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INCIDENCE AND DETERMINANTS OF DOUBLE BROODING IN WRENTITS¹

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Abstract. The Wrentit (*Chamaea fasciata*) has been reported to raise only one brood per year. Nesting data on a marked known-age population of Wrentits in central coastal California revealed that 20% of the breeding pairs during the 4 years 1982–1985 attempted a second brood after successfully fledging young from an earlier brood. The probability of a pair attempting a double brood significantly decreased the later the first clutch was completed. No second broods were attempted if the first clutch was completed later than 5 May (14% of breeding pairs) or if the first attempt failed (41%). The remaining pairs (24%) attempted only one brood although they appeared to have the opportunity to attempt two broods. Adults attempting a second brood reduced the amount of postfledging care given to the young of the previous brood. Double-brooding individuals tended to be older, have better nest survivorship, and fledged significantly more young per season than single-brooding individuals. Survival of the adults to the next breeding season was independent of the number of broods attempted. Young males had significantly lower nest success than older males and young females began nesting significantly later than older females, which may explain the lower incidence of double brooding in young birds.

Key words: Wrentit; *Chamaea fasciata*; double brooding; nest success; parental age; length of breeding season; productivity; parental care; survivorship; California coastal scrub.

INTRODUCTION

The number of successful broods produced by a pair of birds is an important contribution to the individuals' seasonal and lifetime productivity (Hotker 1988). Maximizing the number of broods raised per season may be good reproductive strategy providing it does not cause excessive decrease of survivorship of the parents or the young produced (Williams 1966, Nur 1988).

Most species of birds raise only one brood per year because the time requirements of breeding, including raising young to independence, cannot be repeated before the ecological conditions that permit breeding have ended for the year (Lack 1968, p. 302). However, many temperate-zone passerines are known to raise more than one brood per year (Middleton 1979, Smith 1982, Boer-Hazewinkel 1987) and most nonmigratory species of California coastal scrub, such as Bewick's Wren (*Thryomanes bewickii*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Song Sparrow (*Melospiza melodia*), and Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) (Mewaldt and King 1977), are known to be multibrooded.

For species that irregularly double brood, food abundance and the corresponding extension of the breeding season appear to be the most important factors determining whether individuals or populations will double brood in any given year (Blancher and Robertson 1982, Hussell 1983, Gavin 1984, Arcese and Smith 1988). Density as well as food may determine whether individual Great Tits (*Parus major*) decide to produce a second brood (Kluyver 1951, Tinbergen and van Balen 1988).

In her extensive study of the breeding biology of Wrentits (*Chamaea fasciata*) occurring in the Berkeley Hills of central California, Erickson (1938) concluded that "only one brood is raised" per breeding season. If the first or further attempts failed, pairs would attempt replacement nests until mid-July. A circumstantial record reported by Miller (1944) and another refuted by Erickson (1938) are the only previously reported instances of a second nest attempt following a successful earlier attempt. In this study, we documented 22 incidents of double brooding in Wrentits.

The Wrentit is a nonmigratory, long-lived (up to 12 years), monogamous babbler restricted to brushy areas and chaparral in cismontane California, Oregon, and Baja California. It differs from other multibrooded species inhabiting

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coastal scrub (i.e., Bewick's Wren, Rufous-sided Towhee, Song Sparrow, and Nuttall's White-crowned Sparrow) in that: (1) both sexes build nests, incubate, and defend territories throughout the year (Erickson 1938); (2) the average nest cycle from first egg to fledging is 7 days longer; (3) the reported period of postfledging of 70 days (Erickson 1938) was longer than the 10–21 days for the four species mentioned above (Geupel and DeSante, unpubl. data) and the average of 8.2 days for all temperate-zone passerines (Ricklefs 1969). These differences may limit the ability of Wrentits to raise multiple broods.

In this study, we investigated the effects of the timing of clutch completion, density, nesting success, postfledging care, and parental age on the irregular occurrence of double brooding, the interrelationship among some of these factors, and examined the role of double brooding on adult survivorship and productivity.

