OLD AGE AND BREEDING BEHAVIOR IN A TROPICAL PASSERINE BIRD *PLOCEUS CUCULLATUS* UNDER CONTROLLED CONDITIONS

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ABSTRACT.—Many tropical species of passerine birds have potentially long reproductive lives in both nature and aviaries, but rate of breeding by old individuals may eventually decline. A group of individually color-banded African Village Weavers (*Ploceus cucullatus*), a polygynous species, was kept in aviaries at Los Angeles for 22 years. At 14–18 years of age, old males built significantly fewer nests per year, displayed to females less often, had fewer mates, and generally fathered fewer clutches than did the same males when 9–13 years old. One male reached 24 years of age, when he rarely sang and no longer wove when provided with nest materials. The females, after reaching "middle age" (9–13 yr), laid significantly fewer eggs per year, and still fewer during "old age" (14–18 yr). When 14 or more years old, weavers of both sexes rested much more than did young adults 4–6 years old in the same aviary.

Individuals differed greatly in the decline of breeding behavior with age. Some individual Village Weavers bred at a surprisingly great age for passerine birds, e.g. fertile copulations by one 19-year-old male and by one 18-year-old female. These seem to be the oldest breeding ages yet recorded for any small passerine bird. Long reproductive life of a small number of individuals that contribute disproportionately to the next generation would give a selection pressure for longevity, and also could help explain the evolution of small clutch size (2–3 eggs) in the Village Weaver and in many other tropical birds. *Received 7 January 1985, accepted 5 December 1985.*

ETHOLOGICAL gerontology deals with the behavioral aspects of the ecology and evolution of animal life spans. Our object is to give a quantitative description of how old age influences the breeding behavior of a tropical passerine bird under controlled conditions. Like people, animals rarely, if ever, die of "old age," but rather of increased susceptibility to some stressful condition. The reactions and behavior of old animals must be compared simultaneously with those of younger control animals to evaluate adequately the effects of advanced age. Our data deal with maximum breeding ages, but we try to relate our results to actual breeding ages in nature. We can find no previous study that presents experimental and quantitative data on the effects of old age on breeding behavior of wild birds under controlled conditions.

Recent studies suggest high adult survival among small land birds in the tropics (Fogden 1972, Snow and Lill 1974, Fry 1980, Lewis 1980, Collias and Collias 1981, Willis 1983), where annual survival rates were 70–90% in over 30 species. By contrast, among small land birds of the north Temperate Zone, adult survival per year seems to be about 40–60% (Ricklefs 1969, Cody 1971: 490).

The relatively great adult survival known in nature for at least some small tropical land birds raises the question of how long and how successfully such old birds are able to breed. If some long-lived individuals continue to reproduce over a number of years, and exclude others from breeding, their contribution to succeeding generations may be much greater than that of the average adult of the same species. Furthermore, the question of senescence among small tropical land birds has not been studied systematically.

For over 20 years we studied the behavior of a breeding colony of a tropical passerine bird, the African Village Weaver (*Ploceus cucullatus*), in outdoor aviaries at the University of California, Los Angeles (UCLA). The birds are polygynous and breed in colonies with many nests in one tree. The male weaves the nest from long strips that he tears from the leaves of palms or tall grasses. Each male occupies and defends from one to a few small branches on which he builds his nests. He endeavors to attract unmated females to his nest with special displays and vocalizations. If a female accepts the nest, she lines it with grass tops and often with feathers as well. She incubates the eggs and, in this subspecies, does virtually all the feeding of the young. The male is normally sexually mature by 2 years of age, the female when 1 year old.

The birds in our aviaries freely competed with each other for food, nest materials, and mates. It gradually became evident that many of these Village Weavers were able to breed at a surprisingly advanced age. A decline in breeding behavior of some very old adults seemed evident, but controlled observations were needed. In 1977, 1979, and 1980 we specifically compared groups of old and young adults, but in 1978 the birds were kept indoors because of construction activities by the university near the outdoor aviaries. We controlled numbers of birds per aviary, sex and age ratios, food supply (ample *ad libitum*), and of course predation. In nature, it would be extremely difficult to compare the behavior of younger and very old birds exposed to exactly the same conditions. But such comparisons can readily be made on captive birds in aviaries under controlled conditions. We have presented two preliminary reports (Collias et al. 1980, 1981).

