Short Communications and Commentaries

Asynchronous Polygyny in the House Wren (*Troglodytes aedon*)

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Polygyny occurs regularly (5% or more males polygynous) in only 14 (5%) of the 291 species of passerines analyzed by Verner and Willson (1969). Orians (1961) suggested that polygyny in passerines is most common in habitats where nest-site availability is limited. Suitable nest sites are limited for many secondary cavity nesting birds (von Haartman 1957, Holroyd 1975, Pinkowski 1979, Minot and Perrins 1986). Secondary cavity nesters, therefore, might exhibit polygynous mating systems if other factors (such as the need for male parental care) do not limit them to monogamy. Evidence from populations of Great Tits (*Parus major*; Kluyver 1951), Pied Flycatchers (*Ficedula hypoleuca*; Alatalo and Lundberg 1984), and House Wrens (*Troglodytes aedon*; Kendeigh 1941) supports this hypothesis.

The question of why females choose to settle with already-mated males, when it is potentially costly to their fitness, is central to the study of avian mating systems. The polygyny-threshold model suggests that a female who chooses an already-mated male obtains a higher-quality breeding situation than if she were to choose an unmated male at the same time (Verner 1964, Verner and Willson 1966, Orians 1969). Although Vehrencamp and Bradbury (1984) suggested that an adequate test has never been made, the polygyny-threshold model is widely cited as the best explanation for the evolution of territorial polygyny in many bird species (Searcy and Yasukawa 1989).

A key prediction of the polygyny-threshold model is that secondary females should be at least as successful as monogamous females that settle at the same time (Garson et al. 1981). Tests of this prediction however, have produced little support (Leonard 1990). We report results that support the prediction for a single-brooded population of House Wrens and discuss how timing of polygyny may have been a factor.

We studied House Wrens in 1986 at the Beaverhill Bird Observatory, 72 km east of Edmonton, Alberta (53°24'N; 112°31'W). The study comprised an area with

210 nest boxes in willow (*Salix* spp.) shrubland and poplar (*Populus balsamifera, P. tremuloides*) forest, and a control area of equal size without nest boxes. Nest boxes (25 cm deep by 13 cm wide, with a 3.8-cm diameter hole) fixed to trees, shrubs or posts were spaced 30 m apart and were 1.2 m above the ground. We used mist nets and a trap door on the nest boxes to catch adult wrens. Each bird was individually color-marked with a combination of aluminum and celluloid leg bands.

We defined mating status of House Wrens by social behavior and not strictly sexual relations. For example, extra-pair copulations occur in House Wrens (Johnson and Kermott 1989), but distinguishing them from others was beyond the scope of our study. Male House Wrens were considered polygynous if they were observed feeding females or young at more than one nest where there was an overlap between the nesting periods of the primary and secondary nests. Males were also considered polygynous if they were observed defending a nest box that later had a female raising young without male assistance. Nest failure that occurred before both adults could be caught and marked often made it impossible to determine mating status.

We estimated the incidence of polygyny by comparing the number of polygynous matings to the total number of nest attempts (at least one egg laid) for which the mating status was known. We used clutch size and number of young fledged to compare reproductive success of monogamous and primary females with secondary females. To correct for the seasonal decline in clutch size and number of fledglings, we standardized the values by dividing the number of eggs or fledglings in each nest by an average value for each day. The average was computed by linear regressions of clutch size or number of fledglings against laying date for monogamous and primary polygynous nests.

There were 74 nest attempts (at least one egg laid) in nest boxes within the experimental area, and 2 in natural cavities in the control area. We were able to determine the mating status of 56 females from the 74 nest attempts. Failure to confirm the mating status of females from the remaining 18 nest attempts was

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TABLE 1. Timing and success of primary (P) and secondary (S) female House Wrens in 10 cases of polygyny.

