

venile was never found more than 170 m from the nest. Over 90% of the observations were within 100 m of the nest. On 27 July, 225 days after fledging, we observed a food transfer from an adult hawk-eagle to the juvenile within 100 m of the nest. Before the transfer the adult and juvenile called repeatedly 160 m apart for 36 min. The juvenile then left its perch and flew to the adult, grabbed the prey item from its talons without landing and continued to a nearby perch. It continued to exchange calls with the adult for 2 min. These observations indicate that the juvenile hawk-eagle was partially dependent on parental feeding 312 days after hatching when the study was concluded. This supports Brown's (1977) generalization that tropical raptors have a long parental dependency period compared to similar sized temperate raptors.

If we assume that Ornate Hawk-Eagles have an incubation period of at least 40 days, they will require well over a year for courtship, nesting, and raising one young to independence. At most, this species may produce one nestling every other year. Such low productivity may make the species sensitive to habitat destruction or hunting pressure.

We appreciated the help of Susan Renner and Antonio Cabral in identifying the nest tree. Antonio Cabral also helped with the construction of the observation platform. Fernando C. Novaes, Jose Maria Cardosa da Silva, and Maria de Fatima Lima identified the prey remains from the nest using reference material at the Museu Goeldi in Belem, Brazil. Rocelino Marajo dos Reis and Luis Raimundo helped with many of the ordeals of living in a remote field site. Scott Robinson

provided unpublished data on prey species. The manuscript benefited from conversations with Jay Malcolm and John Eisenberg. This study was supported by the World Wildlife Fund-US, the Instituto Nacional de Pesquisa da Amazonia (INPA), and the Instituto Brasileiro de Desenvolvimento Florestal (IBDF), and represents publication number 32 in the Minimum Critical Size of Ecosystems Project (Dinamica Biologica de Fragmentos Florestais) technical series.

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*The Condor* 90:241-245  
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## A CASE OF COMMUNAL NESTING IN THE EUROPEAN STARLING<sup>1</sup>

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*Key words:* Communal nesting; hole-nesting species; European Starling; *Sturnus vulgaris*; parentage; polygyny; electrophoresis; nest-site competition.

The most common type of avian communal breeding system involves helpers at the nest, in which one or more nonreproductive conspecifics help to raise the

brood of a single breeding pair (e.g., Skutch 1961, Brown 1978, Emlen 1978). A less common system involves two or more females and one or more males contributing gametes to a single brood that they raise cooperatively (Koenig and Pitelka 1981). The latter phenomenon is well known in Groove-billed Anis (*Crotophaga sulcirostris*; Vehrencamp 1978) and Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig and Pitelka 1979). In other species, in which nonreproductive helpers are common, a minority of nests contain the clutches of more than one female (Zahavi 1974, Rowley 1978, Lawton and Lawton 1985). Few other cases of communal laying and subsequent cooperation in parental care have been reported (Bellrose 1943, Hawksley and McCormack 1951, Brackbill 1952, Frith

<sup>1</sup> Received 25 February 1987. Final acceptance 27 August 1987.

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TABLE 1. Egg laying and fates of eggs at I-14 in 1986. Only visits to the nest at which new eggs were found or eggs were discovered to be missing are included, although the nest was checked three times a day during this period.

Date	Time	Eggs removed or new eggs found	Fate of eggs
24 April	08:09	Egg 1 found and marked	Removed
	11:54	Egg 1 gone	
25 April	07:54	Egg 1a found and marked	Fledged
	12:10	Egg 2 found and marked	Fledged
26 April	07:45	Egg 3 found and marked	Died during hatching
27 April	09:00	Egg 4 found and marked	Removed during incubation
		Egg 5 found and marked	Removed
	12:17	Egg 5 gone	
		Egg 5a found and marked	Fledged
28 April	12:26	Egg 6 found and marked	Fledged
29 April	08:47	Egg 7 found and marked	Removed 2 days after all others hatched

and Davies 1961, Sauer and Sauer 1966, Pinkowski 1975, Gibbons 1986).

Here we report a case in which two European Starlings (*Sturnus vulgaris*) laid eggs in the same nest in three breeding attempts: one brood in 1986 and two broods in 1987. Both females cooperated in incubating the eggs and in feeding the nestlings. The same male fed the young in two of the three broods. Electrophoretic data support observations that each female was the mother of at least two of the nestlings that fledged from each of the three broods. Results of electrophoresis also support the observation that both females were mated to the same male in at least two of the three broods. Although starling nests may often contain the eggs of more than one female as a result of intra-specific brood parasitism (Yom-Tov et al. 1974, Evans 1980, Power et al. 1981), cooperation between starling females in incubation and feeding nestlings has not been reported previously.

