

EXTRA ADULTS AT THE NEST IN BARN SWALLOWS¹

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Extra adults at the nest have been noted in a wide variety of bird species (for reviews, see Skutch 1961, Lack 1968, Ricklefs 1974, Brown 1978, Emlen 1978). We use the neutral term "extra adult" to refer to non-breeding adults that interact frequently and nonhostilely with the primary breeding pair at or near the nest, regardless of whether they care for the young or later breed. In Barn Swallows, extra adults at the nest have been reported in two populations (Myers and Waller 1977; Crook 1984; Crook and Shields, in press). The purpose of this note is to report our findings on extra adults at the nest in a third population, and to point out notable differences, in plumage and behavior, among the three populations.

METHODS

In 1979 and 1980, we studied 13 solitary nests on the grounds of the Woodland Park Zoo and in the surrounding neighborhood, in Seattle, Washington. In 1979, we monitored eight second or late clutches at the nest, and for several weeks after fledging. In the latter context, we identified family groups by color marking young; family groups typically stayed together for one to two weeks (Medvin and Beecher 1986). In 1980, we watched five nests during both first and second clutches. Observation periods averaged 30 min, for a total of approximately 175 hr. We sexed breeding adults by tail length (Samuel 1970), and song. Extra adults at each nest were identified by plumage markers (see section below); such identifications were independently confirmed by at least two observers. In addition, we marked the breeding pair at 4 of the 13 nests (Table 1).

RESULTS

PLUMAGE DIFFERENCES

While the typical plumage of the adult Barn Swallow includes a reddish-brown breast, and deeply forked, long tail feathers, the extra adults all had either white or light colored breasts and/or short tail feathers, and resembled juveniles of the first clutch. The plumage of the extra adults was so distinctive that we could easily distinguish them from both primary adults and juveniles. There may have been extra adults who lacked these unique plumage markers. In virtually all cases

where we saw three birds together at a nest, however, one of them had the distinctive plumage of an extra adult. Moreover, in only one instance did we ever see more than three adults at a nest.

The retention of juvenal plumage, as seen in our extra nest attendants, has not been reported in other studies of Barn Swallow extra adults (Myers and Waller 1977, Crook and Shields 1985, in press). Retention of juvenal plumage features has been found in Tree Swallows (*Tachycineta bicolor*; Kuerzi 1941, Sheppard 1977) and Mexican Jays (*Aphelocoma ultramarina*; Brown 1963, see also Brown 1978).

FREQUENCY OF EXTRA ADULTS

Extra adults were seen at 12 of the 13 nests (Table 1). Extra adults were seen at the nest as early as the initial courtship of the primary pair. At two of the nests, the extra adult ultimately nested with the male (see below). At the remaining 10 nests, we compared the number of days an extra adult was seen with the family group, relative to the number of days the male and female were seen. On average, an extra bird was present during 24% of the observation periods, compared to 84% and 90% for the male and female respectively. We cannot be sure that we always saw the same extra adult at a particular nest rather than one of several different birds. We favor the first alternative, however, for two reasons. First, some of the extra adults had distinctive markings, and identification was unequivocal. Second, in general, a breeding pair interacted with the light-colored extra adult in a tolerant fashion, suggesting familiarity, which contrasted sharply with their aggressive reaction to the occasional dark-colored intruder.

The high proportion of nests with extra adults in our study is similar to that seen in the New York population studies by Crook and Shields (in press), where 78% of the nests were attended. The proportion differs from that seen in the Ohio population studied by Myers and Waller (1977) in which attendants were reported at less than half of the nests.

HELPING BEHAVIOR OF EXTRA ADULTS

The extra adults infrequently fed at nests. In 40 observation hr during the nestling period, we saw only 12 feedings by extra birds (distributed over three nests); parents typically feed that much in an hour. In the postfledging family groups, we observed an extra adult feeding fledglings in two groups. The feeding rate we observed is much lower than the 15% of the total feeding visits at nests with extra adults observed by Myers and Waller (1977), but it is much higher than the two feedings observed by Crook and Shields (in press) in

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TABLE 1. Extra adult sightings.

Nest	When seen? ^a				Number of days			
	CB	I	N	PF	Nest observed	Male seen	Female seen	Extras seen
Aur/79	—	y	y	y	33	31	32	12
Cam/79	—	—	—	y	3	2	3	2
Comm/79	—	y	y	y	44	41	41	16
Day/79 ^b	y	—	—	—	15	11	9	2
Duck/79	y	y	y	y	29	25	29	8
Pony/79	—	—	y	y	12	11	12	2
Zeb N/79 ^c	—	—	y	y	15	15	15	11
Zeb F/79	n	n	n	n	6	6	6	0
Zeb/80	y	n	n	—	23	16	19	2
Comm/80 ^{c,e}	y	y	—	—	16	14	14	2
Duck/80 ^c	y	y	y	—	67	52	55	10
Ele/80	y	y	y	—	64	52	59	11
Pony/80 ^{d,e}	y	y	—	—	21	11	13	8

^a When an extra adult was seen. CB = courtship/nest building, I = incubation, N = nestling, PF = postfledging, y = yes, n = no, — = no observations during this phase.