METHODS

We studied Wrentits during 6 years (1980–1985) on 36 ha of coastal scrub at the Palomarin Field Station of the Point Reyes Bird Observatory. The study area was located just inside the southern boundary of the Point Reyes National Seashore immediately adjacent to the Pacific Ocean. For a description of the study site see DeSante (1981).

We banded Wrentits for individual recognition with a U.S. Fish and Wildlife Service aluminum band on one leg and three plastic color bands on the other leg. Many birds were color-banded as nestlings when they were 9–10 days old. We captured free-flying birds by: (1) trapping with four-cell "Potter" traps baited with cracked corn in the nonbreeding season; (2) a spring and summer netting program in which portable mist nets were operated in favorable locations, and (3) the daily operation of 20 mist nets that bordered the study plot. The age of birds not banded as nestlings was determined by the stage of skull pneumatization or the color of the outer iris (Pyle et al. 1987). Sex was determined in the field by differences in song (Grinnell 1913).

The entire study plot was censused two times per month throughout the year. We determined the location of territorial boundaries by spot-mapping censuses. We made concentrated efforts during each census to locate all nests for all breeding pairs in the study area. Some nests that failed early in the incubation period may have been missed. We visited nests every 1–4 days to

obtain clutch size, date of clutch completion, number of eggs hatched, hatching date, number of young fledged, and fledging date. We defined the date of predation or desertion as the midpoint between the date the nest was last active and the date the nest was first found to be inactive.

We considered a nest successful if at least one young fledged. Confirmation of fledging was obtained by direct observation of the fledglings or of food carrying by the adults. Predation was assumed if all the nest contents were missing. Desertion was assumed if all the cold eggs or dead nestlings were present. Predation was the cause of nest failure in 94% of all failed nests, while desertion, usually caused by inclement weather, accounted for the other 6% of the failed nests.

Each nesting attempt of each pair was classified into one of the following four categories: (1) first attempt (first nest of the season where at least one egg was laid); (2) replacement attempt (a second, third, or fourth nest where the previous attempt failed). No pairs attempted to replace a failed double brood attempt; (3) double brood attempt (a second nesting attempt following a successful first attempt; and (4) unknown attempt (chronology of nest unknown).

Elements of nesting success were: clutch size; hatchability (the proportion of eggs surviving the incubation period that hatched); number of young fledged; and the nest survivorship during the egg-laying, incubation, and nestling periods, and over the entire nesting period. The entire nesting period was defined as beginning on the day of laying of the first egg and ending on the day of departure of the last nestling, and on average equaled 33 days. Only nests where at least one egg was laid were considered as a nesting attempt. The mean survivorship of nests during these four periods was estimated by the Mayfield (1961, 1975) method. We estimated the variance and statistical significance of these survivorship values as recommended by Johnson (1979).

The period of parental care was defined as the number of days between a juvenile's fledging date and the last date it was seen within 30 m of its natal territory. Because a few individuals remained on their natal territory as long as 200 days and others were known to return to their natal territory after becoming independent, we defined the upper limit of parental care as 41 days. This was the maximum number of days an individual Wrentit has been observed being fed by its parents. We set a lower limit of 18 days,

TABLE 1. The number of double broods, the number of first broods located, the proportion of pairs double brooding, density (number of breeding pairs per hectare), the mean clutch completion dates of first attempts, and latest nest of Wrentits over the 6 years 1980–1985.

Year	No. of attempts		Proportion of pairs double brooding	Density*	Mean of all first attempts ^b Date (SD)	Latest nest date
	Double brood	First brood				
1980	1+?	14	?	1.25	30 April (16.70)	19 June
1981	?	30	?	1.33	30 April (14.34)	12 June
1982 ^c	6	21	0.286	0.97	28 April (12.68)	1 July
1983 ^c	1	27	0.037	1.11	28 April (16.73)	27 June
1984 ^c	7	30	0.233	1.06	19 April (16.95)	26 June
1985 ^c	8	33	0.242	1.31	21 April (10.99)	29 June

* Logistic regression analysis of proportion double brooding with density; Likelihood ratio statistic = 0.003, df = 1, $P > 0.9$.