We studied starlings breeding on our trail of nest boxes during 1986 and 1987 on the Kilmer Campus of Rutgers University in Piscataway, New Jersey. The breeding biology of starlings nesting in these boxes has been monitored since 1979. All breeding adults are marked with USFWS bands and many are marked with unique color-band combinations to allow identification at a distance.

During an evening census of nest boxes on 2 March 1986 we found female 66214 and a previously unbanded female (given band 66597) roosting together in box I-14. Female 66214 bred in box I-14 in 1983, 1984, and 1985. In each of those years her mate was male 66218. Female 66597 was again captured at I-14 on 23 April. Box I-14 contained a complete nest with no eggs at this time. Female 66597 was captured in the nest box again on 26 April. She was repeatedly observed entering and exiting the box between 10:00 and 11:30 on 27 April. Female 66214 was found in box I-14 twice on 27 April and was also repeatedly observed entering and exiting the nest box between 10:00 and 11:30 on 27 April. She was found on the nest three more times between 29 April and 10 May.

Egg laying began in box I-14 on 24 April (Table 1). All eggs were numbered as they were found; a total of nine eggs were laid in the nest. More than one egg

appeared in the nest on both 25 and 27 April. A total of four eggs hatched on 9 and 10 May. All embryos were uniquely dyed so the egg from which each nestling hatched could be determined (Rotterman and Monnett 1984). Nestlings were then individually marked by clipping their toenails in a unique pattern (Hoffenberg et al. 1988).

The two eggs that appeared in I-14 on 25 April (Table 1) must have been laid by different females; a single female is physiologically unable to produce two eggs in 1 day (Wolford et al. 1964, Woodard and Mather 1964; see also Gould 1986). Similarly, three eggs appeared in I-14 on 27 April, suggesting that three different females (66214, 66597, and an unknown brood parasite) laid in the nest on the morning of 27 April.

Females 66214 and 66597 were found brooding together in I-14 at 21:20 on 14 May. Both females were observed feeding nestlings on 21, 22, 24, and 27 May. Male 66218 was observed feeding the nestlings on 14, 22, 24, and 27 May. Four nestlings fledged between 28 May and 1 June.

The same two females also laid eggs in I-14 in each of two broods in 1987. The clutch in I-14 went from three eggs (Eggs 1-3) at 14:28 on 15 April to eight eggs (Eggs 1-8) at 16:26 on 17 April. The appearance of five eggs in a 2-day period indicated that at least three different birds (66214, 66597, and an unknown brood parasite) laid in I-14 during that period. Egg 9 appeared on 18 April. A total of eight eggs (Eggs 1-8) hatched on 28, 29, and 30 April. Embryos were dyed and nestlings were toeclipped as in 1986.

All three adults cared for the nestlings in the first brood in 1987. Female 66214 was found incubating at 15:28 on 16 April and was found brooding at 20:51 on 5 May. Females 66214 and 66597 and male 66218 were observed feeding nestlings on 9 and 10 May. The nestling from Egg 8 died between 2 and 4 May. Nestlings from Eggs 1-7 fledged on 19 and 20 May.

Second-brood laying began in I-14 on 31 May 1987, when one egg (Egg 1) appeared. Two new eggs were found each day on 1 June (Eggs 2 and 3), 2 June (Eggs 4 and 5), and 3 June (Eggs 6 and 7), producing a clutch of seven eggs. All eggs hatched between 13 and 15 June. Female 66214 was caught incubating at 13:23 on 13 June. Females 66214 and 66597 were both observed

feeding nestlings on 16, 18, 19, and 22 June, but no male was observed feeding. The nestling from Egg 2 died during hatching on 13 June. The nestling from Egg 1 died between 15 and 17 June, the nestling from Egg 7 between 25 and 27 June. Nestlings from Eggs 3–6 fledged between 3 and 6 July.

