

POLYGyny AND THE BREEDING SUCCESS OF
THE GREAT REED WARBLER
ACROCEPHALUS ARUNDINACEUS

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INTRODUCTION

The great reed warbler *Acrocephalus arundinaceus*, a summer visitor to Japan, is known to be a marsh nesting polygynous species. Polygyny has been recorded in many local populations in Europe and Japan. HANEDA and TERANISHI (1968b) and SAITOU (1976a) showed that 15.2% and 15.8% of territorial males of *A. a. orientalis* were polygynous, respectively. DYRCZ (1977) also reported that at least 12% of nests of *A. a. arundinaceus* belonged to polygynous groups. Compared with other *Acrocephalus* warblers, e.g. marsh warbler *A. palustris* (6.7% of which are polygynous; calculated from DOWSETT-LEMAIRE, 1979), reed warbler *A. scirpaceus* and sedge warbler *A. schoenobaenus* (in which rare cases of polygyny have been reported; CATCHPOLE, 1980) in Europe, the occurrence of polygyny is clearly a fundamental attribute of the great reed warbler populations.

There have been many studies of its social organization and/or social behavior, in particular territorial behavior and the territoriality (KLUYVER, 1955; HANEDA and TERANISHI, 1968b; SAITOU, 1976a, b), female behavior and intra- and inter-pair relations (EZAKI, 1981), breeding behavior of polygynous families (KIKUCHI et al., 1957; HANEDA and TERANISHI, 1968b), the characteristics of polygynous males and their territories (PELTZER, 1972; SAITOU, 1976a; DYRCZ, 1977; BEIER, 1981), and the dispersal and the age structure of a population (BEIER, 1981). SAITOU (1976a) showed that males which established territories earlier had greater mating success than late settlers.

The seasonal settling pattern of females and mate changes, i.e. divorce and remating, within a breeding season are likely to be important in the understanding of the occurrence of polygyny in warblers, because the former strongly influences the probability of mate attraction and acquisition by males (EMLEN and ORING, 1977) and the latter concerns the strength of pair bonds. However, previous studies have not clarified these aspects because many of them dealt with poorly marked populations.

Since 1980, I have been carrying out an intensive marking study to clarify the polygynous mating system of this species. In this paper, I show 1) the observed frequency

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of mating patterns, 2) the relationship between settlement date and mating status, and 3) the breeding success in relation to mating status, for five breeding seasons, and discuss the significance of seasonal mating pattern in the population as an important factor affecting the mating system of this species.

STUDY AREA

The field study was carried out throughout the breeding season (late April–mid August) from 1980 to 1984. The study area was a marsh lying between a channel and a dike surrounding the Kahokugata reclaimed land ($36^{\circ}40'N$, $136^{\circ}42'E$, near sea level), Ishikawa Prefecture, central Japan.

The size of the study area varied between years; it was 420 m long in 1980, 820 m in 1981–82, and 510 m in 1983–84 (Fig. 1). The width of the marsh was reduced from 20–40 m to 10–30 m by repair work to the dikes in the 1981/82 winter.

Reed *Phragmites communis* predominated over the marsh accompanied with Manchurian wild rice *Zizania latifolia* in the outer part and cat-tail *Typha australis*, bugleweed *Lycopus lucidus*, and other grasses (Gramineae, Cyperaceae, Juncaceae, etc.) in the inner part. Willow *Salix subfragilis*, Japanese alder *Alnus japonica*, and false-acacia *Robinia pseudo-acacia* were scattered in the northern part of the study area. The vegetation of the marsh appeared on the whole to be rather stable over the five years.

The inner part of the reclaimed land consisted of dry reed beds which the warblers inhabited during the earlier years of the study. However, their number has steadily decreased as a result of reclamation and the commencement of cultivation. The warblers consistently established their territories and bred in the reed marsh during the study period.

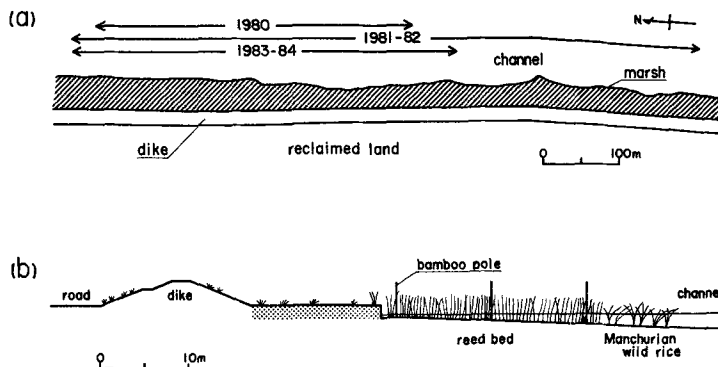


Fig. 1. (a) Map of the study area. Lines with arrowheads indicate the length of the study area in each year, and the hatched area indicates the marsh. (b) Schematic profile of the study area. Stippled area indicates the area reclaimed by the repair works in 1981/82 winter.

METHODS

(1) Marking, sexing, and aging

Birds were captured in mist nets and individually marked with a numbered aluminium ring and a combination of colored plastic leg rings. The birds were released near the point of capture after ringing, sexing, and measuring.

Sexually active adults were sexed in the hand by cloacal protrusion and a search for brood patch (see SVENSSON, 1975). Differences in behavior between the sexes were useful to confirm the sexes of resident adults. Juveniles were discriminated from the adults in the latter part of the breeding season and the pre-migration period by the presence of a pair of black spots on the base of the tongue in juveniles and by the differences in the color of iris and mouth (see KAKIZAWA, 1974).

A total of 826 birds (178 adults, 7 juveniles, and 641 nestlings) were marked in and near the study area in five breeding seasons. The number of marked males which established territories in the study area was 18 in 1980, 33 in 1981, 44 in 1982, 31 in 1983, and 27 in 1984. As females were more difficult to capture than males, the number of marked females that bred in the study area was smaller than that of males: 6 in 1980, 3 in 1981, 22 in 1982, 28 in 1983, and 29 in 1984.

(2) Observation

Individual behaviors were observed with 8 x binoculars and a 20 x spotting scope from the dike. Bamboo poles 2–5 m tall were placed in the marsh forming a 10 m × 20 m grid pattern for recording the location of the birds. Two to seven hours of observations were made mainly in the morning and late in the evening almost every day during the study period in 1980–82 and before mid June in 1983–84; however, on and after mid June in the last two years, observations were made once every two or three days.

(3) Pair bond and definition of mating status

When a male sang frequently in a particular area which was not shared with other males for at least three days, he was regarded as a territorial male.