Materials and Methods

The Village Weavers belonged to the West African race (*P. c. cucullatus*); the original stock came from Senegal, where we studied the behavior of this subspecies in the field (Collias and Collias 1970). Dr. Jean Delacour sent us 18 males and 8 females in the fall of 1958, from which the birds of this experiment were descended over three generations. The breeding behavior of the birds in our five outdoor aviaries (from 9.2 m long × 5.2 m wide × 5.2 m high, to 7.9 × 6.1 × 4.2 m) at UCLA was essentially similar to that seen in nature. The birds were allowed to choose their own mates.

Usually, a similar number of males and females were kept in each aviary (Table 1). Males typically weighed 41-51 g ($\bar{x}$ = 46, n = 9), females 31-39 g ($\bar{x}$ = 36, n = 9). Because the sex ratio has a profound effect on amount of breeding activity (Collias et al. 1971), the overall sex ratio was kept about equal each year. It was more difficult to keep age ratios constant, because by the nature of the experiment the oldest birds tend to die. We included in the experimental analysis only those birds that lived through the breeding season of any given year. Each of the two outdoor aviaries contained both older and younger (control) birds, except for one aviary in 1979. The results from both aviaries were merged for statistical analysis. All the birds in each aviary, regardless of their ages, were exposed to the same number of adults of the opposite sex.

Table 1. Sex and age composition of birds in two experimental aviaries. (M = number of males, F = number of females.)

	Aviary 1 M:F	Aviary 2 M:F	Total M:F
1977[a]			
Older birds (12–15 yr)	3:3	4:3	7:6
Young adults (2–3 yr)	4:4	5:5	9:9
Total	7:7	9:8	16:15
1979			
Old birds (14–17 yr)	—	6:6	6:6
Young adults (4–5 yr)	5:5	3:4	8:9
Total	5:5	9:10	14:15
1980			
Old birds (15–18 yr)	2:2	2:2	4:4
Young adults (5–6 yr)	4:5	4:4	8:9
Total	6:7	6:6	12:13

[a] Starting figures: during 1977 all the males of the two aviaries were interchanged at either 4- or 6-week periods.

Each bird carried two colored leg bands on each leg, with the same individually distinctive color combination on each leg. Each bird was named from its leg bands; thus, Male OG had an orange over a green band on each leg. The birds were fed on parakeet seed mixture, fresh lettuce, cuttlebone, grit, a vitamin supplement (Vionate), meal worms regularly, and crickets when the birds were raising broods. Fresh water was given daily. The 5–10 males usually kept in each aviary commonly built up to 100 or more nests during the breeding season of April to September. During the cool winter months we brought the birds indoors, where they were maintained in cages or small aviaries.

With the exception of one male (RA), all the birds we report on here were hatched in our aviaries on known dates. Records were kept routinely for each male of the number of nests he built, number of mates he secured, and number of clutches he presumably fathered. Of several hundred copulations observed, only twice was a female seen to copulate with a male other than her own mate. We made sample counts 1

TABLE 2. Individual records of numbers of nests built (N), mates obtained (M), and clutches fathered (C) by older and younger adult male Village Weavers during the last four years of the study.[a] In 1978 birds were indoors and not allowed to breed.

	Age in 1977	Life span (yr)	1977			1979			1980		
			N	M	C	N	M	C	N	M	C
Older males											
Wbr	12	17.9	31	8	14	17	4	12	23	7	27
yrB	12	16.7	33	4	15	7	1	1	1	1	1
yrA	12	15.4	25	5	7	2	0	0	0	0	0
OG	12	15.2	25	2	8	0	0	0	0	0	0
AR	12	14.6	25	9	9	3	0	0		*	
Brb	12	14.1	13	3	13	4	2	5		*	
Awr	15	16.2	10	0	0		*				
Younger adult males											
OY	2		24	1	1	19	3	9	14	4	9
GW	2		14	0	0	10	2	6	7	3	9
YW	2		10	0	0	3	0	0	6	0	0
WO	2		15	1	1	20	3	11	14	1	6
AO	2		6	0	0	15	2	8	0	0	0
RG	3		20	3	4	10	1	2	26	4	19
WB	3		18	2	6	14	6	19	8	5	12
YA	3		16	3	8	4	1	1	0	1	2
WR	3		25	3	9		*				

[a] An asterisk indicates that the bird died.

h each day of the frequency with which each male gave nest-invitation displays to females, counting each time the male hung beneath the nest entrance flapping his wings. For each female, we recorded her mates and the number of clutches and eggs laid. In occasional tests for fertility of old birds, we cracked open the eggs and checked for presence or absence of an embryo. "Old age" was arbitrarily defined as about 14 years. Time samples of specific behaviors engaged in by every bird also were taken during the last two years. To stimulate more nest building and more nest acceptances by the females, we generally removed clutches. This was done shortly after the eggs were laid to prevent wide variations in the interval before a female laid her next clutch. Prompt removal of clutches (experimental predation) made the data more comparable within and between the different years, and allowed us to test the reproductive capacity of the females in relation to their age. In September 1980 we terminated the experiments.

