AGE AND BREEDING PERFORMANCE OF EUROPEAN BEE-EATERS

C. M. LESSELLS[1] AND J. R. KREBS[2]

[1]Department of Animal and Plant Sciences, University of Sheffield,
Sheffield S10 2TN, United Kingdom, and
[2]Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom

ABSTRACT.—We studied breeding biology of the European Bee-eater (Merops apiaster) at a colony in southern France from 1983 to 1987. Approximately 50% of the breeding birds were juveniles (hatched the previous calendar year), and ca. 34% of the breeding birds in any year were known to return to the colony in a subsequent year. The proportion of birds banded as chicks and not recorded breeding until 2 years of age suggests that most females attempted to breed at 1 year of age, but that a larger proportion of juvenile males failed to attempt to breed. Pairs that survived tended to breed together in successive years, and the return to the colony in any year of one member of a breeding pair was not independent of the return of the other. Bee-eaters mated assortatively with respect to age. There was a nonsignificant tendency for breeding adults to be more likely than breeding juveniles to have helpers at the nest. At nests without helpers, adult females bred earlier and laid larger clutches than juveniles, brood size at fledging was unrelated to the age of either parent, recruitment rate of offspring of adults of both sexes was about twice that of offspring of juveniles, and provisioning rate was unrelated to parental age. Neither habitat saturation nor low breeding success of juveniles provide complete functional explanations of helping at the nest in European Bee-eaters. Received 16 May 1988, accepted 19 January 1989.

WE attempted to document differences in breeding performance between age classes of European Bee-eaters (Merops apiaster). The question of how breeding success is related to age is of particular interest in this species because ca. 25% of breeding pairs that hatch chicks have one or more helpers at the nest. Helpers feed the chicks, but apparently do not help at an earlier stage. In at least some cases helpers are close relatives of the breeding pair.

There are two main questions that relate to age and breeding biology in species with helpers at the nest. The first is the frequency of occurrence of young birds among the breeding population, and in particular whether any of the young birds attempt to breed at all. The second concern is whether young birds are as successful as older birds when they attempt to breed. These questions are of interest because some explanations of helping behavior posit that young birds either are excluded from breeding because suitable breeding habitat is saturated or mates are not available, or are not as competent as older birds at producing offspring and hence are selected to help relatives rather than attempt to breed (Emlen 1982, Brown 1987). These two phenomena (the exclusion of young birds and incompetence of young birds) are not necessarily mutually exclusive.

In many bird species, young birds breed less successfully than their older conspecifics (Richdale 1949, Lack 1966, see Rohwer in press for a recent review). The components of breeding success most frequently known to be affected are clutch size and timing of breeding. In some cases these differences result in differences in the number of young fledged or recruited into the breeding population (e.g. Perrins and McCleery 1985). Egg size, hatching success, fledging success, frequency of renesting, and interclutch intervals may also be influenced by the age of the female. In many studies, differences in breeding success are sought only between first time and older breeders, but even in species in which breeding success continues to increase with age, the largest differences are often between first and second time breeders (Rohwer in press).

In general, there are three explanations of correlations between breeding performance and age (Lack 1966, Curio 1983, Harvey et al. 1985, Hamann and Cooke 1987, Nol and Smith 1987, Rohwer in press). First, individuals may improve with age or breeding experience. If this were the case, changes in reproductive performance should be detectable in the breeding histories of individuals (Aldrich and Raveling 1983, Harvey et al. 1985, Hamann and Cooke 1987).

Second, individuals may not change within their lifetimes, but selective mortality of birds with certain phenotypes occur. In this case, reproductive performance should differ between the birds of any age class that subsequently do and do not survive to the following year (van Balen et al. 1986). Last, individuals may not change within their lifetimes, but more successful birds defer breeding until a greater age. In order for this last explanation to hold, individuals must vary at the age at which they start breeding.

When breeding success increases with age, selection may favor those birds who choose their mates on the basis of age, which results in assortative mating (Ridley 1983, Perrins and McCleery 1985). However, assortative mating is not unequivocal evidence for such mate choice; it may also arise in populations in which pairing is random, but some pairs remain together in successive breeding seasons, or in which pairing is random at any time, but juveniles and adults seek mates at different times of year.

