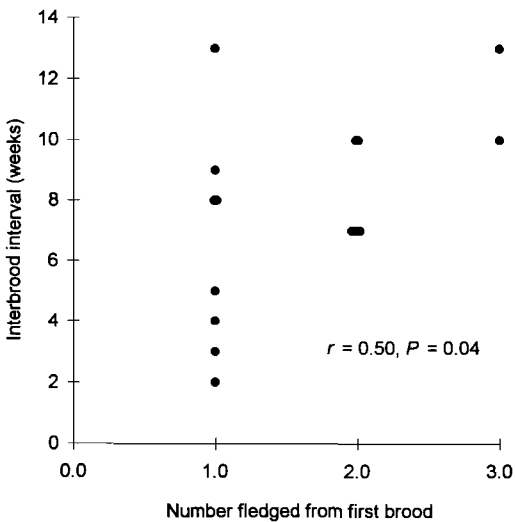


FIG. 2. Length of the interbrood interval in relation to number fledged from the first nesting attempt for double-brooded Crested Caracaras in south-central Florida, 1994 to 1996.

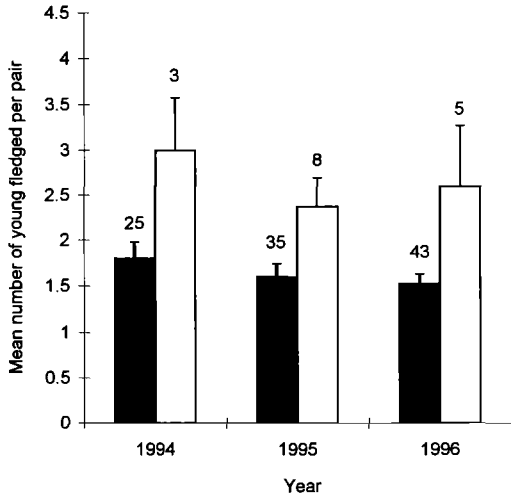


FIG. 3. Annual productivity ($\bar{x} \pm SE$) for single-brooded (solid bars) and double-brooded (open bars) pairs of Crested Caracaras nesting in south-central Florida, 1994 to 1996. Number of pairs shown above each bar.

the natal territory of first-brood fledglings ($11 \pm SE$ of 2.56 weeks, $n = 18$) was significantly shorter ($U = 290.5$, $P < 0.001$) than that of fledglings from single-brood pairs (33 ± 1.61 weeks, $n = 34$) or of second-brood fledglings

(29.7 ± 1.73 weeks, $n = 9$; $U = 33.0$, $P = 0.01$). Postfledging 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. Length of the period of postfledging care for single-brood fledglings did not differ from that of second-brood fledglings ($U = 54.4$, $P = 0.40$). In many cases, single-brood fledglings remained in the natal territory until their parents began breeding the following year.

Estimates of the probability of survival to recruitment differed between young from first and second broods (Kaplan-Meier survival function, $\chi^2 = 8.51$, $P = 0.004$; Fig. 4). Survival estimates for young from first broods also were higher than estimates for young from single broods ($\chi^2 = 75.95$, $P < 0.001$; Fig. 4).

Correlates of double brooding.—Timing of initiation of the first brood was the more important of the two variables in the model predicting the occurrence of double brooding (Table 3). 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 of young fledged in the pre-