RESULTS

Effects of age on amount of breeding.—Old and young adults were compared in two ways for breeding performance. First, they were compared during the same year to control for difference in circumstances in different years. Second, the breeding behavior of the same individual was compared during different times in its life.

In 1977, the older males (all but one then 12 yr old) exceeded the younger adult males (2–3 yr old) in number of nests built, number of mates, and number of clutches fathered (Tables 2 and 3). In 1979, these same younger males (then 4–6 yr old) significantly exceeded the old males (then 14 yr old) in number of nests built. The change from 1977 to 1979, comparing survivors only, was statistically significant for all aspects of behavior mentioned. Frequency of nest-invitation displays to the female by the males varied greatly, but here too the old males declined significantly from 1977 to 1979 when compared with the young males (rank-sum test, $P = 0.004$). The old males dropped from an average of 168 displays$\cdot$month$^{-1}\cdot$male^{-1} to 47, whereas the young males stayed essentially the same in both years (64:61).

Although the males normally mature at 2 years of age, these differences could be a function of increasing experience of the young adults as well as aging of old adults. The change with age from 1979 to 1980 was not significant, but only four old males survived; three of them had poor records in both years (Table 2), while in 1980 one vigorous 15-year-old male (Wbr) had the most mates and fathered 59% of the clutches in his aviary (with 2 old and 5 young adult males).

When each of eight old males was compared

TABLE 3. Breeding behavior of older and younger adult male Village Weavers; same birds (survivors) each year. Averages per male are given in parentheses.

	Total				
	1977[a]		1979		1980
Age of older : younger males (yr)	12–13:2–3		14:4–5		15:5–6
No. of older : younger males	7:9		6:8		4:8
No. of nests built					
Older males	162 (23.1)		33 (5.5)		24 (6.0)
Younger males	148 (16.4)		95 (11.9)		75 (9.4)
Probability[b]	NS (0.06)	0.001	0.041	NS	NS
No. of mates					
Older males	31 (4.4)		7 (1.2)		8 (2.0)
Younger males	13 (1.4)		18 (2.2)		18 (2.2)
Probability[b]	0.024	0.002	NS	NS	NS
No. of clutches fathered					
Older males	66 (9.4)		18 (3.0)		28 (7.0)
Younger males	29 (3.2)		56 (7.0)		57 (7.1)
Probability[b]	0.02	0.001	NS	NS	NS

[a] In 1977 only one male was older than 12 years.
[b] Probabilities are based on rank-sum test (Dixon and Massey 1969: 344), comparing totals for older and younger males within and between years.

against his own record, the males built significantly more nests on the average each breeding season after reaching "middle age" (9–13 yr) than as young adults (3–8 yr) (Table 4). Average annual number of nests built per male declined greatly ($P = 0.01$) when the males reached "old age" (14–18 yr). The average number of mates each male obtained per year also decreased significantly after age 14, but not the average number of clutches fathered (Table 4), because of one exceptional old male (Wbr), who fathered two-thirds of all the clutches fathered by the eight old males. For the other seven males together, there was a significant decline ($P = 0.016$) from middle to old age in clutches fathered. The term "bird-years observed" (Table 4) refers to the fact that the different birds were observed for 1–4 seasons each during each 5- or 6-yr period of life, varying with each bird. Not all birds were allowed to breed every year, but the data were grouped to

TABLE 4. Changes in breeding behavior by eight adult male Village Weavers as they aged.

		Yearly averages per male[a]		
Age	Bird-years observed	Nests built	No. of mates	Clutches fathered
Young adult (3–8 yr)	20	15	2.7	5.5
Middle age (9–13 yr)	29	23*	3.7	7.8
Old age (14–18 yr)	13	6*	1.5*	3.7[b]

[a] * = significant change ($P < 0.05$) from preceding age by Wilcoxon matched-pairs signed-rank test.
[b] Not significant ($P = 0.078$); see text.