We investigated the effect of age on the breeding biology of European Bee-eaters. We concentrated on the frequency of young birds among breeders and the occurrence of nonbreeding in this segment of the population, the persistence of the pair-bond and occurrence of assortative mating, and the relationship between breeding performance and age.

METHODS

We studied European Bee-eaters at a colony of ca. 100 pairs in an earth bank at Mas des Sarcelles, ca. 8 km south of Arles in the Camargue region of southern France. Observations were made from May to August in 1983–1987. Fully grown birds were caught in mist nets in the colony or with small nets over nest burrows. These birds were marked individually with metal bands and acrylic paint on their tails. Tail painting allows individual identification in the field, but birds must be caught and repainted each year. Birds were classified on the basis of plumage as juveniles (hatched the previous calendar year) or adults (hatched at least two calendar years before marking). Juveniles have primary coverts which are more worn and browner than feathers in the surrounding feather tracts. This technique was validated on 84 known juveniles and 124 known adults. Birds were sexed in the hand using the extent on the orange patch on the median and greater coverts and secondaries. This technique is not completely reliable, but sexes were confirmed in breeding pairs, and if necessary determined from behavioral observations (courtship feeding and copulation) or winglength (Lessells and Ovenden 1989).

We identified breeding adults at their nests as early as possible, and monitored the outcome of each breeding attempt. Juveniles were more easily mist-netted (pers. obs.), however, and tended to be identified earlier in their breeding attempts than adults, which gave a bias towards juveniles among breeding attempts that failed early. The age distribution of breeding adults was therefore estimated from those birds that hatched at least one chick. Similarly, in order to exclude from the estimate of return rates birds that died during their breeding attempt, we included in the analysis only birds that fledged chicks. Under these limitations, data for estimating the proportion of juveniles among breeders were available only from 1984 to 1987, and data for estimating return rates, from 1984 to 1986.

Breeding success.—Breeding success was analyzed separately with respect to the age of the male and female, and birds were included in the analysis irrespective of whether the age of their mate was known. Helping behavior may increase breeding success (Avery, Lessells, and Krebs unpubl.), so pairs with helpers were excluded from this analysis. Variables were also excluded from the analysis when one member of the pair died sufficiently early in the breeding attempt to influence that variable. On the basis of identified breeding birds, males disappeared from 2.5% of breeding attempts ($n = 279$), and females from 3.6% ($n = 282$). Five variables related to breeding success were analyzed. (1) *Hatching date* was determined in 1984–1987 by observing nests for 1 h daily from late incubation onwards. The hatching date was the date on which food was first observed being delivered to the nest. Infrequently birds took single items of food into the nest, and no further items for at least two days. Inspection of some of these nests with an industrial endoscope showed that no chicks had hatched, and such feeds were excluded from the determination of hatching date. Inspection of nests also revealed that prey items were generally first recorded being taken into the nest on the day on which the chicks hatched, but occasionally up to two days afterwards. No correction was made for this. The date of first egg lay is commonly used as a measure of the timing of breeding in avian studies. We collected comprehensive and systematic data on laying dates only in 1987. In that year, laying date and hatching date were strongly correlated ($r = .974$, $n = 41$, $P < .001$). (2) *Clutch size* was determined in 1985–1987 by endoscopic inspection of nest burrows. In 1985 we inspected nests at various stages during incubation, and in 1986 and 1987 generally at clutch completion. Clutches were augmented by intraspecific nest parasitism (pers. obs., Emlen and Wrege 1986), but no attempt was made to correct for this. (3) *Brood size at fledging*: Some nests were excavated by enlarging the nest tun-