Since it was difficult to be sure of the exact date of pair formation, the date on which the first egg of the first clutch was laid was used as a reference point (after ORIAN, 1980). A pair bond was regarded to have been established if 1) a female repeatedly brought nest material to a nest site and the territorial male consorted with her, or 2) an active nest, containing at least one egg or one nestling, was found in the territory. In this paper, a pair bond is regarded as continuing from the onset of nest building until either a female with her fledglings left the territory or a female disappeared from the territory after a failure in breeding. This period is called the period of association.

Three types of mating status were observed for males; the terms and definitions given here are based on CAREY and NOLAN (1979) with slight modification.

- 1) polygyny: males were mated simultaneously with two or three females,

the periods of association overlapping.

- 2) monogamy: males mated with only one female.
- 2') successive monogamy: males mated with two or three females with no overlap in the periods of association. This is referred to as monogamy, because males had single pair bond with only one female at a time.
- 3) bachelors: males formed no pair bonds during their residence.

All sexually mature males established territories. The mating status of females was defined in terms of the status of their mates, i.e. polygynous or monogamous females. Among polygynous females, the "primary female" was the first female mated with the polygynous male, and "secondary females" were those with which the male mated later. Since trigamy was rare, the third females are included among "secondary females", instead of using the term "tertiary females", in this paper.

(4) Estimation of mortality and breeding success

Nest contents were usually inspected in the afternoon or evening at two to four day intervals. However, nest contents due to hatch were checked daily for a few days. The first egg laying date was not confirmed for 24% of nests; instead the date of first egg laying for these nests was estimated by assuming the most common incubation period of 11–12 days and a laying rate of one egg per day. The age of a nestling was estimated by comparing its body size, growth of quills or feathers with those of nestlings of known age. Nestlings were marked on day 9 in 1980 and on day 7 in 1981–84 (the date of hatching of the first nestling in each brood was defined as day 0).

a. Mortality of eggs. Eggs hatched 11–12 days after the last egg of a clutch was laid. The number of eggs hatched was counted directly. Losses which occurred around the hatching date were included in egg mortality unless hatching was confirmed. Five mortality factors were identified as follows:

Unhatched: eggs were left unhatched for at least three days after the first egg hatched in the same clutch.

Desertion: female ceased incubating.

Weather: nest collapsed or was flooded due to bad weather.

Predation: although predation was rarely observed, loss of all the eggs in a clutch at one time was considered to be the result of predation.

Cuckoo: eggs were ejected from the nest by nest parasitizing young common cuckoos *Cuculus canorus*.

Unknown: loss of part of a clutch without trace, which possibly due to predation.

b. Mortality of nestlings. When all the nestlings in a brood were lost at one time, it was probably due to either weather or predation. Young cuckoos also ejected host nestlings. Other possible mortality factors, however, were difficult to identify because parent birds carried the dead bodies of nestlings away from the nest (HANEDA and TERANISHI, 1968a).

Unknown: loss of part of a brood; possibly due to starvation, sickness, chilling or overheating, falling from the nest, and predation.

In this paper, the number of young counted on day 9 was referred to as the number of fledglings and used as an index of the breeding success of the parents, though young fledged between days 10 and 13.

RESULTS

(1) Frequency of mating status

Observations of the mating status of male indicated that monogamous males were most common (except in 1984), bachelors were least common, and polygynous males consisted of 17–43% of the resident males (see Table 1).

Forty-five polygynous matings were observed during the study: 29 were bigamous, three trigamous, and one either trigamous or bigamous. In addition, one male mated bigamously twice within the same season. His first two mates both disappeared, one during nest building and one after unsuccessful breeding. The male subsequently acquired two new mates. The remaining 11 cases were of males with an undetermined number of mates, because unmarked primary or secondary females failed to breed and then either re-nested or were replaced by other unmarked females.

One hundred and three monogamous matings included four cases of successive monogamy and 13 cases where new nests of unidentified females were found after the breeding failure of the unmarked monogamous female in the same territory. In three of the four cases of successive monogamy, the first females disappeared during nest building. One of them mated with another male later.

As females usually mated with only one male in a breeding season, the mating status of females could be defined in terms of the status of their mates. One female, however, mated with two males and reared two broods of young. In 1982, female #592 (here, # indicates a marked individual) reared her first brood successfully as the primary female of bigamous male #308. Thereafter, she mated with male #838, who replaced #308 and occupied the same territory, and reared her second brood. Some females mated with two males during a breeding season, but these females remated with the second

Table 1. Frequency of mating status of males. The study area varied in size between years (see Fig. 1a).

| Mating Status | 1980 <i>n</i> (%) | 1981 <i>n</i> (%) | 1982 <i>n</i> (%) | 1983 <i>n</i> (%) | 1984 <i>n</i> (%) | 1980–84 <i>n</i> (%) |
|----------------|----------------------|----------------------|----------------------|----------------------|----------------------|-------------------------|
| Polygynous | 3(16.7) | 10(19.6) | 11(20.8) | 9(27.3) | 12(42.9) | 45(24.6) |
| Poly. or Mono. | 5(27.8) | 2(3.9) | 2(3.8) | —(—) | —(—) | 9(4.9) |
| Monogamous | 9(50.0) | 34(66.7) | 34(64.2) | 17(51.5) | 9(32.1) | 103(56.3) |
| Bachelor | 1(5.5) | 5(9.8) | 6(11.3) | 7(21.2) | 7(25.0) | 26(14.2) |
| Total | 18 | 51 | 53 | 33 | 28 | 183 |

mates only after unsuccessful breeding.

(2) Mating status in relation to settlement date

a. Settlement date of male. Males settled from late April or early May to mid July, a period of 37 days in 1980, 78 in 1981, 71 in 1982, 77 in 1983, and 64 in 1984 (\bar{x} = 65.4 days); the settlement peaked in early or mid May (Fig. 2). The proportion of males which settled in the first half of the settling period was 83.3% in 1980, 87.8 in 1981, 86.0 in 1982, 75.8 in 1983, and 78.6 in 1984.

The earlier settlers tended to be polygynous, while many of the late settlers remained bachelors (Fig. 2). Polygynous males were the earliest to settle, followed in order by monogamous males and bachelors in all five seasons (see Table 2). The date of settlement differed significantly between males of different status in 1981 (Kruskal-Wallis test, $H=14.377$, $P<0.001$), 1982 ($H=19.315$, $P<0.001$), 1983 ($H=9.499$, $P<0.01$), and 1984 ($H=10.480$, $P<0.01$), though no significant difference was found in 1980 ($H=4.522$, $0.1<P<0.2$).