TABLE 5. Numbers of clutches and of eggs (in parentheses) laid during the last four years of the study by individual older and younger adult female Village Weavers.[a] In 1978 birds were indoors and not allowed to breed.

	Age in 1977	Life span (yr)	1977	1979	1980
Older females					
WA	15	18.4	9 (24)	2 (5)	2 (2)
Oar	13	16.2	7 (14)	0 (0)	1 (1)
brG	12	17.5	2 (3)	0 (0)	4 (4)
Bya	12	15.1	1 (1)	2 (4)	0 (0)
Aba	12	14.4	13 (27)	1 (2)	*
Aya	12	13.9	5 (9)	0 (0)	*
Younger adult females					
RY	3		7 (15)	11 (31)	8 (21)
AB	3		8 (16)	7 (13)	8 (17)
YB	3		7 (13)	6 (12)	9 (20)
LW	3		3 (6)	5 (10)	8 (16)
RO	2		7 (13)	9 (25)	9 (20)
GY	2		10 (21)	5 (15)	9 (25)
OL	2		4 (8)	9 (20)	7 (13)
YL	2		9 (19)	10 (24)	10 (23)
LG	2		3 (6)	5 (8)	4 (8)

[a] An asterisk indicates that the bird died.

TABLE 6. Number of clutches and eggs laid by older and younger adult female Village Weavers; same birds (survivors) each year. Averages per female are given in parentheses.

	Total				
	1977[a]		1979		1980
Age of older : younger females (yr)	12–15:2–3		14–17:4–5		15–18:5–6
No. of older : younger females	6:9		6:9		4:9
No. of clutches					
Older females	37 (6.2)		5 (0.8)		7 (1.8)
Younger females	58 (6.4)		67 (7.4)		72 (8.0)
Probability[b]	NS	0.004	<0.001	NS	0.001
No. of eggs					
Older females	78 (13.0)		11 (1.8)		7 (1.8)
Younger females	117 (13.0)		158 (17.6)		163 (18.1)
Probability[b]	NS	0.005	<0.001	NS	<0.001

[a] In 1977 only one female (WA) was older than 13 years.

[b] Probabilities are based on rank-sum test (Dixon and Massey 1969: 344), comparing totals for older and younger females within and between years.

show general trends by yearly averages per male for young, middle-aged, and old adults. The clutches fathered by old males dropped significantly from 1977 to 1979, including Male Wbr, when the birds went from 12 to 14 years of age (Table 3).

In 1977 the average number of clutches and eggs laid by the older females (all but one were then 12–13 yr old) was about the same as the number laid by young adult females (2–3 yr old). By 1979 the same older females laid significantly fewer clutches and eggs than did the same young females (Tables 5 and 6). The average number of clutches and eggs laid each season by eight females over their lifetime decreased significantly when they reached middle age and again in old age (Table 7).

The modal clutch was two eggs. We removed the eggs of each female as soon as she had completed her clutch, and this procedure may have contributed to an earlier decline in reproductive behavior of the females compared with the males because the females no doubt laid many more clutches than birds in nature would, under this strong experimental "predation."

TABLE 7. Average number of clutches and eggs laid per year by eight adult female Village Weavers as they aged.

Age	Bird-years observed	Yearly averages per female[a]	
		Clutches	Eggs
Young adult (3–8 yr)	8	9.7	20.7
Middle age (9–13 yr)	24	5.3*	11.2*
Old age (14–18 yr)	15	2.4*	5.8*

[a] * = significant decline ($P < 0.05$) from preceding age by Wilcoxon matched-pairs signed-rank test.

Interest in males or their nests may persist longer than egg laying in females that were previously good layers. During the breeding season of 1980, a 16-year-old female accepted nests four times without laying eggs, although she copulated with the male owner each time. She laid only one egg all season. This egg was addled and could not be checked for fertility. Another female still visited nests but was not seen to copulate and laid no eggs at 15 years of age in the last breeding season she was observed. She carried a little lining material into the nests. Very old females incubated their eggs, and in the case of three females (15–18 yr old) allowed to incubate, kept the eggs covered for about the same percentage of time as did four younger females that were incubating eggs at the same time. The oldest female given the opportunity to raise young was 12 years old, and she fed and cared for her nestlings.