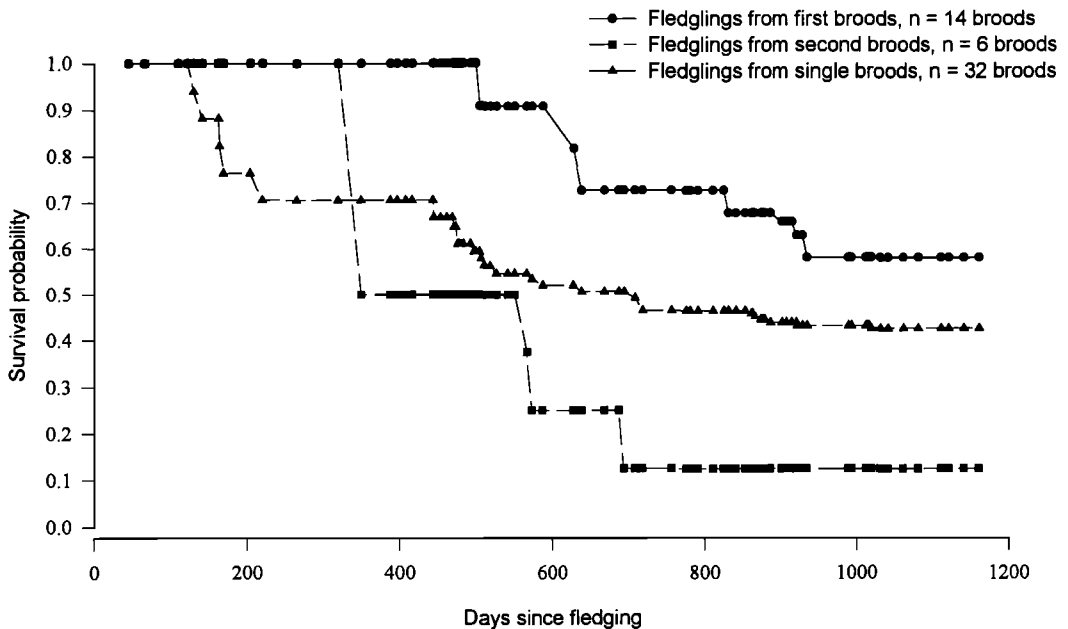


FIG. 4. Kaplan-Meier survival functions estimated for young Crested Caracaras from first, second, and single broods in south-central Florida, 1994 to 1996.

TABLE 3. Results of logistic regression analysis of the influence of timing of initiation of the first brood and number of young fledged in the first brood on the occurrence of double brooding in Crested Caracaras in south-central Florida, 1994 to 1996 ($n = 16$ double-brooded pairs, 103 single-brooded pairs).

Variable	Coefficient	SE	P
Constant	7.50	2.22	0.001
Timing of initiation	-0.52	0.12	<0.001
Number young fledged	0.01	0.43	0.97

vious year, or the date of fledging during the previous year (Table 4).

DISCUSSION

Life-history theory predicts that a breeding attempt will occur when the potential benefits to lifetime reproductive success exceed the expected costs (Williams 1966, Stearns 1992). In Florida's population of Crested Caracaras, only a small proportion of pairs apparently attempt a second brood in any year. This strategy likely is maintained, however, because double-brooded individuals may incur higher fitness (Perrins 1970, Boer-Hazewinkel 1987). Although the probability of recruitment is lower for second-brood young, successful double-brooded individuals are more productive and so potentially have more young recruited into the breeding population.

Second clutches may reduce the reproductive value of the first brood because the latter receive less postfledging care (Verhulst and Hut 1996). I found no evidence that first-brood young incurred reduced postfledging survival, despite reduced postfledging care. First-brood fledglings had the highest probability of survival to recruitment. This suggests that juvenile caracaras can forage independently in a period as short as seven to eight weeks.

The occurrence of double brooding in Crested Caracaras in Florida may be related to the length of the breeding season and to food availability. These two factors largely determine the number and the timing of broods produced by a breeding pair (Perrins 1970, Newton 1979, Tinbergen and van Balen 1988). The subtropical climate of southern Florida (Chen and Gerber 1990) allows Crested Caracaras to extend their breeding season from September

TABLE 4. Results of logistic regression analysis of the influence of double brooding the previous year, fledging date, and number of young fledged the previous year on the occurrence of double brooding in Crested Caracaras in south-central Florida, 1994 to 1996 ($n = 11$ double-brooded pairs, 34 single-brooded pairs).

Variable	Coefficient	SE	P
Constant	2.40	0.28	0.39
Previous double brooding	0.72	0.92	0.44
Fledging date	-0.12	0.86	0.15
Number young fledged	0.27	0.55	0.63

throughout the winter and into June or early July (Morrison 1996). Timing of breeding apparently is the most important factor influencing individual productivity and reproductive success in this population (Morrison unpubl. data), and some early nesting pairs have sufficient time to raise two broods.

Numerous studies have examined the influence of food supply on the occurrence and timing of breeding in raptors (e.g. Cavé 1968, Dijkstra et al. 1982, Newton and Marquiss 1984). Food supply apparently influences 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 does not have to be synchronized with the availability of particular foods. Caracaras typically inhabit areas associated with human activity, such as cattle ranches, farmlands, and urban dumps (Rodríguez-Estrella 1996, pers. obs.). These habitats may provide a diversity of predictable food resources, in some part due to regular schedules of management activities related to the production of livestock. The combination of a relatively mild climate and the availability of a variety of food resources apparently allows early initiation of breeding and double brooding by some pairs. Whether individuals attempt a second brood, or even attempt to nest early in the season, may depend on the age and quality of individuals, the experience of pairs, and the quality of territories. The occurrence of double brooding in any year was not influenced by the previous year's reproductive effort, suggesting that double-brooded individuals are the most fit.