^b Observations during second clutch; courtship seen, but no eggs laid.

^c Female marked.

^d Male and primary female marked.

^e Pony/80 was a case of polygyny; Comm/80 a replacement female. The number of times the extra female was seen is tabulated only to the point where she nested.

2,000 to 5,000 observation hr. Crook and Shields (in press) also describe eight instances of infanticide by extra adults, whereas neither we nor Myers and Waller (1977) observed any such instances.

EXTRA ADULTS SOMETIMES NEST

At 2 of the 12 nests with extra adults, the extra adults mated with the primary male. At one of these nests, the primary female died, and the third adult became a replacement female. At the other, the male and third adult mated shortly after the primary female's nest failed. Subsequently, the primary female renested with the same male, thus forming a polygynous trio. We describe these two cases in some detail here.

The extra adult (second female) at nest Comm/80 became a replacement nester. This bird was easily identified because of a light-colored band on her breast. The bird was first seen at this nest on 6 May 1980, during the nest building stage. The primary female of this nest completed a clutch of four eggs on 18 May. We found her dead of unknown causes two weeks later, with only two eggs remaining in the nest. The next evening, the male was found sleeping by the nest with the third bird; the following day the nest had fresh mud and new feathers. Within another week, the former third bird laid her first egg, and she completed a clutch of four eggs on 12 June. The pair stopped incubating on 19 June for unknown reasons, and subsequently began a replacement clutch of six eggs, which was completed on 4 July. Four of the six eggs hatched on 19 July, and the young fledged by 9 August.

The extra adult (second female) at Pony/80 eventually nested polygynously. All three birds were first seen on 3 May 1980. From the start, the three birds interacted frequently (e.g., vocalized antiphonally, foraged together). On 14 May, the primary female completed a clutch of five eggs, and for the next two weeks she incubated. The third adult occasionally incubated

as well. At the end of the normal incubation period of 15 days, however the eggs had failed to hatch. On 3 June, the third adult and the male were building a new nest, approximately 10 m from the old one. The male assisted the third bird with nest building on that day only; she completed the nest by herself. On 8 June, the male and primary female copulated and engaged in renesting activities. The primary female completed a clutch of six eggs on 16 June, and the third adult, now the secondary mate of the male, completed a clutch of five eggs on 18 June. The primary female's eggs hatched on 1 July; the secondary female's eggs on 3 July. During the nestling stage, each female fed only at her own nest. The male fed once at the secondary female's nest, but otherwise fed only at the primary female's nest, and spent most of his time with her. The primary female's young fledged on 23 July; the secondary female's on 29 July. We did not see the secondary female again. The primary female completed a second clutch that hatched on 13 August; these birds fledged 11 September.

DISCUSSION

A REPRODUCTIVE STRATEGY?

In Tree Swallows, yearling females retain juvenile-like plumage (brown versus blue-green) (Kuerzi 1941, Sheppard 1977, De Steven 1978). Since our extra adults also retained juvenile-like plumage, perhaps they were yearlings. In support of this idea, the lighter plumage and shorter tail feathers seen in the extra adults may indicate an incomplete postjuvenile molt (Rohwer, pers. comm.; Palmer 1972). In addition, Crook and Shields (in press) reported that a high proportion of their extra adults were yearlings.

In several earlier anecdotal reports of nest attendants in Barn Swallows it was assumed that the extra birds were juveniles of the first clutch (Astley 1934, White

1941, Williamson 1941). Myers and Waller (1977) verified that juveniles of the first clutch may sometimes feed nestlings of the second clutch. Our study suggests, however, that some of the extra nest attendants seen in these earlier studies may have been yearling adults, who owing to the retention of juvenile-like plumage were mistaken for juveniles.