Individual Village Weavers varied greatly in the apparent effect of old age on their breeding. The oldest female averaged twice as many clutches and almost four times as many eggs per season as did the best of seven other very old females, all of whom were at least 2 years younger. During the 1980 breeding season, two 15-year-old males failed to establish territories and did not breed. That same season another 15-year-old male built only one nest, obtained only one mate, and fertilized only one clutch. But a fourth 15-year-old male held a territory,

TABLE 8. Percentage of instantaneous time samples in which old and young adult male Village Weavers engaged in various activities.

	1979			1980		
	Old	Young	P	Old	Young	P
No. of males (territorial : nonterritorial)	4:3	3:0		2:3	6:3	
Resting (perch, preen, sleep)						
Territorial	62	55	NS	46	26	0.01[a]
Nonterritorial	—	—	—	81	62	0.05[a]
Forage, eat, drink	11	8	NS	11	7	NS
Building by territorial males	20	21	NS	21	24	NS
Singing	1	0	NS	3	8	0.07
Display of nest	3	7	0.058	10	15	NS
Precopulatory and copulatory behavior	1	4	0.055	2	2	NS
Total samples	200	200		110 120	110 120	

[a] Differences statistically significant. Probabilities are based on relative frequencies and binomial test (Siegel 1956).

dominated the six other males in his aviary, and built more nests (23 during that season) than any other male in his aviary. He also obtained 7 mates, and fathered 27 clutches, far more than any of the other 13 males that season in either of the aviaries (Table 2). By 1983, in his 18th year and living in the Los Angeles Zoo, he had outlived all the other old males but had not yet built a nest that season, although four young adults in his aviary at the zoo had done so. He died later that season of unknown causes.

Some Village Weavers continue to breed, or retain high dominance, at a surprisingly advanced age. One wild-trapped adult was still fertile at a minimum age of 19 years when last checked for fertility. At 20 years old he still held a territory, wove nests, courted females, and copulated, although he died near the end of that season (1976). One 20-year-old male did not breed, but despite an old wing injury, dominated the other nine males in his aviary. His wing had been broken in a fight and had healed imperfectly. Our oldest female laid 24 eggs at 15 years of age. When she was 18 years old, she still lined nests, laid fertile eggs, and incubated.

Frequency of various behaviors in old and young adults.—Instantaneous samples of all activities by each bird were taken by scanning the aviary every 6 min for 1-h periods (Altmann 1974). In 1979 samples were taken for 20 h and in 1980 for 11 or 12 h in the two aviaries (Tables 8 and 9).

Resting includes perching, self-preening, or sleeping. In 1980 the old birds of both sexes

TABLE 9. Percentage of instantaneous time samples in which old and young adult female Village Weavers engaged in various activities.

	1979			1980		
	Old	Young	P	Old	Young	P
No. of females	5	4		4	9	
Rest (perch, preen, sleep)	72	60	0.078	57	27	0.0003[a]
Forage, eat, drink	11	13	NS	20	14	NS
Visit male's territory	4	8	0.076	4	7	NS
Gather nest materials	1	2	NS	2	6	NS
Inside a nest	11	17	0.071	12	38	0.00007[a]
Total reproductive activities	16	27	0.012[a]	17	52	<0.00003[a]
Total samples	200	200		110 120	110 120	

[a] Differences statistically significant. Probabilities are based on relative frequencies and binomial test (Siegel 1956).

rested significantly more than did the young adults (Tables 8 and 9). Sleep is objectively defined here as tucking the beak back among the scapular feathers. Although not within the conventional bounds of statistical significance, the old males tended to sing less, to display their nests less often to visiting females, and to engage in less precopulatory and copulatory activity than did younger adult males (Table 8). Old males more often failed to establish a territory. Males without territories never obtain mates. There was little or no difference between the old and young territorial males in building activity.

In 1980 the old females, compared with the younger adult females, were inside nests less often (Table 9). In both years the young females engaged in significantly more reproductive activity than did the old females.

In May 1982, over a two-week period, the frequencies of various activities by our oldest bird, a 23-year-old male, were compared with those of a 7-year-old adult male in his prime. These males were hand raised in isolation to adulthood, both were very tame, and both could be observed closely without disturbing them. They were maintained indoors in separate individual cages (92 cm long, 42 cm wide, 43 cm high) in different buildings. Both males were in full breeding plumage at the time of the test. All activities each bird performed were recorded during 1-min time samples every 5 min for 1-h periods. All hours of the day from 0700 to 1900 were sampled for a total of 12 h per bird. Each activity was sampled for occurrence or nonoccurrence for a total of 144 1-min time samples per bird.