Blood and pectoral muscle tissue samples were collected from females 66597 and 66214, male 66218, and all but one of the nestlings surviving to 19 days after hatching (see Hoffenberg et al. 1988 for collection methods). (The nestling not biopsied was from Egg 7 in the first brood in 1987, which escaped during handling before being biopsied. In the following discussion this bird is considered to have fledged.) Results of polyacrylamide gel electrophoresis are shown in Table 2. Plasma amylase phenotypes indicated that 66597 could not be the mother of Nestling 6 in 1986 or Nestling 3 in the second brood in 1987, as she could not have contributed an F allele. Similarly, 66214 could not be the mother of Nestling 5a in 1986, Nestling 3 in the first brood in 1987, or Nestling 6 in the second brood in 1987, as she could not have contributed an S allele. Neither female can be excluded from the maternity of any heterozygous nestlings. Male 66218 could not be excluded from the paternity of any nestling. These results support the hypotheses that (1) both females were mated to 66218 in at least the first two broods and (2) both females laid their clutches in I-14.

This is the first time we have positively identified two females sharing feeding and incubation duties. Observations on the study population suggested that intruding adults may occasionally carry food into nest boxes containing nestlings but do not repeatedly feed nestlings. Anderson (1961) reported twice seeing two different starling females feeding a brood but gave no further information regarding the circumstances. Kessel (1957) mentioned that Grabham (1895), Newstead (1908), and Kluijver (1933) all reported observations of a trio of adults feeding a brood of starlings, with the extra bird being a male in each case.

The absence of a USFWS band when 66597 was captured on 2 March 1986 showed that she did not fledge from one of our nest boxes. We have monitored the breeding activities of female 66214 and male 66218 since 1983; all progeny of this pair were banded prior to fledging. Electrophoretic results (Table 2) verify that female 66214 cannot be the mother of female 66597, although male 66218 cannot be excluded from the paternity of female 66597. Close kinship is often found among birds cooperating at the same nest (Brown 1978, Emlen 1978, Woolfendon and Fitzpatrick 1984), and kin selection has been proposed as an important force in the evolution of such systems (Brown 1974, Ricklefs 1975). Other authors theorize that it is not kin selection, per se, that is necessary for the evolution of cooperative breeding, but that ecological limiting factors reduce the reproductive success of birds that leave the family unit (Koenig and Pitelka 1981, Woolfenden and Fitzpatrick 1984).

The case we describe may be the result of a lack of suitable nest sites for a nonexcavating cavity-nesting bird. We reduced the number of nest boxes on the field site where I-14 is located from 48 to 25 between 1985 and 1986. In 1985 to 1987 all boxes were used for breeding by starlings. Reduction in the number of nest

TABLE 2. Results of polyacrylamide gel electrophoresis of parents and nestlings at I-14. Nestling numbers correspond to egg numbers mentioned in the text or in Table 1.

Bird	Plasma amylase phenotype
Female 66597	SS
Female 66214	FF
Male 66218	FS
1986	
Nestling 1a	FS
Nestling 2	FS
Nestling 5a	SS
Nestling 6	FF
1987—First brood	
Nestling 1	FS
Nestling 2	FS
Nestling 3	SS
Nestling 4	FS
Nestling 5	FS
Nestling 6	FS
1987—Second brood	
Nestling 3	FF
Nestling 4	FS
Nestling 5	FS
Nestling 6	SS

boxes was associated with an increase in the number of nest boxes containing multiple parasite eggs in 1986 over 1985, probably due to increased competition among females for nest sites. Polygyny is probably not due to a lack of unmated males, as male starlings outnumber females in other populations (Kessel 1957).

Discovery of female starlings fighting in nest boxes ( $n = 4$  fights in 1986), and entire clutches being removed after the addition of multiple parasite eggs ( $n = 7$  in 1986) are not unusual events in the study population. The typical result of such conflict is the loss of a breeding opportunity for both birds at the box being disputed. These events are probably not due to an unnatural density of nest boxes in the study site (e.g., Semel and Sherman 1986), as all boxes were at least 33.2 m apart in 1986 and 1987. Natural cavities are often more clumped in distribution (e.g., several cavities in the same tree) and may all be used by starlings (Stouffer, pers. observ.).

In the cases reported here both females and the male benefited from cooperation between the females. In each of the three broods both females achieved higher reproductive success than did the average monogamous female in the study population in 1986 (1.72 fledglings/complete [incubated] clutch for all clutches in 1986). (Data from 1987 are not applicable for comparison because most clutches were subjected to manipulations influencing reproductive success.) Based upon laying chronologies and electrophoretic data, each female fledged two young in 1986, three young in the first brood in 1987, and two young in the second brood in 1987. The male thus fledged four, six, and four young

in the three broods, compared to 1.72 fledglings/clutch for monogamous males in 1986. This is the only case of simultaneous polygyny that we know of in the study population. Compared to the average reproductive success of monogamous males, communal nesting appeared to be to the selective advantage of the male (but see below), although the simultaneous fertility of two females may have increased the male's vulnerability to cuckoldry. Cuckoldry has been documented in the study population (Hoffenberg et al. 1988), as has behavior to prevent cuckoldry (Power et al. 1981).