Case	Distance between P and S (meters)	Days between first eggs of P and S	Days of overlap between P and S nestling periods	No. young fledged		Cause of mortality
				P	S	
1	90	21	0	8	7	
2	30	22	0	7	7	
3	30	2	11	7	0	Starvation
4	30	11	4	0	5	Infanticide
5	30	11	3	7	5	
6	30	22	0	7	5	
7	30	17	0	0	5	Infanticide
8	60	20	0	7	0	Abandoned
9	60	22	0	6	6	
10	30	20	0	7	0	Infanticide

due to predation, intraspecific interference, or abandonment before both adults could be caught and marked (Quinn 1989). There were 10 confirmed cases of polygyny in the 56 matings for which the mating status was known (21.7% of mated males were polygynous, 35.7% of females were mated to polygynous males).

Young were successfully fledged from 15 of the 20 (75.0%) nests with polygynous males (Table 1). In only 1 of the 10 cases of polygyny did clutch initiation of the secondary female precede incubation by the primary female; the result was starvation of the young from the secondary nest nine days after hatch. We observed the male feeding the young at both nests until the third day after the hatch of the secondary clutch, after which he was seen only at the primary nest. The timing of clutch initiation in the other nine cases of polygyny resulted in short (two cases, four and five days, respectively) or no overlap between the nestling phases of primary and secondary nests.

In absolute numbers, the clutch size and number of young fledged did not differ significantly between primary/monogamous females and secondary females (Table 2). Regressions of clutch size and number of fledglings on the date of first egg (Figs. 1 and 2) revealed a significant decline in both as the season progressed ($t = 7.32$, $P < 0.01$; $t = 6.35$, $P < 0.01$, respectively). When the correction for time of season was applied, the clutch size of the secondary females was significantly greater than that of primary/monogamous females, while the number of young fledged did not differ significantly.

Secondary female House Wrens laid significantly larger clutches and fledged at least as many young as primary or monogamous females that settled at the same time. These results are consistent with a key prediction of the polygyny-threshold model. In addition, the timing of primary and secondary nests implies that the costs of polygyny might be reduced by a settlement pattern that avoids a significant overlap in the nestling periods of the primary and secondary females.

The incubation and nestling periods of House Wrens are nearly equal (13 and 14 days, respectively), and incubation begins with the final egg (Kendeigh 1941). Therefore, a secondary polygynous mating that is initiated midway or further through the incubation period of the primary female results in the secondary clutch hatching near or after the time that the first brood fledges. Nine of the 10 cases of polygyny in our study had little or no overlap in the primary and secondary nestling stages. The one case of polygyny where there was an almost complete overlap of the primary and secondary nestlings resulted in starvation of the secondary nestlings.

The reproductive costs to females that share or lose

TABLE 2. Clutch size and number of young fledged for monogamous (M) and primary (P) female House Wrens compared to secondary (S) females at Beaverhill Lake, Alberta.

	Monogamous/primary $\bar{x}$ + SE (n)	Secondary $\bar{x}$ + (n)	Comparisons[a]
Absolute clutch size	6.56 + 0.16 (46)	6.50 + 0.31 (10)	ns
Adjusted clutch size	1.00 + 0.02 (46)	1.09 + 0.04 (10)	$P < 0.05$
Absolute number of young	5.85 + 0.19 (41)	5.43 + 0.20 (7)	ns
Adjusted number of young	1.00 + 0.02 (41)	1.09 + 0.05 (7)	ns

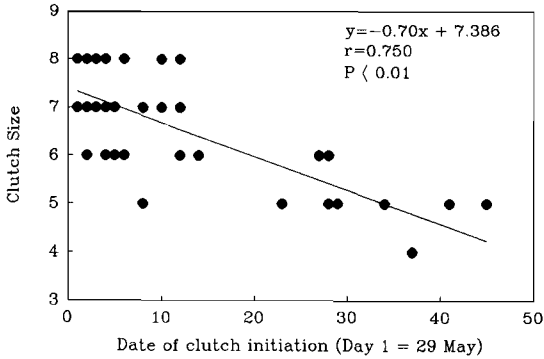[a] Mann-Whitney U-test. ns, $P > 0.05$.