Territory boundaries of great reed warblers sometimes shift slightly in response to neighboring male's territorial behavior (HANEDA and TERANISHI, 1968b; SAITOU, 1976a; URANO, unpublished). Besides these shifts, there were two cases of distant shifts: both

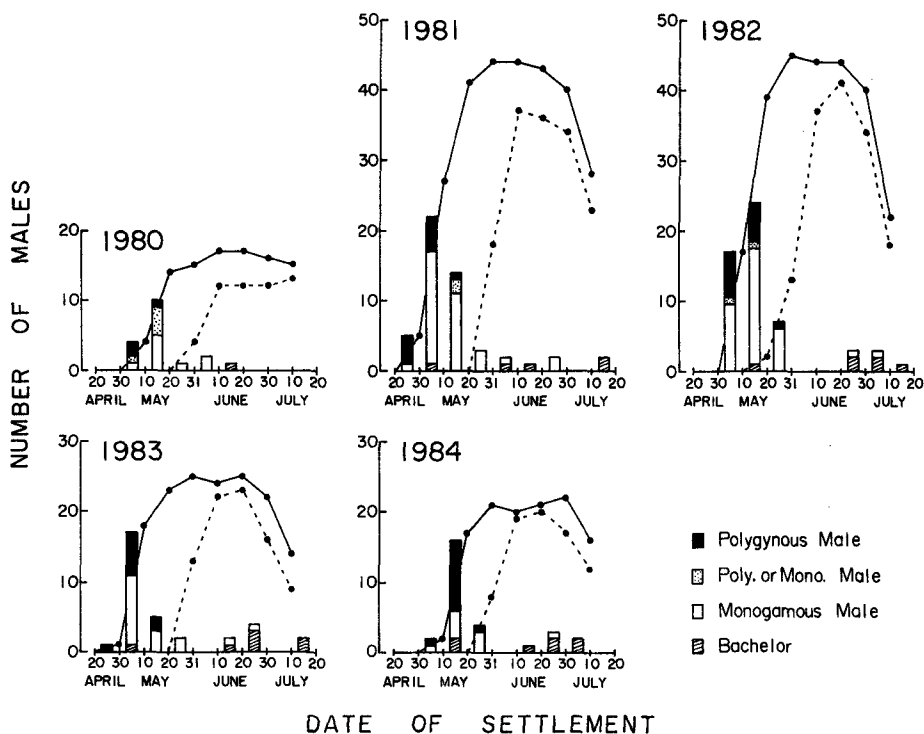


Fig. 2. The number of males in each mating status which settled in each ten (or 11) day period. Solid and broken lines show changes in the total number of territorial and mated males, respectively. The number of mated males, in this figure, does not include males of which mates did not start egg laying of their first clutches.

Table 2. Mean settlement dates of males of different mating status. Mean \pm SD; (): Number of males.

| Year | | Polygynous | Monogamous | Bachelor |
|------|-----|-------------------|------------------------|-------------------------|
| 1980 | May | 11 \pm 4.7 (3) | May 20 \pm 11.2 (9) | June 13 (1) |
| 1981 | May | 3 \pm 5.5 (9) | May 15 \pm 13.9 (33) | June 17 \pm 28.7 (5) |
| 1982 | May | 10 \pm 4.7 (10) | May 18 \pm 13.2 (32) | June 26 \pm 20.5 (6) |
| 1983 | May | 4 \pm 5.8 (9) | May 15 \pm 15.0 (17) | June 21 \pm 25.3 (7) |
| 1984 | May | 13 \pm 4.8 (12) | May 22 \pm 14.4 (9) | June 15 \pm 24.2 (7) |

involving males moving into the study area from outside, showing that the late settlers could be males which had once established their territories but moved from them.

The number of territorial males decreased due to both the disappearance of males and the cessation of territorial behavior in the late breeding season (Fig. 2).

b. Date of the first egg laying. As females were less conspicuous before nest building, they were not always found immediately after their arrival. Females were first seen in the study area on May 18 (1980), May 15 (1981), May 14 (1982), May 10 (1983), and May 20 (1984), which was 8 to 17 days after the first settling date of males. Seventy-two per cent (1980), 60.0 (1981), 48.1 (1982), 45.5 (1983), and 60.7 (1984) of males had already settled before the appearances of the females.

The duration from females' appearances in the territories to first egg laying usually spanned from 7 to 10 days. Females laid their first eggs from around May 20 to mid July, over a period of 43 days in 1980, 46 in 1981, 60 in 1982, 54 in 1983, and 40 in 1984 (\bar{x} = 48.6 days); first egg laying peaked in early June in all five seasons (Fig. 3). The first

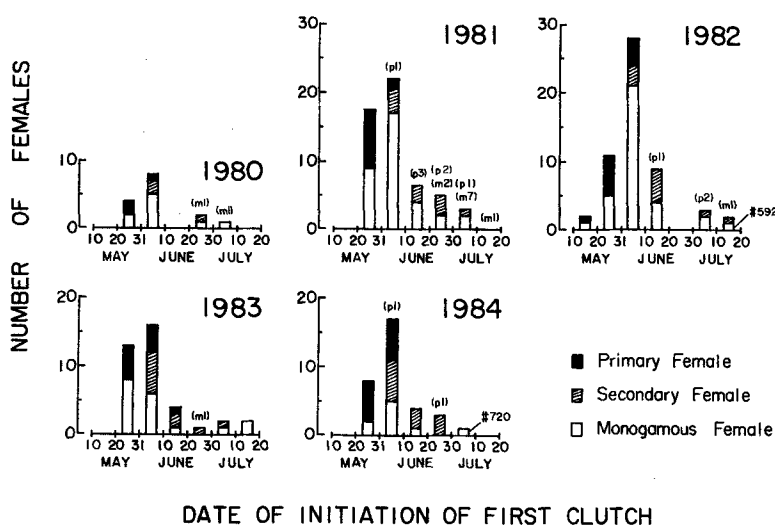


Fig. 3. The number of females in each mating status which initiated their first clutches in each ten (or 11) day period. The first egg laying at the second mating by females (#592 and #720) are treated as the laying of the first clutch. Numerals in parentheses show the number of new nests found after unsuccessful breeding of unmarked females in the territories of polygynous (p) and of monogamous (m) males, respectively (see text for details).

clutches of 73.3% (1980), 74.1 (1981), 90.9 (1982), 84.2 (1983), and 78.8 (1984) of females were initiated in the first half of the laying period.

The proportion of primary to monogamous females, both initiating their first clutches in each ten (or 11) day period, was significantly higher in late May (1.06) than in early June (0.31) ($\chi^2=10.375$, $P<0.01$, data were pooled for five seasons). This means that males which mated earlier tended to have multiple mates.

Secondary females laid their eggs in and after early June (Fig. 3). Their first clutches were begun 4 to 35 days later than those of the primary females which mated with the same males ($\bar{x}=14.9$, $SD=7.4$, $n=43$), indicating that the breeding cycles of females of different status are separated from one another.