nel on day 23 (where the hatching date = day 1) in order to band the chicks. Fledging begins a few days later, and usually extends over several days. Brood size at fledging is the brood size on day 23. Chicks cannot be reliably counted at this age with the endoscope, so brood size at fledging is known only for the restricted sample of nests in which chicks were banded in 1984–1987. (4) *Recruitment rate of offspring:* Between 15 and 20% of chicks banded at fledging return to the colony in subsequent years. More males than females return (Lessells and Ovenden 1989) and the return of chicks from a brood tended to be non-independent (i.e. there tended to be an excess of broods where zero or at least two chicks returned, and a deficit of broods where a single chick returned). Because of this, we analyzed the proportion of chicks returning from a brood. Broods were included in the analysis only if they were banded on day 23, so the analysis includes broods from only 1984–1986. (5) *Provisioning rate* is not directly a component of breeding success, but may influence it, especially in view of the tendency for the lightest chicks in broods to die of starvation (Lessells and Avery 1989). We observed nests daily for 1 h from day 1 to day 23, and recorded all prey items taken to the nest by the male or female. Provisioning rate is the total number of prey items brought by the male or the female during these 23 h of observation.

Data from this study are held in a data-base on the University of Sheffield's IBM 3083 computer. Data manipulation and most statistical analyses were carried out using SAS (SAS Institute Inc. 1985), and 2- and 3-way analyses of variance using SPSS-X (SPSS Inc. 1986).

RESULTS

The age of breeding birds.—Approximately 50% of the breeding birds (including those with and without helpers) that hatched chicks each year were juveniles, and there was no difference in the proportion of juveniles among breeding males (51%, $n = 174$) and females (54%, $n = 180$; $\chi^2 = 0.14$, df = 1, $P > 0.70$). The proportion of juveniles that bred did not vary greatly from year to year (range 43–65% for 4 yr in males and females separately; for difference between years—males: $\chi^2 = 2.8$, df = 3, $P > 0.30$; females: $\chi^2 = 7.4$, df = 3, $P > 0.05$).

The return rate of breeding birds (with or without helpers) was somewhat lower than expected on the basis of the proportion of adults among breeders. Of birds that fledged chicks, we recorded 33% ($n = 104$) of males and 35% ($n = 111$) of females in the colony in a subsequent year. There was no difference in the return rates

of males and females, or of juveniles and adults (3-dimensional G test [Sokal and Rohlf 1981]— sex: $G = 0.14$, df = 1, $P > 0.70$; age: $G = 0.92$, df = 1, $P > 0.30$).

Nonbreeding by juveniles.—Given the high proportion of juveniles among breeders, it seems likely that most juveniles attempt to breed. Because we did not identify all breeding birds in the colony each year, we cannot be certain that any particular bird did not attempt to breed. However, the relative proportions of juveniles and adults known to be alive (but not recorded to breed) can be used to estimate the relative frequency with which juveniles and adults failed to attempt to breed. Among the birds banded as nestlings in the colony, and subsequently recorded to breed at two years of age or older (with or without helpers), 55% ($n = 11$) of males and 40% ($n = 5$) of females were not recorded to breed as juveniles. These percentages represent the maximum frequency of nonbreeding by juveniles. The actual proportion will be lower because we failed to identify some birds who attempted to breed. In comparison, among breeding birds whose first and last recorded breeding attempts were at least 2 yr apart, no breeding attempt was recorded in 23% ($n = 16$) of the males in intervening years, and 50% ($n = 18$) of the females in intervening years. If we assume that all adults attempt to breed, we can estimate the number of breeding attempts overlooked for each recorded breeding attempt (3/13 for males and 9/9 for females). Additionally, if we assume that breeding attempts by juveniles and adults are equally likely to be overlooked, and that the pattern of breeding dispersal (*sensu* Greenwood 1980) within and between colonies is the same for juveniles and adults, these ratios apply also to juveniles, and we can estimate the number of juveniles who attempted to breed, but were not recorded by us ($5 \times 3/13$ males and $3 \times 9/9$ females). Hence we estimate the true proportion of nonbreeding juveniles to be 44% of males [(6 − [5 × 3/13])/11; i.e. the number of juvenile males who appear not to have bred, minus the number we estimate to have bred and been missed by us, all divided by the total number known to be alive] and −20% of females. The estimate is negative for females because the proportion of juvenile females recorded to breed was higher than the proportion of adult females recorded to breed. These estimates suggest that males are

TABLE 1. Assortative mating with respect to age in European Bee-eaters. If pairs were recorded to breed in more than one year, data are included only for the first recorded breeding attempt ($\chi^2 = 68.6$, df = 1, $P < 0.001$).