The very old male rested more often (54% vs. 1% of time samples) and moved about much less than the younger male. He showed very little interest in nest materials (4:38) and did not weave at all, whereas the younger male wove in 38% of the time samples. The old male sang only about half as often as the younger adult male, and ate only about a third as often. The old male showed no difference in drinking or bathing and preened himself about as often as did the young adult male.

Bill and plumage cycles in advanced age.—During the nonbreeding season, the lower mandible of the male Village Weaver turns a pale ivory. Blackening of the bill in the breeding season, singing, territoriality, and nest building are stimulated by male hormone from the testis (Collias et al. 1961). Both old and young males showed the usual seasonal cyclic changes in bill color and plumage color before and after the breeding season, when allowed to breed. A 24-year-old male still developed black bill coloration, indicating that he was still secreting testosterone.

Causes of death in the aviary birds.—The average age of 35 birds that had attained at least one year of age in our aviaries was 11.2 years, but some lived much longer. Nine males (26%) and 8 females (23%) reached 14 years of age or more. Of 17 birds that died in the last five years of the study, 3 died during a severe heat wave and 4 from the cold one winter night when their heat lamp failed. These 7 birds included 3 old (15–19 yr) and 3 young adult (6–7 yr) females and one old (16 yr) male. One young adult male subject to convulsions drowned in the water pan, and another young adult male was killed in a territorial fight. An 8-year-old male died from cancer of the liver, while our oldest bird, a male, died of an impacted intestine. The remaining 6 birds, which were 14–19 years old, died of disease, especially from viral, bacterial, and protozoan infections of the intestine.

None of the birds died of "old age," although advanced age may have increased their susceptibility, because all of the birds that died of infections were old. Combinations of factors probably are often the cause of death in caged birds. Autopsy of one 15-year-old male showed "microscopic extended areas of atrophic muscle fibers in the heart, fibrosis of the endocardium and of liver vessels, and severely congested lungs" (autopsy by H. Niewisch, D.V.M.). This male became so ill that he stopped eating and had to be force fed. Another died of an impacted intestine and enteritis (R. Kray, D.V.M.) when 24 years old. He was the oldest member of his species we know of for whom the dates of hatching and death are both known. His heart (examined by R. J. Gayek, D.V.M.) showed no histopathology, but there was arteriosclerosis of the coronary artery with 90% closure.

DISCUSSION

We draw four main conclusions from our results. (1) Old age in both male and female Village Weavers is eventually accompanied by a decline in general activity and in breeding behavior. (2) Very old males are generally chosen less often as mates than are young adult males. (3) There is great variability between individuals in length of life under supposedly favorable conditions. (4) Some individuals of this tropical species continue to live and breed in captivity to a surprisingly great age for a passerine bird.

(1) Decline in activity and breeding behavior in old age.—Our oldest weaverbirds rested a great deal (Tables 8 and 9), which suggests a low energy level. Botkin and Miller (1974) and Calder (1985) reviewed the question of age-independent adult mortality in birds and concluded on both empirical and theoretical grounds that it is more reasonable to assume, at least in older birds, that mortality is age-dependent. Among nonpasserine birds, Coulsen and Wooler (1976) found a significantly lower annual survival in both sexes of breeding Black-legged Kittiwakes (*Rissa tridactyla*) among older birds (6–17 yr breeding experience) than among younger birds (1–5 yr breeding experience). Among tropical passerine species, Willis (1983) reported significantly lower survivorship in color-banded male Spotted Antbirds (*Hylophylax naevioides*), 7–10 or more years old, in Panama forests. Two very old males sang little and had lost their mates to younger males.

Very old male Village Weavers generally showed a decline in breeding behavior (Tables 2–4) related to a decline in nest building. Old female Village Weavers laid fewer eggs (Tables 6 and 7) and showed less interest in the nests woven by the males (Table 9) than did younger adult females.