Although both females were able to fledge at least as many nestlings in each of the three broods as did the average monogamous female in the study population in 1986, it is unlikely that communal breeding is a selectively advantageous strategy for starling females. Monogamous pairs in the study population can fledge four or five nestlings. Egg removal and infertile eggs (Table 1) cost females 66214 and 66597 the opportunity to rear larger broods. The first female to lay in 1986 may have had her first egg(s) removed by the second female. Starling females have been shown to remove eggs added to their nests before they have begun laying their own eggs (Stouffer et al. 1987). (This pattern of egg removal from communal nests also occurs in Acorn Woodpeckers [Mumme et al. 1983] and in Groove-billed Anis [Vehrencamp 1977, 1978].) Also, a single starling may not be able to adequately incubate large clutches (see Biebach 1981); Egg 7 in 1986 and Egg 9 in the first brood of 1987 did not hatch. The cases of communal nesting reported here were probably not advantageous in comparison with successful monogamy, but enabled the parents to avoid total reproductive failure as a result of conflict over nest sites.

We thank T. Vail and R. Ziemciwicz for their assistance in collecting field data. This study was supported by NSF grant BSR 8316361 to H. W. Power and T. R. McGuire, by a Busch Memorial Grant from Rutgers University to H. W. Power, and by a Carl N. Steinetz Memorial Fund grant from the Department of Biological Sciences of Rutgers University to P. C. Stouffer. We thank M. F. Lawton and an anonymous reviewer for their comments on an earlier version of this manuscript.

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*The Condor* 90:245-246  
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## EARLY PAIR AND EXTRA-PAIR COPULATIONS IN WILLOW PTARMIGAN<sup>1</sup>

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*Key words:* Copulation; extra-pair copulation; kleptogamy; Willow Ptarmigan.

In Willow Ptarmigan (*Lagopus lagopus*), males and females are paired from the onset of territoriality until after independence of the brood, a situation unique among grouse. Despite pairs being together on the territory for up to 33 days prior to laying, copulations have rarely been observed in the wild. Copulations between pairs have been seen immediately before and during egg laying and during incubation in Red Grouse (*L. l. scoticus*, Watson and Jenkins 1964), Rock Ptarmigan (*L. mutus*, MacDonald 1970), and White-tailed Ptarmigan (*L. leucurus*, Schmidt 1969). The three species of ptarmigan are the only monogamous grouse in North America and no instances of extra-pair copulation have been reported for them (McKinney et al. 1984). Here we document nine copulations between pairs of Willow Ptarmigan that occurred much earlier in the season than reported previously for ptarmigan and five instances of attempted extra-pair copulations between paired females and unpaired males.

### STUDY AREA AND METHODS

Copulation behavior was observed opportunistically at the Chilkat Pass (CP) in northwestern British Columbia, and at La Perouse Bay (LPB) near Churchill,

Manitoba, Canada. We considered a copulation to be completed if both members of the pair placed their tails to make cloacal contact. The majority of copulations were observed in 1986 and 1987 at CP while we monitored monogamous and experimentally-produced polygynous hens for over 100 hr, 2.5 weeks prior to and up to egg laying. Except when indicated otherwise, observations occurred at Chilkat Pass. In both areas birds were color-banded and the pairing and territorial status of each bird were known. Date of first egg was determined by backdating from hatch date (subtracting 21 days for incubation period and 1 day for each egg laid) or was known directly for hens whose nests were found during egg laying. Terminology for calls and postures follow that of Watson and Jenkins (1964).

### OBSERVATIONS

Completed copulations were observed between mated birds in May between 7 and 16 days before hens laid their first eggs (Table 1). Copulations were similar to those described for Red Grouse by Watson and Jenkins (1964). In addition, an apparently unsuccessful copulation between a mated pair was observed on 22 May 1986 when a hen approached her mate who was engaged in a border dispute. The other male ran toward her and she flew away, followed by her mate. Without preliminary display he jumped on her back, grabbed her nape feathers and treaded on her back. The female struggled throughout, and when her mate flew away to continue the border dispute, she remained crouched

<sup>1</sup> Received 25 February 1987. Final acceptance 8 July 1987.