^b Logistic regression analysis of proportion double brooding with date; Likelihood ratio statistic = 1.39, df = 1, $P > 0.2$.

^c Logistic regression analysis of the 4 years 1982–1985; Likelihood ratio statistic = 7.70, df = 3, $P > 0.1$.

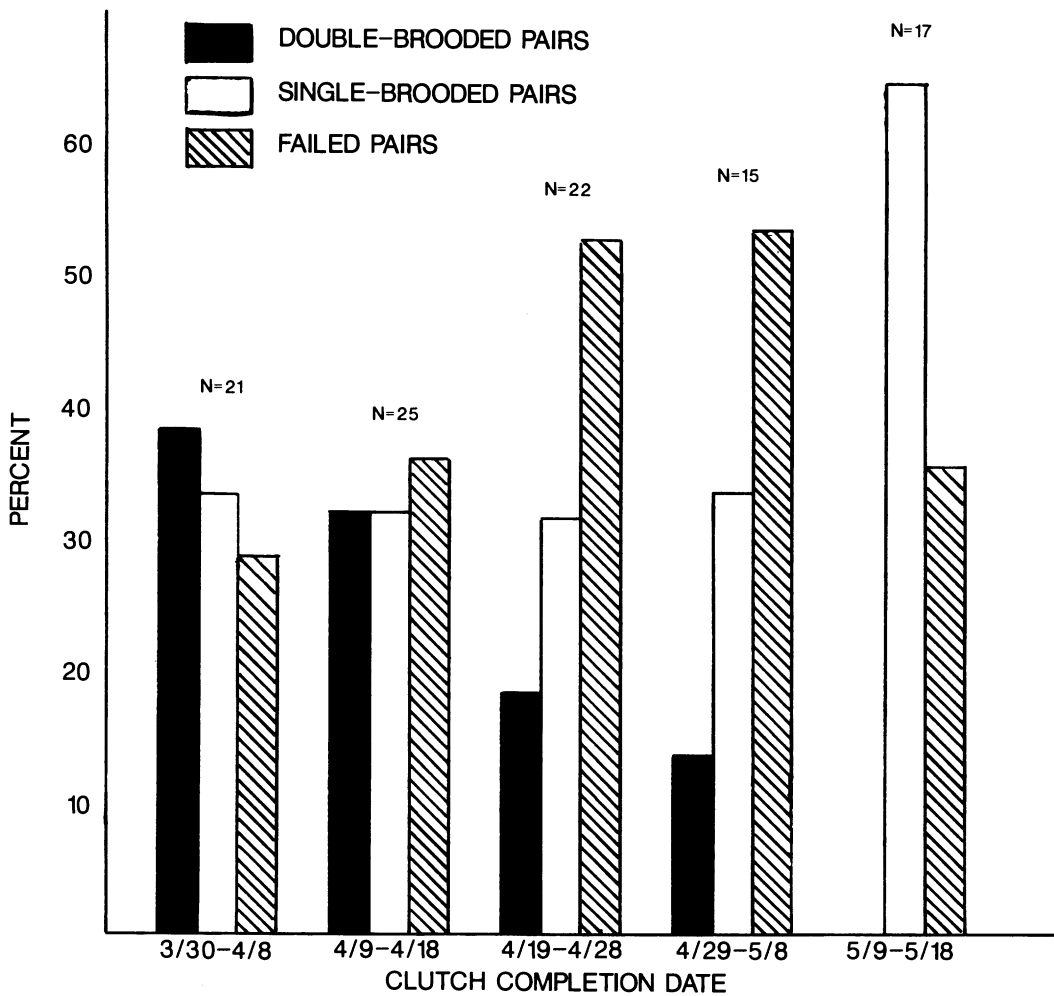


FIGURE 1. The percent of Wrentit pairs; double brooding, single brooding, or failed on their first-brood attempt based on their first-brood clutch completion date over the 4 years 1982–1985. Logistic regression analysis of the percentage of pairs double brooding compared to date (log-likelihood ratio statistic = 10.75, $P < 0.01$).