	Juvenile male	Adult male
Juvenile female	111	21
Adult female	19	56

less likely to breed as juveniles than females, but because the proportion of birds known to be alive that breed does not differ between adults and juveniles either for males (Fisher exact test, $P = .064$) or females ($P = .54$), these results should be treated with caution.

Pair fidelity.—Pairs (with or without helpers) of which both members survived to the next breeding season generally remained together. Only 12% ($n = 26$ pair-years, involving 23 pairs) of surviving pairs acquired new mates. Of the 3 pairs that separated, both members of 2 pairs bred with new mates; in the remaining pair, the male bred with a new mate and the female was not recorded breeding. This method of estimation will tend to underestimate the frequency of separation because pairs that remained together were more likely to both be recorded as alive. However, we believe that separation is a relatively rare event.

The known return of one member of a breeding pair was not independent of the known return of the other member of the pair. Of 98 pairs fledging chicks (with or without helpers), both birds were recorded in subsequent years from 19% of pairs, the male only from 14% of pairs, the female only from 19% of pairs, and neither from the remaining 47% of pairs (3-dimensional G test, controlling for year [Sokal & Rohlf 1981]—male return × female return independence: $G = 7.34$, df = 1, $P < .01$). Part of this nonindependence may be due to our failure to identify all breeding pairs in combination with pair fidelity by the birds.

Assortative mating.—Over 80% of breeding pairs consists of two juveniles or two adults (Table 1). We have insufficient data to test for assortative mating in known newly formed pairs (cf. Lessells 1982), and the nonindependence of return of pair members confounds a null model of the type used by Perrins and McCleery (1985). It was therefore not possible to determine the

extent to which the observed assortative mating arose from active mate choice rather than passively through pair fidelity.

Presence of helpers.—Adults tended to be more likely than juveniles to have helpers at the nest, but this difference was not significant (Males: 24% ($n = 85$) of adults and 18% ($n = 89$) of juveniles; $\chi^2 = 0.5$, df = 1, $P > 0.30$. Females: 26% ($n = 83$) of adults and 14% ($n = 97$) of juveniles; $\chi^2 = 3.35$, df = 1, $0.05 < P < 0.10$).

Breeding success.—We included five components of breeding success with respect to male and female age. Because of the strong assortative mating for age, it was often not possible to determine whether it was male or female age, or both, that were causally related to breeding success.

(1) Hatching date was related to the age of the female, but not the male (Table 2). The clutches of adult females started hatching about 2.5 days earlier than those of juveniles. We recorded hatching dates for 20 females in two or more years. We controlled for annual variation in laying date by expressing values as deviations from the median laying date, and individual females laid an average of 1.29 days earlier (± 1.69 [SE], $n = 14$) as adults than as juveniles, and adults bred 1.00 day earlier (± 3.96, $n = 7$) at successive known breeding attempts. Although neither of these values differ significantly from zero, they are commensurate in magnitude and direction with the difference in the mean of all juveniles and adults. There was no difference between the hatching dates of females that did or did not return to the colony in subsequent years (3-way ANOVA [age, year, return]—return: $F_{1,87} = 0.05$, $P > 0.80$).

(2) Clutch size was also related to the age of the female, but not of the male (Table 2). Adult females laid clutches that were about half an egg larger than those of juveniles. There were insufficient data to examine this difference for individual females. There was no difference between the clutch sizes of females that did or did not return to the colony in subsequent years (3-way ANOVA [age, year, return]—return: $F_{1,56} = 0.2$, $P > 0.60$).

In common with many other bird species, clutch size decreased seasonally (Fig. 1) in juveniles (clutch size = $9.67 - 0.0629$ [hatching date], $F_{1,50} = 6.56$, $P = 0.013$) and adults (clutch size = $8.97 - 0.0470$ [hatching date], $F_{1,43} = 3.92$, $P = 0.054$). Clutch size controlled for hatch date

TABLE 2.   Breeding performance of juvenile and adult European Bee-eaters. Sample sizes are in parentheses.