Year-round residency and persistence of the pair bond between nesting seasons may facilitate double brooding in Crested Caracaras because of the familiarity of individuals with habitats and resources in their territories. 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 probably is a regular but uncommon occurrence in Florida's population of Crested Caracaras and may occur in other populations as well (Dickinson and Arnold 1996, Rodríguez-Estrella and Rivera-Rodríguez unpubl. data). The extended breeding season and postfledging dependency period in Crested Caracaras may have contributed to the lack of confirmation of double brooding until now.

Because only a small percentage of pairs attempt second nests and contributions by these pairs to overall productivity seem only marginal, why does this strategy persist? The ultimate value of double brooding must be that these individuals produce more young that have some probability of recruitment into the breeding population. Of greater interest is why more individuals in this population do not attempt a second brood. For many avian species, the occurrence and timing of breeding efforts are influenced by the age and experience of the parents and/or the 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. Additional studies of conditions that influence the 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 individual lifetime reproductive success and to the overall dynamics of the Crested Caracara population in Florida.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds, 6th ed. American Ornithologists' Union, Washington, D.C.
- ASKENMO, C., AND U. UNGER. 1986. How to be double-brooded: Trends and timing of breeding performance in the Rock Pipit. *Ornis Scandinavica* 17:237-244.
- BEDNARZ, J. C. 1987. Successive nesting and autumnal breeding in Harris' Hawks. *Auk* 104:85-96.
- BENT, A. C. 1938. Life histories of North American birds of prey. Part 2. U.S. National Museum Bulletin No. 167.
- BOER-HAZEWINKEL, J. 1987. On the costs of reproduction: Parental survival and production of second clutches in the Great Tit. *Ardea* 75:99-110.
- CAVÉ, A. J. 1968. The breeding of the Kestrel, *Falco tinnunculus*, in the reclaimed area Oostelijk Flevoiland. *Netherlands Journal of Zoology* 18:313-407.
- CHEN, E., AND J. F. GERBER. 1990. Climate. Pages 11-34 in *Ecosystems of Florida* (R. L. Myers and J. J. Ewel, Eds.). University of Central Florida Press, Orlando.
- COX, D. R., AND D. OAKES. 1984. Analysis of survival data. Chapman and Hall, New York.
- DE VRIES, T. J. 1975. The breeding biology of the Galapagos Hawk, *Buteo galapagoensis*. *Gerfaut* 65: 29-57.