TABLE 2. Nesting success of first-brood, replacement, and double-brood nesting attempts by Wrentits for the 3 years 1982, 1984, and 1985.

	Clutch size ^a	Hatchability ^a	Nest survivorship ^b
First-brood attempt	3.71 (0.551) 63	0.890 (0.166) 66	0.458 ^c (0.338–0.618) 83
Replacement attempt	3.74 (0.526) 27	0.854 (0.200) 28	0.533 ^c (0.364–0.777) 31
Double-brood attempt	3.85 (0.555) 13	0.913 (0.161) 20	0.616 ^c (0.350–1.073) 21

^a Mean, (SD), sample size (differences between the three groups were not significant, *t*-test).

^b Survivorship (determined by Mayfield's [1961, 1975] method), 95% confidence limits (Johnson 1979), number of nests.

^c Survivorship values not significantly different (pairwise *z*-tests, Johnson 1979).

which was the earliest a juvenile was observed off its natal territory.

Less than 1% of breeding adult Wrentits moved territories between breeding seasons. No adults were known to skip a breeding season. Therefore, we defined adult survival as the number of adults returning to breed on the study area the following year. Differences in survivorship rates were compared using a log-likelihood ratio test (*G*-test).

The proportion of pairs double brooding from 1982–1985 were compared with clutch-completion dates, breeding density, and between years using logistic regression analysis (log-likelihood ratio test). Components of nesting success except survivorship were compared by *t*-tests and paired *t*-tests. Significance was assumed at the 0.05 level. Data for 1980, 1981, and 1983 were excluded from analysis of nesting success except with regard to age because of the low or unknown occurrence of double brooding in those years. Because age-distribution samples represent the same individuals over different years, values are not independent and no statistical tests were performed.

RESULTS

Of the 111 pairs that had known first-brood nesting attempts between 1982 and 1985, 22 (20%) went on to attempt a second brood. They involved 39 individual Wrentits (19 males and 20 females). All adults except five were individually

color-banded, thus providing conclusive proof of double brooding in 17 cases (see Peck 1984). The number of double-brood attempts per year was consistent in three out of four years. The proportion of pairs that double brooded was not significantly correlated with the mean date of first brood attempts, breeding density, or the latest nest (Table 1). The low incidence of double brooding in 1983 was associated with high rates of nest desertion, the result, we suspect, of late spring rains (DeSante and Geupel 1987) associated with a major El Niño Southern Oscillation. The fact that no cases of double brooding were recorded in 1980 or 1981 with the exception of a single female that acquired a new male (Geupel 1981) may be a result of incomplete observation.

In 46 cases (41%) Wrentit pairs failed on their first attempt. None of these pairs went on to attempt two successful broods. The only exception to this pattern (less than 1%) was a pair that abandoned two eggs prior to clutch completion and successfully fledged young from their second and third attempts.

Of the 64 successful first attempts 15 (14%) were from pairs that had clutch completion dates later than 3 May. None of these pairs attempted a double brood. The probability of a pair attempting a double brood significantly decreased the later the first clutch was completed (Fig. 1). The remaining 27 pairs (24%) were successful on their first brood, had clutch completion dates

TABLE 3. The number of young fledged from successful nesting attempts by Wrentits over the 4 years 1982–1985.

	\bar{x}	SD	<i>n</i>
Double-brood pairs first attempt	2.88 ^{bc}	1.021	17
Double-brood pairs second attempt	3.18 ^b	1.051	17
Single-brood pairs first attempt ^a	3.14 ^c	0.728	21
Replacement attempts	2.89	0.817	29

^a Nests with clutch completion dates before 5 May.

^b Paired *t*-test, *t* = 0.202, *P* > 0.5.

^c *t*-test, *t* = 0.176, *P* > 0.5.

TABLE 4. The number of days between fledging and the day the Wrentit juvenile was last seen on its natal territory in relation to the fledgling's brood status.