Only two out of 87 marked females laid second clutches.

c. Behavior after breeding failure. After failing at a first breeding attempt, females either re-nested with the same mate or disappeared from the territories; thereafter, perhaps to mate with another male (Table 3). Ten marked females disappeared and two of them were found later: one of them, female #720 had bred as the secondary mate of male #580 in 1984. Their nestlings were lost between June 26 and 28 and the female disappeared from the territory. Thereafter, female #720 laid the first egg of her repeat clutch on July 4 in the territory of her new mate (male #80x) as his monogamous mate. The distance between the territories of male #580 and #80z was about 250 m.

Mate change by females was also indicated by another case. Female #601 had a developing brood patch when she was caught on May 31, 1982, suggesting that she was about to lay eggs. She was next found on July 10 when she was building a nest (as the secondary female of male #322) at a site 260 m south of the previous site. This female had probably divorced her first mate outside the study area and moved into the territory of #322. These two cases suggest that females which disappear from territories in June may move into other male's territories to breed.

The number of new nests which were found in the same territories after unsuccessful breeding by unmarked females (case c in Table 3) are shown in Fig. 3. It was not possible to determine whether the same female re-nested or not, however, since mate changes only occurred in three (case b1) out of 30 cases (case a+b1), most of the nests were likely to have been repeats. Therefore, at least 32.5% ($b/(a+b+c)$) of females

Table 3. The behavior of males and females after breeding failure (first attempt).

| | June | July | (Total) |
|--|------|------|---------|
| a. re-nested with the same mate (females were marked) | 24 | 3 | (27) |
| b. female disappeared from the territory | | | |
| b1. male mated with another female (females disappeared were marked) | 2 | 1 | (3) |
| b2. male did not mate (seven females were marked) | 9 | 13 | (22) |
| c. new nest was found in the territory but whether mate change occurred or not was unknown (females were unmarked) | 24 | 1 | (25) |
| (Total) | 59 | 18 | (77) |

Table 4. Numbers of territorial males and breeding females, and the sex ratio. The minimum (or maximum) numbers of unmarked females are estimated by assuming that all males classified as "polygynous or monogamous" in Table 1 were monogamous (or bigamous) and all nests of case c in Table 3 were repeat nests (or new nests by different females). The maximum and minimum estimates of females for 1980 and 1981 are not shown, because 28% of males were "polygynous or monogamous" in 1980 and case c was as large as 16 in 1981. The sex ratios were not significantly skewed from 1.00 (χ^2 test at 5% significance level).

| | 1982 | 1983 | 1984 | 1982-84 |
|---|---------------|---------------|---------------|-----------------|
| No. of males | 53 | 33 | 28 | 114 |
| No. of females (females marked) | 57-64 (22) | 38-40 (27) | 33-35 (29) | 128-139 (78) |
| Sex Ratio ($\frac{\text{♀}}{\text{♂}}$) | 1.08-1.21 | 1.15-1.21 | 1.18-1.25 | 1.12-1.22 |

disappeared after failing at their first breeding attempt. A few males acquired new mates after their mates disappeared (case b1 in Table 3).

d. Presence of unmated male. Females outnumbered males in the breeding seasons of 1982, 1983, and 1984, though the sex ratios were not significantly skewed from 1.00 (χ^2 test at 5% significance level) (see Table 4).

Unmated males were always present in the study area (Fig. 2). Even when unmated males outnumbered newly settling females, some females mated with already mated males. In addition, five mated males whose territories adjoined those of unmated males, acquired new mates (i.e. the secondary females). While the unmated males were unable to acquire mates.

(3) Clutch size, mortality, and breeding success

a. Clutch size. Females laid an average of 4.57 eggs per clutch (one clutch of two eggs, 6 of three, 87 of four, 132 of five, and 3 of six). The mean clutch size of each ten day period was $4.86 \pm 0.41\text{SD}$ ($n=43$) in late May and gradually decreased to $3.90 \pm 0.33\text{SD}$ ($n=10$) in mid July. Clutches laid later in the season included repeats which had fewer eggs. The details on the clutch size variation will be shown elsewhere (URANO, in preparation).

Primary females had the largest clutches ($4.77 \pm 0.48\text{SD}$, $n=47$), followed in order by monogamous ($4.58 \pm 0.59\text{SD}$, $n=117$) and secondary females ($4.43 \pm 0.62\text{SD}$, $n=46$). The difference only between primary and secondary females was significant ($t=2.961$, $P<0.05$). Females of all three statuses laid eggs in early June and the same order was found again, i.e. primary -4.93, monogamous -4.86, and secondary -4.59, although the differences were not significant. It is suggested therefore that the differences in mean clutch size between females of various mating status were not only due to differences in the timing of the initiation of egg laying (Fig. 3).

b. Mortality of eggs and nestlings. Many eggs and nestlings were lost before fledging; out of 1093 eggs, 812 eggs (74.3%) hatched and only 487 young (44.6%) survived until day 9. Both annual variation and variations between birds of different mating status

Table 5. Life table of eggs and nestlings for each mating status of female. Data were pooled from 1980 to 1984.

| Stage | Cause of change in numbers* | Mating status of females | | | | | | | | | | | |
|----------------|-----------------------------|--------------------------|----------|----------|-----------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost** | L_x *** | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 263 | | | 100.0 | 233 | | | 100.0 | 597 | | | 100.0 |
| | unhatched | | 9 | 3.4 | | | 9 | 3.9 | | | 28 | 4.7 | |
| | predation | | 48 | 18.3 | | | 36 | 15.5 | | | 66 | 11.1 | |
| | cuckoo | | 1 | 0.4 | | | 4 | 1.7 | | | 1 | 0.2 | |
| | weather | | 8 | 3.0 | | | 9 | 3.9 | | | 4 | 0.7 | |
| | desertion | | 2 | 0.8 | | | 3 | 1.3 | | | 9 | 1.5 | |
| | unknown | | 10 | 3.8 | | | 10 | 4.3 | | | 24 | 4.0 | |
| | total | | 78 | 29.7 | | | 71 | 30.5 | | | 132 | 22.1 | |
| Egg hatched | | 185 | | | 70.3 | 162 | | | 69.5 | 465 | | | 77.9 |
| | predation | | 33 | 17.8 | | | 43 | 26.5 | | | 130 | 28.0 | |
| | cuckoo | | 1 | 0.5 | | | — | — | | | — | — | |
| | weather | | 13 | 7.0 | | | — | — | | | 26 | 5.6 | |
| | unknown | | 20 | 10.8 | | | 15 | 9.3 | | | 44 | 9.5 | |
| | total | | 67 | 36.2 | | | 58 | 35.8 | | | 200 | 43.0 | |
| Young on day 9 | | 118 | | | 44.9 | 104 | | | 44.6 | 265 | | | 44.4 |

* cause of change in numbers are defined in Methods (4).