	Juveniles ($\bar{x} \pm$ SD)	Adults ($\bar{x} \pm$ SD)	P[a]	
			Age	Yr
Hatching date[b]				
Males	61.8 ± 6.30 (70)	60.1 ± 6.22 (63)	NS	***
Females	62.2 ± 6.35 (79)	59.7 ± 6.48 (61)	*	***
Clutch size				
Males	5.80 ± 1.08 (55)	6.02 ± 0.96 (52)	NS	NS
Females	5.73 ± 1.02 (60)	6.18 ± 1.01 (49)	*	NS
Brood size at fledging				
Males	4.67 ± 1.30 (43)	4.57 ± 1.63 (40)	NS	NS
Females	4.42 ± 1.39 (50)	4.81 ± 1.58 (36)	NS	NS
Recruitment rate of offspring[c]				
Males	10.1% (21)	19.6% (27)	*	NS
Females	11.0% (28)	21.2% (22)	*	NS
Provisioning rate				
Males	156.5 ± 69.2 (49)	153.5 ± 68.5 (47)	NS	**
Females	128.0 ± 55.0 (52)	131.0 ± 66.9 (42)	NS	*

[a] Two-way ANOVA, no significant interactions. NS = $P > 0.05$. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[b] Hatching date = days after 30 April (i.e. 1 = 1 May).

[c] Recruitment rate was not normally distributed; we confirmed the results of the 2-way ANOVA by a Mann-Whitney U test: males, P (2-tailed) = 0.038; females, P = 0.015.

does not differ between adults and juveniles (combined data: clutch size = 9.53 − 0.0588 [hatching date], $F_{1, 95}$ = 12.23, $P < 0.001$. Age of females: $F_{1, 94}$ = 1.64, $P = 0.20$). Thus, juvenile females laid smaller clutches later in the year than adults, but at any laying date, juveniles laid the same size clutches as adults (Fig. 1). In regression equations, hatching date is expressed as days after 30 April (i.e. 1 = 1 May).

(3) Brood size at fledging was unrelated to the age of either the male or female (Table 2). This was unexpected when we considered the difference in clutch size between juveniles and adults. Although the difference in brood size at fledging was not significant, adult females fledged about 0.4 more chicks than juveniles, and this difference might prove significant in a larger sample.

(4) The recruitment rate of chicks was related to the ages of both the male and female (Table 2). The fledged chicks of adults were about twice as likely as those of juveniles to return to their natal colony in a subsequent year. There was no difference in brood size at fledging between juveniles and adults (see above), nor was there a relationship between recruitment rate and hatching date ($F_{1, 65}$ = 0.4, $P > 0.50$), so the difference in recruitment rate between juveniles

and adults cannot be attributed to differences in brood size or hatching date. There were insufficient data to examine the relationship between recruitment rate and age for individual males or females. Parents who returned to the colony had offspring with a higher recruitment rate (Table 3).

(5) Provisioning rate of the chicks was not related to the ages of either the male or female (Table 2).

DISCUSSION

In common with many other bird species, juvenile European Bee-eaters are less successful breeders than adults. Juvenile females lay smaller clutches later in the year, and offspring of juvenile males and females are less likely to return to the colony. In view of the high proportion of females that start to breed at 1 year of age, it is unlikely that any of the relationships are due to deferred breeding of individuals with superior breeding performance. Neither clutch size nor hatching date differ between females who do or do not return to the colony in subsequent years, so the relationship of these variables to female age cannot be due to selective mortality. In addition, although the difference
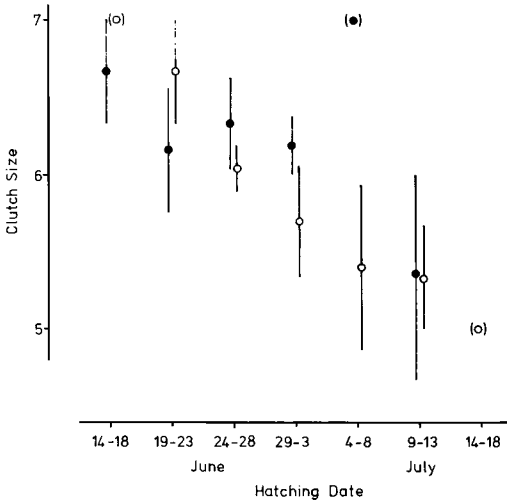
Fig. 1.   Seasonal decline in clutch size in juvenile (O) and adult (●) female European Bee-eaters. Vertical bars are standard errors. Single values for sample are in parentheses.