Fledglings from	<i>n</i>	\bar{x} (SD) ^a	Range ^b
Single brood	70	31.9 (6.5)	18–200
First brood of two broods	24	29.9 (5.2) ^{cd}	25–179
Second brood of two broods	22	33.6 (7.7) ^c	28–158
All except first brood of two broods	92	32.5 (6.8) ^d	18–200

^a Data truncated at lower limit of 18 days and upper limit of 41 (see text).

^b Data not truncated.

^c *t*-test, *t* = 1.63, *P* = 0.11.

^d *t*-test, *t* = 1.97, 0.05 < *P* < 0.1.

early enough to permit two broods, but did not attempt a second brood.

Second-brood nests had a mean clutch completion date of 10 June (SD ± 9.9 days) and were not attempted after 1 July. The number of days between the fledging of the first brood and the laying of the first egg of the second brood was 28.9 ± 8.8 days (*n* = 21, range = 10–47 days). Clutch size and hatchability of second-brood nests were similar to other nests (two sample *t*-test, *P* > 0.05, Table 2). Nest survivorship of second-brood attempts were 34% greater than first-brood attempts (*z* = 1.08, *P* > 0.2, Table 2). Comparison of nest survivorship values over nine 10-day periods revealed no positive or negative seasonal trends.

The mean number of young known to have fledged from second-brood nests was not significantly different than that from first nests of double-brooded pairs, nor was it different from single-brood pairs' first and only nest (Table 3). Thus, pairs that successfully fledged two nests in a year produced significantly (*t* = 9.726, *P* < 0.001) more young per season (5.75 ± 1.65 SD, *n* = 16, range = 3–9) than birds that raised only one successful brood per year (3.06 ± 0.794, *n* = 63, range = 1–4).

First-brood young of parents who went on to double brood tended to receive less parental care (\bar{x} = 29.9 days) than the young of single-brooding parents (\bar{x} = 31.9 days) or the young from sec-

ond-brood nests (\bar{x} = 33.6 days) (difference not significant; Table 4). These periods were considerably less than the 70 days reported by Erickson (1938). In most cases, young from first-brood nests were off, presumably excluded from their natal territory, at the time of incubation of the second brood.

Adults who attempted two broods survived to breed the following year at a higher rate (81%) than adults that raised only a single brood (64%) (Table 5). These results were similar for both sexes.

Younger (second-year) male and female Wrentits in their first breeding season tended to double brood less often than older (after-second-year) birds (Table 6). Two of the four second-year females were banded as nestlings and both were offspring of parents who had double brooded at some time in their lives.

We investigated the two factors previously identified as important influences on double brooding: date of first brood and success of first nesting attempt. Older females tended to nest earlier than younger females: Clutch completion dates for first-brood nests were on average 11 days earlier for older females (*t* = 3.69, *P* < 0.001, Fig. 2). Age did not influence clutch completion dates among males. The single, unusually late, first-brood clutch completion date of June 16 (1985) involved a known young female floater (Brown 1969) that finally paired with an un-

TABLE 5. The number of adult Wrentits surviving to breed the following year based on the previous year's nesting attempt(s).

	Males ^a			Females ^a		
	Number	Observed	Percent	Number	Observed	Percent
Single successful brood	32	49	65.3% ^c	28	45	62.2% ^d
Replacement attempt ^b	12	17	70.6% ^c	11	17	64.7% ^d
Double-brood attempt	15	17	88.2% ^c	15	20	75.0% ^d

^a Number returned, number observed, percent returned.

^b First attempt failed and at least one or more attempts.

^c Log-likelihood ratio test, *df* = 2, *G* = 3.212, *P* = 0.073.

^d Log-likelihood ratio test, *df* = 2, *G* = 0.948, *P* > 0.3.

TABLE 6. Age distribution of single-brooded (SB)^a and double-brooded (DB)^b Wrentits.