Few data are available on the decline of breeding with advanced age among passerine birds in nature, such as we observed with our weavers in aviaries. Great Tits (*Parus major*) have been studied a very long time near Oxford, England. The average age of adults is 1.9 years for females, 2.5 for males. Most die before the age of 5 or 6. The number of young that a female raises to independence increases steadily until the female is about 3 or 4 years old, but thereafter breeding success steadily declines (Perrins 1979). Dhondt (1985) found evidence that Great Tits sometimes forego breeding once they reach 5 years of age. In a 15-year study of color-banded Florida Scrub Jays (*Aphelocoma coerulescens*) Fitzpatrick and Woolfenden (1984) found that success in producing offspring that reach breeding age improves annually over the first four years as a breeder, then levels off, and may decline slightly after eight years as a breeder.

Most research on the physiological basis of aging has been done with mammals, especially humans (Finch and Hayflick 1977, Behnke et al. 1978, Walford 1983). Decline in general activity with old age could be caused by a general reduction in enzyme activity (Gafne 1981). Recent evidence indicates that in old female rats the decline in the ability to release gonadotropins from the anterior pituitary results mainly from decrements in hypothalamic function, but a decrease in pituitary responsiveness to hypothalamic gonadotropin-releasing hormone or of the ovaries to gonadotropin, or both, may contribute to loss of regular estrous cycles (Meites 1982). Rather similar factors may hold in the aging of reproductive capacity and behavior in birds.

The decline in activity and reproductive capacity of very old birds suggests that they will be at a disadvantage in competition under natural conditions, but they may have compensatory assets for competing such as greater experience and wariness, relatively high dominance, and ownership of a familiar territory, all of which would aid reproduction. According to McClure (1974: 294), summarizing returns from more than 100,000 Ploceidae ringed in Asia, only young individuals are readily caught. He states, "Old ringed birds will remain in an area for many years and never be captured again, even though they are seen readily." In a 15-year study of Black-capped Chickadees (*Parus atricapillus*) in Missouri, Elder and Zimmerman (1983) found significantly higher annual survival based on resightings of color-banded individuals compared with recapture data in the same population. The birds became wary of traps as they grew older. There is need for caution in the interpretation of banding returns.

Medawar (1957: 22) defined senescence "as that which predisposes the individual to death from accidental causes of random incidence." He suggested that senescence consists of an innate portion, indicated by the genetic decrease in vitality and in the growth capacity of tissues with aging beginning virtually at birth, and an environmental portion, comprised of the accumulated sum of the effects of recurrent stress or injury or infection. Medawar explained the evolution of senescence by suggesting that genes will be selected for if they confer high fitness at a time of life when the individual concerned has high reproductive value, whereas genes that act later in life will be relatively unimportant (see also Wilson 1975). However, it seems possible that a postreproductive phase of life could evolve by means of family selection if old individuals in some way continue to aid the survival or reproduction of their descendants after the latter reach maturity. There is no extensive evidence as yet of a postreproductive phase of life for most birds in nature. We have given experimental evidence for a definite decline in breeding capacity with old age in captive Village Weavers, and have cited evidence for senescence in nature among two other passerine species, Great Tits and Spotted Antbirds.

(2) Old males less successful in competition for mates.—In the Village Weaver the female generally selects her mate. After reaching 14 years of age, the males built fewer nests and obtained fewer mates in this polygynous species than when they were younger (Table 4). In the monogamous Rock Dove (*Columba livia*), individuals of both sexes over 7 years of age were definitely and significantly discriminated against (Burley and Moran 1979).

(3) Great individual variability in maximum life span.—We have shown that individual Village Weavers under presumably favorable conditions vary greatly in length of life. Great variability among individuals in maximum life span may turn out to be a general principle. Coulsen and Horobin (1976) found that Arctic Terns (*Sterna paradisaea*) ringed on the Farne Islands, Northumberland, usually began breeding at about 4 years of age, with a further life expectancy of 7 years. But one 29-year-old tern successfully reared young. One of the oldest recorded living birds was a Royal Albatross (*Diomedea epomophora sanfordi*) that was still breeding in New Zealand when at least 55 years old (Robertson 1980, John Warham pers. comm.). Fisher (1975), however, found that of 742 Laysan Albatrosses (*Diomedea immutabilis*) banded on Midway Island in the Pacific, only 3% lived to be more than 40 years old.

In 70 years of banding returns over the world for several million birds, mostly from the north Temperate Zone, Rydzewski (1978) listed 86 species of passerine birds in which some individuals lived for at least 10 years. But the vast majority of individuals lived a much shorter time. Occasional individuals in 22% of 141 species of frequently banded species of North American passerine birds lived 10 years or more in the wild (Clapp et al. 1983, Klimkiewicz et al. 1983).