TABLE 3.   Recruitment rate of European Bee-eater chicks in relation to the return of their parents to the colony in subsequent years. Sample sizes are in parentheses.

	Recruitment rate ($\bar{x}$)			
	No return	Return	P^a	P^b
Males				
Juvenile	5.9% (16)	23.7% (5)	0.038	<0.05
Adult	15.6% (19)	29.0% (8)	0.064	
Females				
Juvenile	6.6% (17)	17.9% (11)	0.093	<0.05
Adult	16.3% (16)	34.2% (6)	0.027	

^{a} One-tailed Mann-Whitney U test.
^{b} Two-tailed combined probability for juveniles and adults (Fisher's method; Sokal and Rohlf 1981).

was not significant, individual females tend to breed earlier as they become older. Thus for clutch size and hatching date the observed relationships with age appear to be due to changes within individuals. Such age-related differences may be due to age per se or to breeding experience. Some authors have attempted to separate these effects, but such interpretations must be treated with caution because of potential differences in quality between birds first breeding at different ages (Harvey et al. 1985, Rohwer in press). We have not attempted to separate the effects of female age and breeding experience on clutch size and hatching date.

Clutch size declines seasonally, and the smaller clutches of juvenile females were explained by this decrease in combination with the later breeding of juvenile females. This contrasts with Lesser Snow Geese (Anser c. caerulescens; Finney and Cooke 1978) in which young females lay smaller clutches even after controlling for laying date. Despite the differences in clutch size, adult females do not fledge significantly more young, although larger sample sizes might reveal this effect.

The most striking relationship between age and breeding success is with the recruitment rate of offspring. Others have shown that adults recruit more offspring (e.g. Perrins and Mc-

Cleery 1985), but they generally fledge more young. We found that there is a difference between juveniles and adults in the proportion of offspring that return to the colony. We believe that European Bee-eaters are the first example of a possible difference in postfledging survival between the young of juvenile and adult parents. Bee-eaters continue to feed their young after fledging and, because the capture of fast-flying insects is a skill which may require time to acquire, bee-eater chicks presumably continue to be dependent on their parents for some time after fledging. The welfare of the offspring at this stage may depend on both the rate at which parents can provision their young, and on the ability of the parents to "shepherd" the brood, particularly during the several days when the brood is partially fledged and the fledged chicks may be being fed at some distance from the colony. Alternatively, the observed differences in recruitment may be due to a difference in dispersal rather than survival, although it is difficult to provide a functional explanation for such a difference.

The lower breeding success of young birds may occur because they make the same reproductive effort, but are less competent (the constraint hypothesis) or because they make a lower reproductive effort because of quantitative differences from adults in a compromise between current and future reproductive value (the restraint hypothesis) (Pugesek 1981, Curio 1983). These hypotheses are difficult to distinguish (Curio 1983, Rohwer in press). However, the equal provisioning rates of juveniles and

adults do not suggest restraint on the part of juveniles.

About 50% of the breeding birds are juveniles, which implies that few juveniles fail to attempt to breed. This is confirmed for females by a calculation based on the frequency with which birds that were known to be alive were not observed to breed. If our population is at demographic equilibrium, the high proportion of juvenile breeders implies an annual mortality rate of breeding birds that would be more typical of a small temperate passerine than of a species with helpers at the nest (Lack 1954, Brown 1987). The 34% return rate of breeding adults is lower than expected on the basis of the age distribution of breeding birds in combination with the observed lack of a systematic decline in colony size or increase in the proportion of juveniles among breeding birds. The observed return rate is deflated to some extent by our failure to record the identities of all breeding birds in any year. An alternative explanation is breeding dispersal between colonies. Such dispersal would be adaptive in the face of variation in colony suitability due to food availability or predation, but is unexpected in a species where helping behavior appears to be dependent on the presence of close relatives, as a result of philopatry (Avery, Lessells, and Krebs unpubl.).