Age (years)	Males			Females		
	SB ^a	DB ^b	% DB	SB	DB	% DB
2	7	1	12.5	9	4	30.8
Total > 2 years	12	15	55.6	9	17	65.4
Unknown age	7	6	46.2	8	1	11.1
Total	26	22	45.8	26	22	45.8

^a Single-brooded birds are those that successfully fledged young from their first nesting attempt in a given year and did not attempt a second nest.
^b Double-brooded birds are those that successfully fledged young from their first nesting attempt in a given year and did attempt a second nest.

mated older male late in the season. Younger males had significantly lower nest survivorship in the egg-laying-incubation period than older males (Table 7). No significant age effects were found for females for any measure of nesting success. Thus the tendency for older birds to double brood more often may be, in part, due to age-related differences in nest initiation in females, and age-related differences in nesting success among males.

DISCUSSION

Double brooding in the coastal population at Palomar is a relatively common event. It is re-

markable that Erickson (1938) did not observe double brooding in an ecologically similar Berkeley population, particularly since she regularly recorded replacement nests as late as 15 July, some 2 weeks later than the latest replacement nest recorded in the Palomarin population. Miller (1944) stated, "There is no reason to doubt Erickson's observations . . . for she was thoroughly acquainted with events taking place in the lives of the many pairs under her surveillance." This apparent enigma may reflect Erickson's fewer years of observation, difference in populations (see Gavin 1984), habitats (Kluyver 1951, Boer-Hazewinkel 1987), density (Tinbergen and van Balen 1988), the origin of races

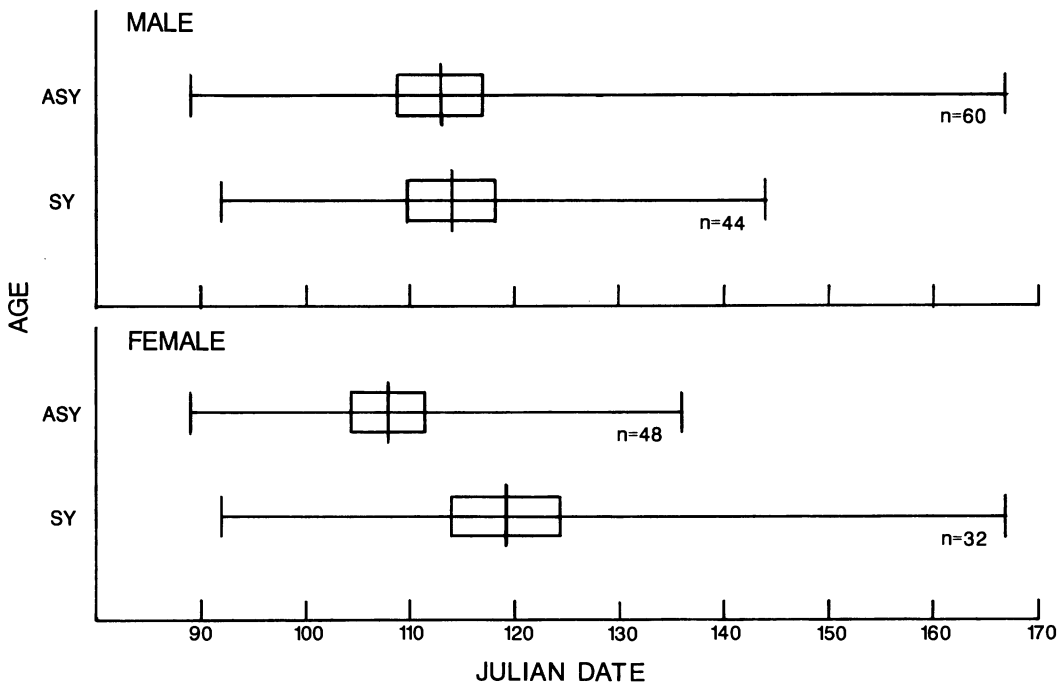


FIGURE 2. Mean, range, and 95% confidence limit (box) of clutch completion dates of first-brood nests (1980-1985) as a function of parental age and sex.

(Erickson studied the more interior *intermedia* race, and we studied the coastal *rufula* race), or perhaps that double brooding is a new behavior.