- DICKINSON, V. M., AND K. A. ARNOLD. 1996. Breeding biology of the Crested Caracara in south Texas. *Wilson Bulletin* 108:516–523.
- DIJKSTRA, C., L. VUURSTEEN, S. DAAN, AND D. MANSMAN. 1982. Clutch size and laying date in the Kestrel *Falco tinnunculus*: Effect of supplementary food. *Ibis* 124:210–213.
- DRURY, W. H. 1961. Studies of the breeding biology of the Horned Lark, Water Pipit, Lapland Longspur, and Snow Bunting on Bylot Island, Northwest Territories, Canada. *Bird-Banding* 32:1–44.
- ELLIS, D. H., D. G. SMITH, W. H. WHALEY, AND C. H. ELLIS. 1988. Crested Caracara. Pages 119–126 in *Southwest Raptor Management Symposium and Workshop*. National Wildlife Federation Scientific Technical Series No. 11, Washington, D.C.
- EVANS OGDEN, L. J., AND B. J. STUTCHBURY. 1996. Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. *Condor* 98:736–744.
- FARGALLO, J. A., G. BLANCO, AND E. SOTO-LARGO. 1996. Possible second clutches in a Mediterranean montane population of the Eurasian Kestrel (*Falco tinnunculus*). *Journal of Raptor Research* 30:70–73.
- FORSMAN, E. D., A. GIESE, D. MANSON, S. SOVERN, AND D. R. HERTER. 1995. Renesting by Spotted Owls. *Condor* 97:1078–1080.
- GUEPEL, G. R., AND D. F. DESANTE. 1990. Incidence and determinants of double brooding in Wren-tits. *Condor* 92:67–75.
- HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: A model, estimators, and simulation results. *Wilson Bulletin* 93:42–53.
- HOCHACHKA, W. 1990. Seasonal decline in reproductive performance of Song Sparrows. *Ecology* 71:1279–1288.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETIT. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321–333.
- HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1991. Numerical and demographic responses of temperate forest birds to annual fluctuations in their food resources. Pages 1559–1567 in *Acta XX Congressus Internationalis Ornithologici* (B. D. Bell, Ed.). Christchurch, New Zealand, 1990. New Zealand Ornithological Congress Trust Board, Wellington.
- HOWELL, A. 1932. *Florida birdlife*. J. J. Little and Ives, New York.
- JANDEL SCIENTIFIC. 1995. SigmaStat, version 2.0. Jandel Scientific, San Rafael, California.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London.
- LACK, D. 1966. *Population studies of birds*. Oxford University Press, Oxford.
- LAYNE, J. N. 1996. Crested Caracara. Pages 197–210 in *Rare and endangered biota of Florida*. Vol. 5, *Birds* (J. Rogers, Jr., H. W. Kale II, and H. Smith, Eds.). University of Florida Press, Gainesville.
- MADER, W. J. 1975. Biology of the Harris' Hawk in southern Arizona. *Living Bird* 14:59–84.
- MALHERBE, A. P. 1963. Notes on birds of prey and some others at Boshhoek north of Rustenburg during a rodent plague. *Ostrich* 34:95–96.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MILLSAP, B. A., AND C. BEAR. 1990. Double brooding by Florida Burrowing Owls. *Wilson Bulletin* 102:313–317.
- MORRISON, J. L. 1996. Crested Caracara (*Caracara plancus*). In *The birds of North America*, no. 249 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- NEWTON, I. 1979. *Population ecology of raptors*. Buteo Books, Vermillion, South Dakota.
- NEWTON, I. (Ed.). 1989. *Lifetime reproduction in birds*. Academic Press, London.
- NEWTON, I., AND M. MARQUISS. 1984. Seasonal trend in the breeding performance of Sparrowhawks. *Journal of Animal Ecology* 53:809–829.
- NUR, N. 1988. The cost of reproduction in birds: An examination of the evidence. *Ardea* 76:155–168.
- ORMEROD, S. J., AND S. J. TYLER. 1993. The adaptive significance of brood size and time of breeding in the Dipper *Cinclus cinclus* (Aves: Passeriformes) as seen from post-fledging survival. *Journal of Zoology (London)* 231:371–381.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–255.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 53:7–15.
- RICHMOND, A. R. 1976. Feeding of nestlings by the Caracara in Costa Rica. *Wilson Bulletin* 88:667.
- RIKLEFS, R. E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65:1602–1616.
- RODRÍGUEZ-ESTRELLA, R. 1996. Response of Common Black Hawks and Crested Caracaras to human activities in Mexico. Pages 355–363 in *Raptors in human landscapes: Adaptations to built and cultivated environments* (D. Bird, D. Varland, and J. J. Negro, Eds.). Academic Press, London.
- SMEENK, C., AND N. SMEENK-ENSERINK. 1975. Observations on the Pale Chanting Goshawk *Melierax poliopterus*, with comparative notes on the Gabar Goshawk *Micronisus gabar*. *Ardea* 63:93–115.
- SMITH, J. N. M., AND D. A. ROFF. 1980. Temporal spacing of broods, brood size, and parental care in Song Sparrows (*Melospiza melodia*). *Canadian Journal of Zoology* 58:1007–1015.
- SMITH, R. D., AND M. MARQUISS. 1995. Production and costs of nesting attempts in Snow Buntings

- Plectrophenax nivalis*: Why do they attempt second broods? *Ibis* 137:469–476.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman, New York.
- STAHLCKER, D. W., AND H. J. GRIESE. 1977. Evidence of double brooding by American Kestrels in the Colorado high plains. *Wilson Bulletin* 89:618–619.
- STEARNS, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- TINBERGEN, J. M., AND J. H. VAN BALEN. 1988. Food and multiple breeding. Pages 380–391 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Sciences, Ottawa.
- TOLAND, B. R. 1985. Double brooding by American Kestrels in central Missouri. *Condor* 87:434–436.
- VERHULST, S., AND R. HUT. 1996. Post-fledging care, multiple breeding and the costs of reproduction in the Great Tit. *Animal Behaviour* 51:957–966.
- VOOUS, K. H. 1983. *Birds of the Netherlands Antilles*. De Walberg Pers, Zutphen, The Netherlands.
- WESTMORELAND, D., L. B. BEST, AND D. E. BLOCKSTEIN. 1986. Multiple brooding as a reproductive strategy: Time-conserving adaptations in Mourning Doves. *Auk* 103:196–203.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687–690.
- WITMER, M. C., AND R. E. PATRICK. 1987. Continuous breeding at a Barn Owl nest in Texas. *Southwestern Naturalist* 32:402–403.
- WOOD, P. B., AND M. W. COLLOPY. 1993. Effects of egg removal on Bald Eagle productivity in northern Florida. *Journal of Wildlife Management* 57:1–9.
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