Juvenile females do not appear to be excluded from breeding by habitat saturation or the lack of a suitable mate. The evidence is more equivocal for juvenile males. Based on the proportion of birds that are known to be alive which are not recorded breeding, we calculated that almost 50% of juvenile males may fail to attempt to breed. However, although this estimate is high, the apparent frequency of nonbreeding does not differ significantly between juvenile and adult males. Moreover, the high proportion of juveniles among breeding males suggests that few juvenile males fail to attempt to breed. Juveniles also have a demonstrably lower breeding success than adults. However, both hypotheses for helping behavior that depend on age-related differences in breeding performance imply that juveniles should help rather than attempt to breed. In European Bee-eaters most juveniles do attempt to breed and many helpers appear to be failed breeders rather than birds adopting a helping strategy from the start of the breeding season. Thus, neither of the age-related hypotheses for helping behavior provides a complete explanation for this behavior in European Bee-eaters.

LITERATURE CITED

ALDRICH, T. W., & D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. Auk 100: 670–679.

BALEN, J. H. VAN, A. J. VAN NOORDWIJK, & J. VISSER. 1986. Lifetime reproductive success and recruitment in two Great Tit populations. Ardea 74: 1–11.

BROWN, J. L. 1987. Helping and communal breeding in birds: ecology and evolution. New Jersey, Princeton Univ Press.

CURIO, E. 1983. Why do young birds reproduce less well? Ibis 125: 400–404.

EMLEN, S. T. 1982. The evolution of helping: I. An ecological constraints model. Am. Nat. 119: 29–39.

———, & P. H. WREGE. 1986. Forced copulations and intra-specific nest parasitism: two costs of social living in the White-fronted Bee-eater. Ethology 71: 2–29.

FINNEY, G. H., & F. COOKE. 1978. Reproductive habits in the Lesser Snow Goose: the influence of female age. Condor 80: 147–158.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162.

HAMANN, J., & F. COOKE. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese *Anser caerulescens*. Ibis 129: 527–532.

HARVEY, P. H., M. J. STENNING, & B. CAMPBELL. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (*Ficedula hypoleuca*). J. Anim. Ecol. 54: 391–398.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

————. 1966. Population studies of birds. Oxford, Clarendon Press.

LESSELLS, C. M. 1982. Some causes and consequences of family size in the Canada Goose *Branta canadensis*. Ph.D. dissertation, England, Univ. Oxford.

————, & M. I. AVERY. 1989. Hatching asynchrony in European Bee-eaters *Merops apiaster*. J. Anim. Ecol. In press.

————, & G. N. OVENDEN. 1989. Heritability of winglength and weight in European Bee-eaters *Merops apiaster*. Condor 91: 210–214.

NOL, E., & J. N. M. SMITH. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. J. Anim. Ecol. 56: 301–313.

PERRINS, C. M., AND R. H. McCLEERY. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major*. Ibis 127: 306–315.

PUGESEK, B. H. 1981. Increased reproductive effort with age in the California Gull (*Larus californicus*). Science 212: 822–823.

RICHDALE, L. E. 1949. The effect of age on laying, size of eggs and size of clutch in the Yellow-eyed Penguin. Wilson Bull. 61: 91–98.

RIDLEY, M. 1983. The explanation of organic diversity. Oxford, Clarendon Press.

ROHWER, F. C. In press. The evolution of reproductive patterns in waterfowl. *In* The ecology and management of breeding waterfowl (B. D. J. Batt et al., Eds.). Minneapolis, Univ. Minnesota Press.

SAS INSTITUTE, INC. 1985. SAS user's guide: basics, version 5. North Carolina, Cary.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry. San Francisco, W. H. Freeman and Co.

SPSS, INC. 1986. SPSS user's guide, 2nd edition. Chicago.