** % lost in nestling period is shown in terms of eggs hatched.

*** L_x indicates % survival in terms of eggs.

in survival rates occurred (see Appendix). When the data were pooled for five years (Table 5), there was no difference in the survival rates of eggs and young among the three mating statuses, except for higher hatching rates of eggs in nests of monogamous pairs compared with primary ($\chi^2=5.653$, $P<0.02$) and secondary females ($\chi^2=6.329$, $P<0.02$), respectively.

The rate of unhatched eggs (Table 5) ranged from 3.4 to 4.7%, but may be underestimated because some infertile eggs were lost by other mortality factors. The modified rate of unhatched eggs was derived by: No. eggs unhatched/(No. eggs unhatched+No. eggs hatched). The rate was 4.6% for primary, 5.2 for secondary, and 5.6 for monogamous females ($\chi^2=0.306$, NS).

Predation on full clutches and full broods was the most important mortality factor despite the variations between years and between the mating statuses (see Appendix). Mortality from egg to fledging by predation was 30.8% (primary), 33.9 (secondary), and 32.8 (monogamous females). Since the loss of part of a clutch or brood was treated as "unknown" in life tables, "real" mortality by predation should be much higher.

Only one case of predation was observed during this study: a snake *Elaphe climacophora* was observed swallowing nestlings from a nest. Other animals which were seen in the study area and which were potential predators were: weasel *Mustela sibirica*, rat *Rattus*

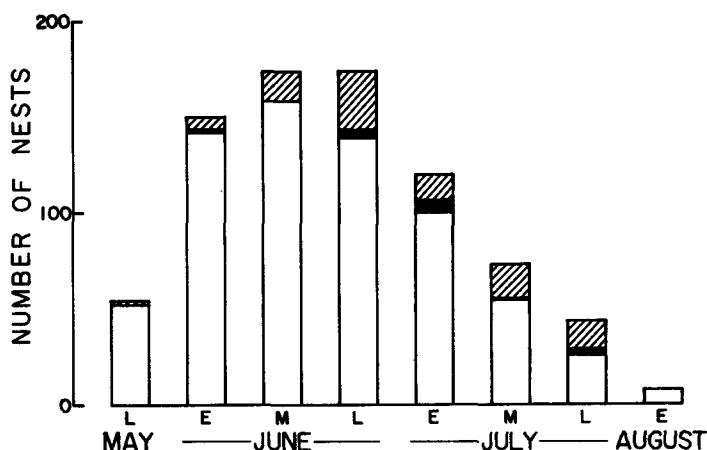


Fig. 4. The number of active nests and those of nests attacked by predators (hatched bar) or destroyed by bad weather (black bar) in each ten (or 11) day period. Data are pooled for five years.

norvegicus, snake *Elaphe quadrivirgata*, Chinese little bittern *Ixobrychus sinensis*, azure-winged magpie *Cyanopica cyana*, and carrion crow *Corvus corone*. Snakes and birds were the most likely predators because more than 70% of nests were attacked without being deformed or collapsed, nor were the reeds around the nests crushed. Five nests were parasitized by the common cuckoo.

The predation pressure on active nests clearly increased after mid June, and nest collapse caused by bad weather was concentrated in late June and early July (see Fig. 4). Mortality from unhatched, desertion, and other unknown factors showed no seasonal trend. The difference in survival rates from egg to fledging was caused by seasonal changes in predation and bad weather: the fledging rate of eggs laid from late May to mid June varied from 44.4 to 51.6%, while those from late June to early July varied from 26.1 to 29.3%.

c. Breeding success and mating status. The mean number of fledglings over five years was 3.19 for primary females, 2.41 for secondary females, and 2.80 for monogamous females. However, no significant difference was detected between the frequency distribution of any two mating statuses in the same year and between those in the pooled data (Kolmogorov-Smirnov two sample test at 5% significance level) (see Fig. 5).

The breeding success of females which initiated their first clutches in the same ten day period was compared in order to examine the relationship between breeding success and mating status. The breeding success of females mated with already mated males (i.e. secondary females) was not lower than that of females mated with unmated males (monogamous or primary females) (Table 6a), and females whose mates acquired additional females later (thus becoming primary females) did not show lower breeding success than females which monopolized their mates (monogamous females) (Table 6b) (Kolmogorov-Smirnov two sample test at 5% significance level). The breeding success of neither primary nor secondary females was lowered by sharing a male with another female.

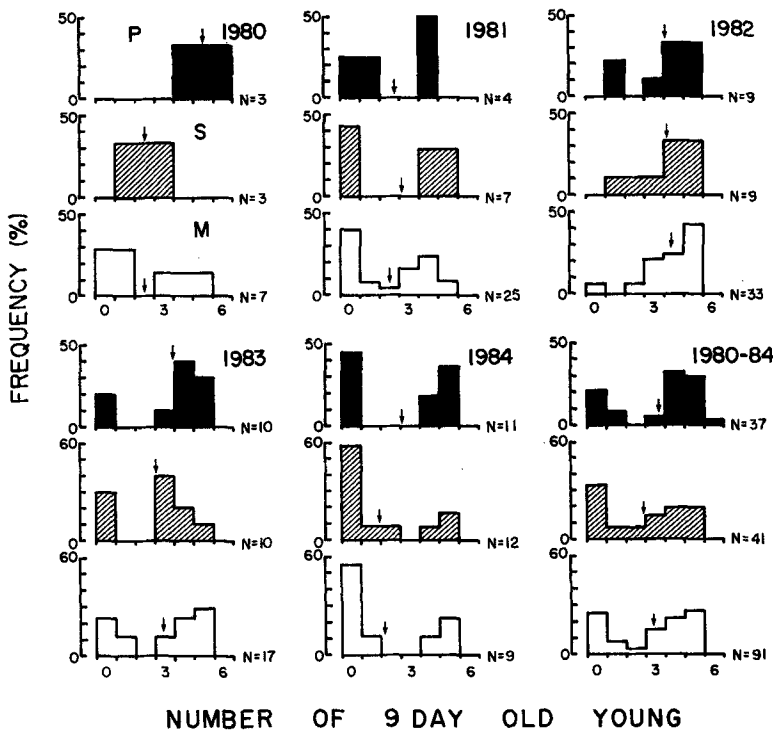


Fig. 5. Comparison of breeding success (number of young surviving on day 9) among the primary (black), secondary (hatched), and monogamous (white) females in each breeding season. Arrows and numerals show the mean number of young and the number of females examined, respectively. Since the females of case c (Table 3) are excluded, the distribution and the mean of monogamous females are slightly different from those of monogamous males (Fig. 6).