The life span of adult birds in captivity also varies greatly within a species. Flower (1938) mentioned several species of passerine birds in which an exceptional individual lived for 20 years or more in captivity. Of 167 individuals of 27 species of Ploceidae (weaverbirds and allies) living in zoos in 1981 [listed by the International Species Inventory System (ISIS); Seal and Olsen 1978], the median age was between 4 and 5 years. Twelve birds were over 10 years old, however, and 3 were over 15 years old. The oldest, a *Ploceus cucullatus*, was over 20 years old. The oldest *Ploceus cucullatus* in the wild that we know of was from the South African race *P. c. spilonotus* and lived over 14 years (Adrian Craig pers. comm.). Of 437 individuals of 47 estrildid finches (Estrildidae) living in various zoos in 1981, the median age was 3 years (ISIS). Only 2 birds were over 10 years old; the oldest was between 15 and 20 years of age. In nature, the tiny estrildid finches also have relatively short lives (Morel 1973, Woodall 1975). In general, longevity in different species of birds correlates well with body size (Linstedt and Calder 1976, Brown and Pomeroy 1984).

We conclude that there is tremendous variability among individuals of bird species in potential, as well as in actual, life span. The cause and significance of this variation are problems for investigation.

(4) Breeding to a relatively advanced age among tropical passerine birds.—Part of the explanation for the length of the reproductive life of some Village Weavers may be in the tropical habitat. Animal species in which population size is variable and frequently below the carrying capacity of the environment usually have short lives, and individuals of species where population size is fairly constant and at or near carrying capacity usually have relatively long lives (Pianka 1970). Pianka believes the latter pattern is probably more characteristic of tropical species; however, investigation of many more species is needed to validate the hypothesis.

Among 95 American Goldfinches (*Carduelis tristis*) 5 years or older, banded in the U.S. and Canada, there was only one bird as old as 9 years (Middleton and Webb 1984). The five oldest goldfinches recovered in Canada were only 5 or 6 years old. Only one 9-year-old bird appeared among 253 Black-capped Chickadees color-banded in Missouri over a 15-year period (Elder and Zimmerman 1983). In 12 other studies a maximum age of 8–10 years was reported for this species (Elder and Zimmerman 1983). In contrast, in Trinidad Snow and Lill (1974) found that ages of 10 years or more were not uncommon in two species of color-banded manakins (Pipridae). One male White-bearded Manakin (*Manacus manacus*) was still resident on the courtship display grounds at a minimum age of 14 years. A male of this species copulated when at least 11 years old, and a female when 10 years old.

Many tropical and subtropical species of birds have helpers at the nest, and such cooperative or communal breeders are long-lived (Rowley 1983, Brown and Pomeroy 1984). For example, in Arizona a Pinyon Jay (*Gymnorhinus cyanocephala*) was still breeding at 15 years (R. P. Balda pers. comm.) and a Gray-breasted Jay (*Aphelocoma ultramarina*) at 16 years of age (J. L. Brown pers. comm.). In 1983 the oldest passerine bird in the San Diego Zoo was a communal breeder, a 26-year-old Apostlebird (*Struthidea cinerea*) from Australia (Marvin Jones pers. comm.). In the cooperatively breeding Florida Scrub Jay there is evidence, based on lifetime breeding success, that most young birds reaching breeding age are produced by relatively few long-lived breeders (Fitzpatrick and Woolfenden 1984, Woolfenden and Fitzpatrick 1984). This finding indicates a selection pressure for longevity in nature.

Among birds, there is generally strong individual competition for nest sites and mates. Many tropical bird species lay very small clutches and suffer high nest predation (Skutch 1985). High adult survival means that fewer places are available for young birds and that fewer young birds are needed to replace losses in the adult population. Thus, long reproductive life might help explain the small clutch size (2 or 3 eggs) in the Village Weaver, as in many other tropical passerines (Collias et al. 1981). Long reproductive life with repeated small clutches and nesting attempts making up losses to predation may well be a major characteristic of many tropical passerine species. This would distinguish them from most passerine birds of the north Temperate Zone. While it is evident that the evolution of clutch size in birds depends on the interaction of many factors (Cody 1966, Lack 1966, Murray 1985, Skutch 1985), we here emphasize the importance of one factor—life span—that has been relatively neglected.

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