J. Field Ornithol., 54(3):319–323

EFFECT OF TIMING OF BANDING ON REPRODUCTIVE SUCCESS OF TREE SWALLOWS

By Edward H. Burtt, Jr. and Richard M. Tuttle

Banding of parent birds captured at the nest is often essential to the study of avian populations (e.g., Lack 1966, DeSteven 1980). However, periodic visits to nests reduce reproductive success (Gillett et al. 1975, Robert and Ralph 1975, Lennington 1979, but see Willis 1973) and capturing parent birds at the nest would appear to be more disruptive than visitation, although the effect of such banding is unstudied. A comparison of several population studies of Tree Swallows (*Tachycineta bicolor*) suggests that parental banding reduces reproductive success (Table 1). However, the diverse studies cited in Table 1 are geographically scattered and subject to the differing techniques of different observers. Using standardized banding and monitoring procedures we compared the reproductive success of banded and unbanded Tree Swallows nesting near Delaware, Ohio. We also compared the reproductive success of Tree Swallows banded at different stages in the reproductive cycle and at different hours of the day.

METHODS

From 1977 through 1980 twenty-five pairs of Tree Swallows nested in the Delaware State Park and HinnenKamp farm near Delaware, Ohio. Although not banded, these pairs were checked every 5 to 7 days and comprise our sample of unbanded birds. In 1981, 57 pairs of Tree Swallows nested in the park and on the farm. Because only females incubate and brood, they were the only sex captured and banded.

As soon as females began nest building they were randomly divided between those to be captured on the nest at night and those to be captured on the nest during the day. Several females disappeared prior to capture, resulting in unequal reduction of experimental groups (25 females banded at night vs 32 females banded during the day). Stage of the reproductive cycle was not known prior to banding, but was recorded at the time of capture. "Prelaying" included the time from initial occupancy of the nest cavity to laying of the first egg. "Laying" was the period from appearance of the first egg through the day on which the last egg appeared. "Early incubation" was the 5 days following the day on which the last egg was laid. "Late incubation" included all subsequent days until hatching of the first egg (=day 6 to 14). All nests were checked briefly every 5 to 7 days. Where the date of laying was unknown, visits occurred daily. Clutch size was the largest number of eggs seen in nest; brood size at hatching was the largest number of young seen in the nest.

The distributions of clutch and brood sizes were checked for normality (Zar 1974). Because several distributions differed significantly from nor-

TABLE 1. Reproductive success of banded and unbanded Tree Swallows.

Young fledged/eggs laid	Number of nests	Geographic area	Source
Parents banded before chicks hatched			
0.45	109	New Brunswick	Burtt, unpubl.
0.49	272	Massachusetts	Austin and Low 1932, Low 1933, 1934
0.52	315	Massachusetts	Chapman 1935, 1939, 1955
0.70	26	Massachusetts	Mason 1968
Parents unbanded or banded after chicks hatched			
0.70	68	Connecticut	Kuerzi 1941
0.74	31	New Brunswick	Paynter 1954
0.77	149	Ontario	DeSteven 1978
0.87	22	New Brunswick	Winn 1949
0.94	60	Montana	Weydemeyer 1935

mal, all comparisons are based on nonparametric statistics. For comparison of two groups, for example clutch size of banded and unbanded females, the Mann-Whitney U test (Roscoe 1975) was used. For comparison of more than two groups, for example clutch size of females banded at different reproductive stages, the Kruskal-Wallis test (Zar 1974) was used. The Chi-square test for independence (Roscoe 1975) was used to compare hatching success and the frequency of abandoned clutches among birds banded at different reproductive stages.