If our extra adults were indeed yearlings, we can consider the hypothesis that they were following an age-related conditional reproductive strategy (Brown 1983, Ligon 1983). Yearlings are at a competitive disadvantage to older birds on the breeding ground in three respects. First, they have no reproductive experience. Second, they are unfamiliar with the area; Barn Swallow yearlings disperse from their natal area, whereas adults typically return to the area where they previously bred (Mason 1953, Samuel 1971, Barrentine 1978, Shields 1984). Third, yearlings generally appear in the breeding area after experienced adults have already returned (Barrentine 1978; Shields, pers. comm.; Medvin and Beecher, unpubl. data). Yearlings arriving on the breeding grounds therefore might respond to reproductively unfavorable circumstances (e.g., habitat saturation, a biased sex ratio) by associating with a breeding pair and using the experience they gain (e.g., knowledge of those individuals and of the area) to improve their breeding success the following year. In addition, if conditions were to become favorable, they might breed later that same breeding season. In line with this hypothesis, we note that along with our observations of two attendant females subsequently mating with the primary male, Crook and Shields (in press) observed six attendant males mating with the primary female within the same breeding season, and three males doing so during the following breeding season. Moreover, 90% of the returning extra adults nested in areas where they had attended the previous season. Crook and Shields (1985), however, focus on a different hypothesis concerning the reproductive behavior of their extra adults. Arguing from the occurrence of infanticide in their population, they suggest that the extra males were actively interfering with the breeding efforts of the primary pair to increase the probability of mate acquisition.

In conclusion, our study and those of Crook and Shields (1985; in press) and Myers and Waller (1977) suggest that conditional reproductive strategies may be more characteristic of Barn Swallows than thought previously. At present, we cannot account for the notable differences among these three studies concerning the characteristics and behavior of the extra Barn Swallows, except to suggest that they may be genuine population differences; e.g., perhaps the sex ratio in our population was female-biased while that of Crook and Shields was male-biased. We hope that future studies will enable us to identify the ecological and life history factors that give rise to these differences.

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DELAYED BREEDING IN YEARLING MALE GROUSE: AN EVALUATION OF TWO HYPOTHESES¹

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Key words: Blue Grouse; *Dendragapus obscurus*; delayed breeding; territory quality; female choice; polygyny; survival.

In most monogamous species of birds males and females commence breeding at approximately the same ages, whereas in species with polygynous mating patterns males often initiate breeding at older ages than females (Selander 1965, Orians 1969, Wiley 1974). Although yearling males in these latter species may be physiologically able to breed (e.g., Orians 1961, Eng 1963, Hannon et al. 1979), they usually are presumed to be nonbreeders if they do not defend breeding territories. In contrast, yearling females of the same species often lay eggs and are capable of raising young.

In papers on the evolution of mating patterns in grouse, Wiley (1974) and Wittenberger (1978) proposed explanations for a postponement of breeding by males relative to females in polygynous species. Both authors believed that females may breed preferentially with older males, and hence that female choice of mates could be a factor selecting for delayed breeding by males. Further, Wiley suggested that the cost of breeding for young males of polygynous species may be greater than that for older males, this possibly owing to their relative inexperience in defending territories, advertising to females, and performing courtship displays, which could increase their susceptibility to mortality. This would be particularly true if young males were relegated to taking low quality territories (Wiley 1981). According to Wiley then, both female choice and a greater cost of breeding for younger males relative to older males likely contributed to the evolution of delayed breeding.

Wittenberger (1978), however, argued that within

species the cost of breeding for young males should be similar to that of older males. He therefore concluded that a difference in cost of breeding for young and old males was unimportant as a factor favoring delayed breeding. The two hypotheses proposed by Wiley and Wittenberger are not mutually exclusive in that both consider female choice to be a factor in the evolution of delayed breeding. However, they differ in that Wittenberger considered female choice by itself sufficient to explain delayed breeding by males, whereas Wiley believed a cost factor also was important in the evolution of this behavior pattern.

We studied the demography and behavior of Blue Grouse (*Dendragapus obscurus*) in two areas of coastal British Columbia from 1977 to 1983. This species has a mating system in which there are no pair bonds between males and females, and thus males breed promiscuously. Our objective is to use information from this intensive study of a single species to evaluate Wiley's and Wittenberger's hypotheses for the evolution of delayed breeding in male grouse. In doing so we recognize that it is problematic to test hypotheses on the origin of a behavior pattern. Nevertheless, we can examine how delayed breeding might currently be maintained by selection pressure. We ask the question: is female choice by itself an adequate explanation for the postponement of breeding by yearling male Blue Grouse?

RESULTS

GENERAL BEHAVIOR OF MALE BLUE GROUSE

Adult male Blue Grouse occupy territories that serve primarily as areas for advertising and displaying to females (Bendell and Elliott 1967, McNicholl 1978). Territories generally range between 1 and 4 ha in size and usually include elevated portions of land such as hills, knolls, or ridges (Bendell and Elliott 1967, McNicholl 1978, Lewis 1985). Males generally hoot (sing) from these elevated regions, which probably fa-

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