Polygynous males were more successful breeders than monogamous males with only 11.4% of the former having no fledglings compared with 30.1% of the latter ($\chi^2=5.895$, $P<0.02$; data pooled for five seasons). Polygynous males had a lower risk of breeding failure than monogamous males, and had twice as many fledglings (5.45 young compared with 2.57). The frequency distribution of the number of young per male was significantly different between polygynous and monogamous males (Kolmogorov-Smirnov two sample test: 1980, $D=1.00$; 1981, $D=0.465$; 1982, $D=0.800$; 1983, $D=0.778$; $P<0.05$) except in 1984 ($D=0.417$, NS) (see Fig. 6).

Table 6. Comparison of the mean number of young on day 9 between females of different categories which initiated their first clutches in the same ten day period. (a) secondary females vs. females mated with unmated males (i.e. primary and monogamous females), (b) primary vs. monogamous females. Mean (\pm): SD; Number of females.

| | 1980 | 1981 | 1982 | 1983 | 1984 |
|---------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| (a) secondary | 2.00 \pm 1.13 (3) | 2.57 \pm 2.55 (7) | 3.67 \pm 1.46 (9) | 2.50 \pm 1.89(10) | 1.42 \pm 2.07(12) |
| pri. & mono. | 2.80 \pm 2.31 (5) | 2.06 \pm 1.98(18) | 4.00 \pm 1.20(30) | 3.23 \pm 1.92(13) | 1.25 \pm 2.09(12) |
| (b) primary | 5.00 \pm 1.13 (3) | 2.25 \pm 2.24 (4) | 3.56 \pm 1.64(9) | 3.40 \pm 1.95(10) | 2.55 \pm 2.46(11) |
| monogamous | 1.40 \pm 2.21 (5) | 1.40 \pm 2.07 (5) | 3.96 \pm 1.43(25) | 3.00 \pm 2.11(14) | 1.57 \pm 2.47 (7) |

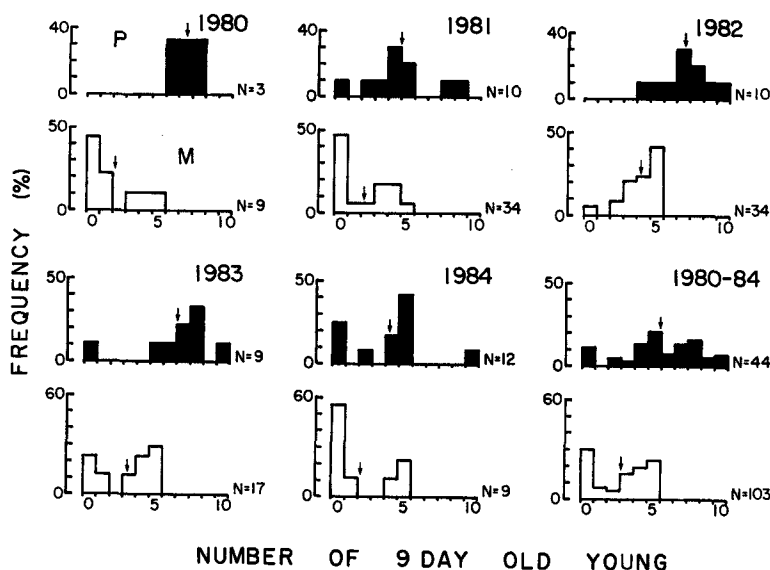


Fig. 6. Comparison of breeding success between polygynous (black) and monogamous (white) males in each breeding season. Arrows and numerals show the mean number of young and the number of males, respectively.

DISCUSSION

(1) The relationship between the chance of mating and the seasonal settling pattern for males

The present study shows that earlier settlers tended to be polygynous, while many bachelors were late settlers (Fig. 2 and Table 2), which is consistent with SAITOU (1976a), and that males which mated earlier were liable to be polygynous (Fig. 3). The seasonal settling pattern of the two sexes was prolonged with a peak in the first half of the period (Figs. 2 and 3, see also Fig. 7a). Males began to settle earlier than females, although 28–54% males settled at the same time as females (see Fig. 7a).

Male great reed warblers that are already mated begin to sing actively and can acquire a new mate again after a short (approximately a week) period of pair-formation and nest-building (KIKUCHI et al., 1957; HANEDA and TERANISHI, 1968a, b; URANO, unpublished), thus unmated males must compete for newly settling females with already mated males. Theoretically, the total number of territorial males could be the same as that of sexually active males. Therefore, the operational sex ratio (OSR) (EMLEN and ORING, 1977) at time t is given by dividing the number of newly settling females by the total number of territorial males (Fig. 7b). The OSR indicates the intensity of competition for acquiring a mate between males at time t (i.e. higher OSR means lower competition). Males which settled earlier have a long time for acquiring mates and suffer lower competition, while males which settled later have a shorter time with higher competition (see Fig. 7b).

To simplify the situation, let us assume that a male's chance of acquiring a mate is