Fig. 1. Linear regression of clutch size on date of clutch initiation for monogamous and primary female House Wrens ($n = 46$).
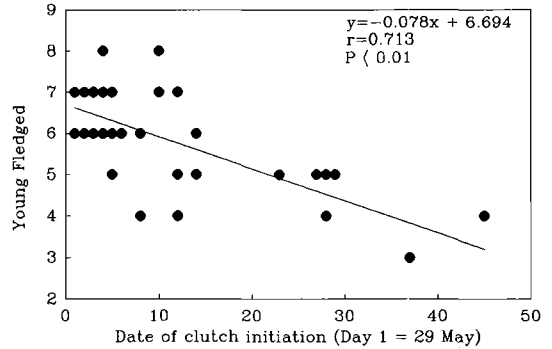

Fig. 2. Linear regression of number of young fledged on date of clutch initiation for monogamous and primary female House Wrens ($n = 41$).

male parental care in polygynous matings might be avoided by asynchronous settlement (Emlen and Oring 1977, Leonard 1990). Lack (1966) proposed that the need for male parental care limits the incidence of polygyny in birds. Male assistance was critical in at least some periods for House Wrens in a male-removal study (Bart and Tornes 1989). Males in our study exhibited territorial behavior and fed young at both the primary and secondary nests.

During the laying stage, male House Wrens spend most of the time with their mate (pers. observ.), probably to prevent extra-pair copulations (Johnson and Kermott 1989). The presence of both sexes during this period also may lessen the risk of egg-dumping (Picman and Belles-Isles 1988, Price et al. 1989), intraspecific nest-content destruction (Belles-Isles and Picman 1986, Quinn and Holroyd 1989), and predation.

Female aggression may also be a factor that limits this population of House Wrens to asynchronous polygyny. If the primary female produced fewer offspring as a result of the addition of another female, then it is in the interest of the primary female to keep the male monogamous (Wittenberger and Tilson 1980, Hannon 1984). The attraction of a secondary female, while the primary female is incubating, greatly reduces the potential for aggression on the part of the primary female, because she rarely leaves the nest (pers. observ.). The risk of intraspecific egg destruction to the secondary female may not be a factor, since there is evidence that females cease breaking eggs once they commence incubation (Belles-Isles and Picman 1986).

Leonard (1990) proposed the asynchronous-settlement model as an alternative to the polygyny-threshold model. The asynchronous-settlement model differs from the polygyny-threshold model in that the former predicts no relationships between: (1) male or territory quality and harem size; and 2) female reproductive success and the order in which territories are settled. The prediction of equal fitness for secondary and monogamous females settling at the same

time is common to both models. Our data are insufficient to adequately determine which of these models best explains the evolution of polygyny in our population, but the question merits future consideration.

Secondary female House Wrens did as well as primary or monogamous females that settled at the same time. These data support one prediction of the polygyny-threshold model that has received little support in the literature. The asynchronous settlement of primary and secondary females may have helped to avoid the reproductive costs usually associated with choosing to settle with an already-mated male.

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Basic Technique for Preparation of Down for Examination with the Scanning Electron Microscope

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The scanning electron microscope (SEM) has aided researchers studying feathers in describing unique structural features (Dyck 1973, Schmalz 1982), making identifications from microscopic characters (Davies 1970, Robertson et al. 1984), and pursuing taxonomic studies (Brom 1990, Reaney et al. 1978). While a number of authors (see above citations) have described preparation of material for SEM examination, their focus was not on material-preparation technique. We have developed a preparation method for plumulaceous feather structures (i.e. down) to be examined with the SEM. Our method is simple, safe, and re-