RESULTS

Effect of banding on reproductive success.—Unbanded females laid clutches of 4.6 ± .3 (mean ± standard error) eggs whereas banded females whose clutches were complete at the time of banding and therefore not influenced by banding procedures laid 5.2 ± .2 eggs/clutch. The difference is not significant ($U_{57,25} = 624.5$, $P > .10$). Unbanded females hatched 4.0 ± .3 chicks/clutch whereas banded females hatched 3.2 ± .3 chicks/clutch. Again the difference is not significant ($U_{55,25} = 577$, $P > .10$). However, the proportion of eggs that yielded fledglings was significantly greater ($\chi^2 = 15.35$, df = 1, $P < .005$) among unbanded females (90 fledglings/107 eggs) than among banded females (182/288). The lower success of banded females resulted from clutches that were abandoned. Banded females fledged the same proportion of chicks as unbanded females in clutches that hatched at least one chick ($\chi^2 = 1.22$, df = 1, $.5 > P > .25$).

Time factors in the disruptive effect of banding.—Among females whose clutches were complete at the time of banding, those banded during the day had a mean clutch of 5.4 (±.2) eggs which was not significantly different ($U_{32,25} = 339.5$, $P > .10$) from the mean clutch size (4.9 ± .3)

TABLE 2. Comparison of clutch or brood size among females banded at different stages of the reproductive cycle. Overall comparison based on Kruskal-Wallis statistic.

	Reproductive stage at banding					Probability of
	Prelaying	Laying	Early incubation	Late incubation	H_c (df = 3)	significant difference
Clutch size (all nests) mean ± SE (n)	4.4 ± 1.0 (8)	5.2 ± 0.3 (18)	5.1 ± 0.2 (21)	5.0 ± 0.3 (10)	1.46	$P > 0.05$
Brood size at hatching (all nests) mean ± SE (n)	3.1 ± 1.0 (6)	1.8 ± 0.5 (18)	3.7 ± 0.5 (21)	4.7 ± 0.4 (10)	11.17	$0.025 > P > 0.01$
Brood size at hatching (only nests with at least one hatching) mean ± SE (n)	5.0 ± 0.7 (5)	3.6 ± 0.6 (9)	4.9 ± 0.2 (16)	4.7 ± 0.4 (10)	3.69	$P > 0.05$

of females with completed clutches banded at night. The mean brood size at hatching of all females banded during the day was 3.1 (±.4); that of all females banded at night was 3.3 (±.5). The difference is not significant ($U_{30,25} = 362$, $P > .10$). Much of the decline was the result of abandoned clutches. Seven of 25 females banded at night deserted their clutches whereas 10 of 32 females banded during the day deserted, a non-significant difference ($\chi^2 = .08$, df = 1, $.9 > P > .75$).

Because reproductive success was unaffected by the time of banding, females banded at night and during the day are combined in the following analysis. Clutch size was not significantly affected by the stage of the reproductive cycle at the time of banding (Table 2). However, reduced brood size at hatching was associated with banding during the prelaying and especially laying stages of the reproductive cycle (Table 2). If clutches in which no eggs hatched are excluded from consideration, the effect of banding disappears (Table 2). Banding early in the reproductive cycle, whether by day or night, is significantly more likely to cause desertion of the nest ($\chi^2 = 8.30$, df = 3, $.05 > P > .02$) than banding later in the cycle. During prelaying, 3 of 8 females abandoned their nests following banding. The proportion of desertions increased to 9 of 18 females banded during laying, then decreased to 5 of 21 females banded during the first 5 days of incubation and 0 of 10 females banded later in incubation.

DISCUSSION

Banding of the female parent significantly increases the probability of desertion among female Tree Swallows banded early in the nesting

cycle, but does not reduce reproductive success of females that remain with their clutches. Recent theories of parental investment predict that as time and energy invested in reproduction increases, the tendency to desert and begin anew decreases (Trivers 1972, Biermann and Robertson 1981). Thus up until early incubation, the disruption caused by capture and banding outweighs the investment in the nest and clutch. To minimize the disruptive effect of banding, females should be banded after the first few days of incubation. Whereas banders often postpone banding until females are feeding young (DeSteven 1978, 1980, Klimkiewicz pers. comm.), our results suggest that, after the first few days of incubation, banding does not significantly reduce reproductive success. Banding early in the reproductive cycle offers the bander two advantages. Birds banded during mid- to late incubation are more likely to be at the nest when the bander visits than are birds feeding young. Furthermore the sooner the bird is banded, the more information is potentially available.