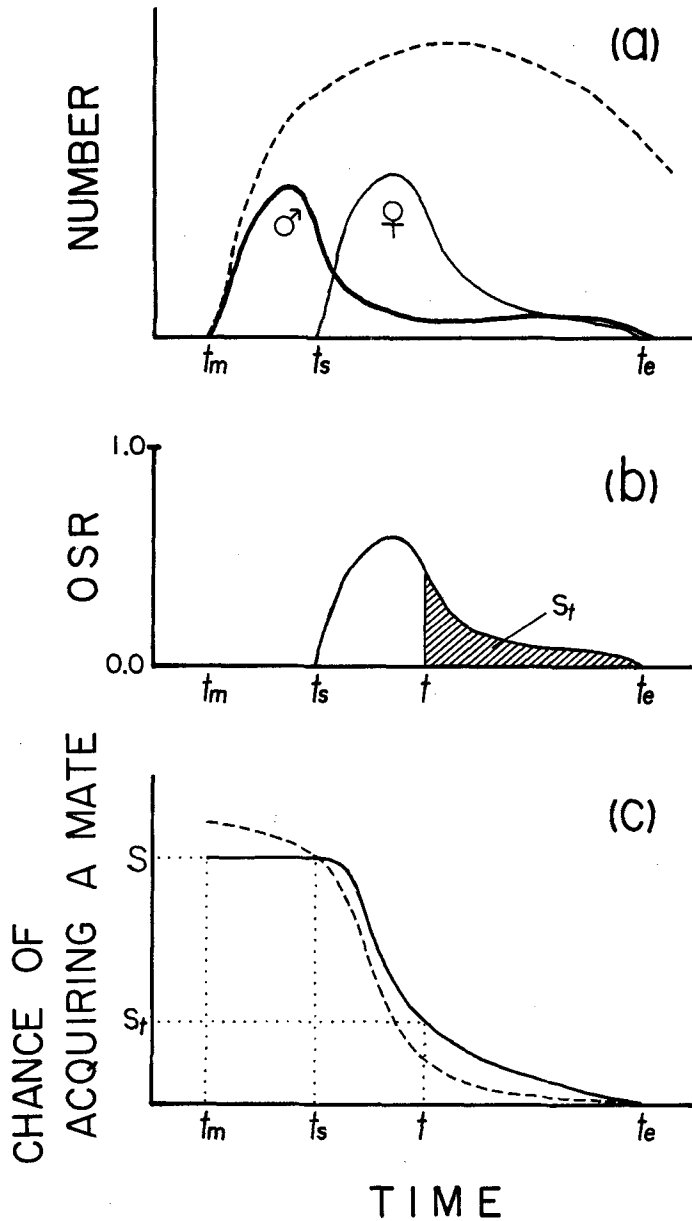


Fig. 7. Schematic representation of the seasonal change in the chance of mating. (a) The seasonal settling pattern of males and females (solid lines). t_m and t_s : time when the first male and female settled, respectively; t_e : time when the last female settled. The broken line indicates the total number of territorial males. (b) Seasonal change in the operational sex ratio. Hatched area (s_t) indicates the chance that a male settling at t can obtain a mate from t to t_e . (c) The chance that a male settled at t can acquire a mate during his residence. Solid line represents the case where the chance is dependent only on area s_t ; Broken line is the case when the chance is dependent on the male's quality as well as s_t .

proportional to the length of his residence and the extent of competition during residence. Under such a condition, a male which established his territory at time t has a chance equal to s_t (the hatched area in Fig. 7b), and males which established their territories before the onset of female settlement had an equal chance, S , the total area enclosed by the abscissa and the OSR curve in Fig. 7b, because the OSR from t_m to t_s is zero (See Fig. 7c).

Later settling males found it more difficult to acquire mates than those arriving earlier (see Figs. 2 and 7c). Males which mated earlier with their first mates can attempt to acquire second mates in the following period with a higher OSR. This means that males which mated earlier have a greater chance of acquiring second mates than males which mated later (see Fig. 3).

Many authors have pointed out the importance of the quality of a polygynous male's territory, in particular, favorable nesting habitat (SARTOU, 1976a; DYRCZ, 1977), near a good feeding site (PELTZER, 1972; DYRCZ, 1977), and of the quality of the males themselves, e.g. age (PELTZER, 1972; BEIER, 1981) and elaborate songs (CATCHPOLE, 1983). The quality of males and/or that of their territories depends on the timing of settlement, i.e. earlier settlers may secure territories with high quality (see SARTOU, 1976a) and older males tend to settle earlier than yearlings (URANO, unpublished). If females choose their mates on the basis of one or more of these qualities, the difference in the chance of acquiring a mate between early settlers and late settlers becomes larger (broken line in Fig. 7c), compared with the case shown by solid line. However, it is usually not easy to separate the relative contribution of these factors in the field.

(2) Breeding success

Mortality due to predation or adverse weather changed with the season, and was highest in the later part of the breeding season (Fig. 4). As predation was the main mortality factor of eggs and nestlings, the fledging rate of young also showed a seasonal decline according to the laying date. This means that late settling females breed under more disadvantageous conditions than earlier settlers. Some females which settled late in a breeding season were not new arrivals but had moved from other males' territories after unsuccessful breeding, as exemplified by female #720 in 1984. The slight difference in the breeding success between females of various mating status, i.e. primary \geq monogamy \geq secondary (Fig. 5), might be affected by the time of settlement (see Fig. 3).

The VERNER-WILLSON-ORIAN model (VERNER, 1964; VERNER and WILLSON, 1966; ORIAN, 1969) predicts that females of different mating status which settle at the same time should achieve equal fitness gains (see also GARSON et al., 1981). To examine the influence of polygyny on breeding success under the same breeding conditions, the breeding success of females which initiated their first clutch at the same time should be compared (GARSON et al., 1981). This study showed that the presence of another female in the same territory did not adversely affect the breeding success of either the primary or the secondary females (Table 6).

Since full clutches or full broods were often lost by predation, polygynous males

which had two or more broods could secure a larger number of offspring by spreading the risk of predation.

In this paper, the number of young counted on day 9 was used as an index of the breeding success for a breeding season. However, individual fitness is actually related to lifetime reproductive success (WITTENBERGER, 1979) and, in a strict sense, reproductive success should be equal to the number of young surviving to maturity. The data related to this problem, including males' parental role (which affects the females' cost of breeding), individual breeding success for successive years, survival rate of adults, and that of young until their first breeding season, will be discussed in forthcoming papers.

SUMMARY

Settlement date, mating status, and breeding success of individually marked great reed warblers, *Acrocephalus arundinaceus*, were studied during the 1980–84 breeding seasons in Kahokugata, Ishikawa Prefecture, Japan. Twenty-five per cent of the territorial males were polygynous, of which the majority were bigamous. The settling periods of both sexes were long, extending for 65 days in males and 49 days in females. About 80% of males and females settled in the first half of the settling period, and the settlement date of 28–54% males overlapped with that of females. Many of the late settlers were bachelors and the males which mated earlier tended to be polygynous. The timing of a male's settlement is important in acquiring mates. Fifty-five per cent of eggs laid were lost before fledging, mainly due to predation. The mean number of fledglings was 3.19 per primary female, 2.41 per secondary female, and 2.80 per monogamous female. Comparison of the number of fledglings of females which mated during the same period showed that the presence of another female in the same territory did not adversely affect the breeding success of either of the polygynous females. Polygynous males have the advantage of decreasing the risk of breeding failure under high predation pressure.

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オオヨシキリの一夫多妻と繁殖成績

浦野 栄一郎

- 1) 1980年から1984年の4月から8月にかけて、石川県河北潟干拓地のヨシ原でオオヨシキリの繁殖個体群を調査した。期間中に826個体に標識を着け、調査地内に定着した各個体について定着時期、なわばりの位置、配偶関係、繁殖成績を記録した。
- 2) なわばり雄の25%は一夫多妻（二妻または三妻）、56%は一夫一妻であった。14%の雄はなわばりを持ちながら雌を得られなかった。
- 3) 調査地への新たな個体の定着は、長期間におよんだ（雄-平均65日間、雌-平均49日間）が雄、雌とも約80%の個体はその前半に定着した。雌の定着開始前に、雄の46-72%はなわばりを確立していた。
- 4) 雄のなわばりへの定着時期が配偶者獲得に大きく影響した。早い時期に1羽の雌を得た雄は一夫多妻になりやすく、一方、定着が遅い雄では、配偶者を得られないものが多かった。
- 5) 総産卵数（1093卵）の54%が巣立ち以前に、主に捕食によって死亡・消失した。
- 6) 雌当りの巣立ち雛数は一夫多妻第一雌3.19羽、第二雌2.41羽、一夫一妻雌2.80羽であった。巣立ち雛数を同じ時期に産卵開始した雌の間で比較したところ、同じ雄と番う他の雌が存在しても、第一雌も第二雌も繁殖成績が低下しなかった。
- 7) 繁殖期を通じて雛を1羽も巣立たせられなかった雄の割合は、一夫一妻雄(30.1%)の方が多妻雄（11.4%）より高かった。高い捕食圧の下での雛の全滅を避け、より確実に雛を巣立たせるには、一夫多妻になることが雄にとって有利と考えられる。

Appendix. Life tables of eggs and nestlings for each mating status of female.