Most species that normally single brood succeed in double brooding by extending the length of the breeding season (Lack 1968, Blancher and Robertson 1982, Hussell 1983). Because Wrentits maintain pair-bonds and remain on territories throughout the year, they may rapidly respond to ecological conditions that exist at the beginning of the breeding season as has been shown for Savannah Sparrows, *Passerculus sandwichensis* (Baptista 1984). The earlier initiation of breeding in 1984 and 1985 did not increase the proportion of pairs double brooding. Furthermore, when the breeding season was delayed approximately 8 days in 1982 the proportion remained high. However, within years pairs that bred earlier were more likely to double brood.

Cliff Swallows, *Hirundo pyrrhonota*, have been shown to vary the incidence of double brooding between years (Samuel 1971), and it has been suggested that this species has evolved the ability to assess whether or not a double-brood strategy is "more favorable under a given set of conditions" (Hussell 1983). In this study we have shown intrapopulation variability under apparently similar environmental conditions (i.e., habitat and year).

The greater survival probability for double-brooded adults compared to single-brooded adults may suggest that only higher quality individuals attempt a double brood and/or individuals only attempt second broods under better environmental conditions such as being on a high quality territory (Nur 1988). The increased incidence of double brooding with age may reflect an association between age and quality of the individual on the territory. Boer-Hazewinkel (1987) reported a similar positive correlation between survival of the parents and production of second clutches in Great Tits, *Parus major*.

In contrast to other normally single-brooded species (Blancher and Robertson 1982, Hussell 1983, Gavin 1984) or multibrooded species (Nol and Smith 1987), Wrentits did not exhibit significant reduction in clutch size, hatchability, or nesting success in the second brood. Furthermore, the number fledged per nest did not vary between first-brood or double-brood attempts. Thus, Wrentits that did double brood greatly increased their productivity. Because Wrentits do not have conflicting pressures to raise young to

TABLE 7. Nesting success of second-year (SY) and after-second-year (ASY) male and female Wrentits over the 6 years 1980-1985.

	Clutch size ^a	Hatchability ^a	Survivorship per period			n
			Laying, incubation ^b	Nesting ^b	Total ^b	
SY males	3.63 (0.492) 24	0.872 (0.202) 26	0.45 ^c (0.27-0.72)	0.71 (0.53-0.96)	0.32 (0.18-0.57)	39
ASY males	3.75 (0.530) 111	0.906 (0.158) 117	0.77 ^c (0.67-0.88)	0.66 (0.56-0.77)	0.49 (0.39-0.61)	134
SY females	3.61 (0.543) 41	0.925 (0.128) 41	0.65 (0.50-0.84)	0.71 (0.56-0.89)	0.46 (0.32-0.65)	54
ASY females	3.82 (0.483) 95	0.888 (0.181) 104	0.73 (0.62-0.86)	0.72 (0.63-0.87)	0.52 (0.42-0.65)	121

^a Mean, (SD), sample size.

^b Survivorship (determined by Mayfield's [1961, 1975] method), 95% confidence limits (Johnson 1979).

^c Values followed by the same superscript are significantly different ($z = 2.166$, $P < 0.05$).

independence or to migrate, they should be able to minimize mortality rates of second-brood young as has been described for Purple Martins, *Progne subis* (Brown and Bitterbaum 1980). Young from double-brood nests, in fact, received the most parental care (Table 5).

As has been suggested for Wood Ducks, *Aix sponsa* (Moorman and Baldassarre 1988), Wrentits gain time for double brooding by reducing the amount of postfledging care that they provide to the young of the first brood. This may be a result of the fact that male Wrentits share nest-building and incubation responsibilities. Thus, males were not free to guard or feed fledglings from the first brood while females began second broods as has been described for Great Tits (Tinbergen 1987).

With reduced parental care (Blancher and Robertson 1982) or late fledging date (Perrins 1965) one would suspect that the progeny from double-brood parents would have a lower probability of survival than progeny from single-brood parents. Alternatively, higher quality individuals might produce higher quality young independent of the amount of parental care or date fledged. Further study is needed to document differences in natal survivorship.

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