The time of day a female is banded has little effect on the probability of desertion. However, our experience suggests that Tree Swallows and many other hole-nesting birds can be banded most efficiently at night. Female swallows incubate at night and are reluctant to fly from the nest even when alarmed. Thus the bander is assured of an occupied nest whose occupant is unlikely to escape. The banded female promptly returns to the nest if placed at the entrance hole. Darkness is a minor handicap to banding, but a headlamp provides sufficient light and leaves both hands free for the tasks of handling, banding, and recording.

SUMMARY

Banding procedures can significantly reduce reproductive success. Female Tree Swallows banded early in the nesting cycle abandoned their clutches significantly more often than females banded late in incubation, whereas reproductive success was unaffected by the time of day of banding. Thus we suggest that Tree Swallows be banded late in incubation or later, when the probability of desertion is low, and at night, when capture is most efficient for the bander.

ACKNOWLEDGMENTS

The Ohio Department of Natural Resources and Elmer and Nance HinnenKamp graciously allowed us to study birds nesting on their land. Analysis and writing were completed while the senior author held an Ohio State Postdoctoral Fellowship and supplemental grant to National Science Foundation grant DEB 7911759. We thank A. John Gatz, M. Kathleen Klimkiewicz, and Charles R. Brown for their critical comments on the manuscript.

LITERATURE CITED

Austin, O. L. Jr., and S. H. Low. 1932. Notes on the breeding of the Tree Swallow. Bird-Banding 3:39–44.

BIERMANN, D. C., AND R. J. ROBERTSON. 1981. An increase in parental investment during the breeding season. Anim. Behav. 29:487–489.
CHAPMAN, L. B. 1935. Studies of a Tree Swallow colony. Bird-Banding 6:45–47.
———. 1939. Studies of a Tree Swallow colony. Bird-Banding 10:61–73.
———. 1955. Studies of a Tree Swallow colony. Bird-Banding 26:45–70.
DESTEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow *Iridoprocne bicolor*. Ibis 120:516–523.
———. 1980. Clutch-size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). Evolution 34:278–291.
GILLETT, W. H., J. L. HAYWARD, JR., AND J. F. STOUT. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492–495.
KUERZI, R. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc., New York 52-53:1–52.
LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford.
LENNINGTON, S. 1979. Predators and blackbirds the "Uncertainty Principle" in field biology. Auk 96:190–192.
LOW, S. H. 1933. Further notes on the nesting of the Tree Swallows. Bird-Banding 4: 76–88.
———. 1934. Nest distribution and survival ratio of Tree Swallows. Bird-Banding 5: 24–31.
MASON, E. A. 1968. Nestling data and notes on a Tree Swallow colony. Bird-Banding 39:187–189.
PAYNTER, R. A. JR. 1954. Interrelations between clutch-size, brood-size, prefledging survival and weight in Kent Island Tree Swallows. Bird-Banding 25:35–38, 102–110, 136–148.
ROBERT, H. C., AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. Condor 77:495–499.
ROSCOE, J. T. 1975. Fundamental research statistics for the behavioral sciences. Holt, Rinehart, and Winston, Inc., New York.
TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 135–179, *in* B. Campbell (ed.), Sexual Selection and the Descent of Man, 1871–1971. Aldine, Chicago.
WEYDEMEYER, W. 1935. Efficiency of nesting of the Tree Swallow. Condor 37:216–217.
WILLIS, E. O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 90:253–267.
WINN, H. 1949. Nestling mortality rate of the Tree Swallow. Bowdoin Sci. Station Bull. 11:19–20.
ZAR, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Department of Zoology, The Ohio State University, 1735 Neil Ave., Columbus, Ohio 43210 (EHB); (Present address: *Department of Zoology, Ohio Wesleyan University, Delaware, Ohio 43015); and 295 West Central Ave., Delaware, Ohio 43015* (RMT). Received 23 Apr. 1982; accepted 12 Oct. 1982.