(1) 1980

| Stage | Cause of change in numbers* | Mating status of females | | | | | | | | | | | |
|----------------|-----------------------------|--------------------------|----------|----------|-----------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost** | L_x *** | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 16 | | | 100.0 | 18 | | | 100.0 | 63 | | | 100.0 |
| | unhatched | | — | — | | | 2 | 11.1 | | | 1 | 1.6 | |
| | predation | | — | — | | | 1 | 5.6 | | | 16 | 25.4 | |
| | desertion | | — | — | | | 1 | 5.6 | | | — | — | |
| | unknown | | — | — | | | 1 | 5.6 | | | 2 | 3.2 | |
| | total | | — | — | | | 5 | 27.8 | | | 19 | 30.2 | |
| Egg hatched | | 16 | | | 100.0 | 13 | | | 72.2 | 44 | | | 69.8 |
| | predation | | — | — | | | 3 | 23.1 | | | 17 | 38.6 | |
| | weather | | — | — | | | — | — | | | 5 | 11.4 | |
| | unknown | | 1 | 6.3 | | | 4 | 30.8 | | | 8 | 18.2 | |
| | total | | 1 | 6.3 | | | 7 | 53.8 | | | 30 | 68.2 | |
| Young on day 9 | | 15 | | | 93.8 | 6 | | | 33.3 | 14 | | | 22.2 |

* cause of change in numbers are defined in Methods (4).

** % lost in nestling period is shown in terms of eggs hatched.

*** L_x indicates % survival in terms of eggs.

(2) 1981

| Stage | Cause of change in numbers | Mating status of females | | | | | | | | | | | |
|----------------|----------------------------|--------------------------|----------|--------|-------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 43 | | | 100.0 | 38 | | | 100.0 | 203 | | | 100.0 |
| | unhatched | | — | — | | | 2 | 5.3 | | | 14 | 6.9 | |
| | predation | | 15 | 34.9 | | | 1 | 2.6 | | | 31 | 15.3 | |
| | weather | | — | — | | | 4 | 10.5 | | | — | — | |
| | desertion | | 2 | 4.7 | | | — | — | | | 4 | 2.0 | |
| | unknown | | — | — | | | 2 | 5.3 | | | 16 | 7.9 | |
| | total | | 17 | 39.5 | | | 9 | 23.7 | | | 65 | 32.0 | |
| Egg hatched | | 26 | | | 60.5 | 29 | | | 76.3 | 138 | | | 68.0 |
| | predation | | 12 | 46.2 | | | 7 | 24.1 | | | 58 | 42.0 | |
| | weather | | — | — | | | — | — | | | 11 | 8.0 | |
| | unknown | | 5 | 19.2 | | | — | — | | | 11 | 8.0 | |
| | total | | 17 | 65.4 | | | 7 | 24.1 | | | 80 | 58.0 | |
| Young on day 9 | | 9 | | | 20.9 | 22 | | | 57.9 | 58 | | | 28.6 |

(3) 1982

| Stage | Cause of change in numbers | Mating status of females | | | | | | | | | | | |
|----------------|----------------------------|--------------------------|----------|--------|-------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 57 | | | 100.0 | 45 | | | 100.0 | 164 | | | 100.0 |
| | unhatched | | 6 | 10.5 | | | 4 | 8.9 | | | 8 | 4.9 | |
| | predation | | 3 | 5.3 | | | 4 | 8.9 | | | 4 | 2.4 | |
| | unknown | | 3 | 5.3 | | | 1 | 2.2 | | | 1 | 0.6 | |
| | total | | 12 | 21.1 | | | 9 | 20.0 | | | 13 | 7.9 | |
| Egg hatched | | 45 | | | 78.9 | 36 | | | 80.0 | 151 | | | 92.1 |
| | predation | | 3 | 6.7 | | | — | — | | | 14 | 9.3 | |
| | weather | | 5 | 11.1 | | | — | — | | | — | — | |
| | unknown | | 5 | 11.1 | | | 2 | 5.6 | | | 8 | 5.3 | |
| | total | | 13 | 28.9 | | | 2 | 5.6 | | | 22 | 14.6 | |
| Young on day 9 | | 32 | | | 56.1 | 34 | | | 75.6 | 129 | | | 78.7 |

(4) 1983

| Stage | Cause of change in numbers | Mating status of females | | | | | | | | | | | |
|----------------|----------------------------|--------------------------|----------|--------|-------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 61 | | | 100.0 | 61 | | | 100.0 | 105 | | | 100.0 |
| | unhatched | | 1 | 1.6 | | | 1 | 1.6 | | | 5 | 4.8 | |
| | predation | | 10 | 16.4 | | | 13 | 21.3 | | | — | — | |
| | cuckoo | | 1 | 1.6 | | | — | — | | | 1 | 1.0 | |
| | weather | | 5 | 8.2 | | | — | — | | | 4 | 3.8 | |
| | desertion | | — | — | | | — | — | | | 5 | 4.8 | |
| | unknown | | 2 | 3.3 | | | 3 | 4.9 | | | 3 | 2.9 | |
| | total | | 19 | 31.1 | | | 17 | 27.9 | | | 18 | 17.1 | |
| Egg hatched | | 42 | | | 68.9 | 44 | | | 72.1 | 87 | | | 82.9 |
| | predation | | 2 | 4.8 | | | 15 | 31.8 | | | 20 | 23.0 | |
| | cuckoo | | 1 | 2.4 | | | — | — | | | — | — | |
| | weather | | — | — | | | — | — | | | 10 | 11.5 | |
| | unknown | | 5 | 11.9 | | | 4 | 11.4 | | | 8 | 9.2 | |
| | total | | 8 | 19.0 | | | 19 | 43.2 | | | 38 | 43.7 | |
| Young on day 9 | | 34 | | | 55.7 | 25 | | | 41.0 | 49 | | | 46.7 |

(5) 1984

| Stage | Cause of change in numbers | Mating status of females | | | | | | | | | | | |
|----------------|----------------------------|--------------------------|----------|--------|-------|-----------|----------|--------|-------|------------|----------|--------|-------|
| | | Primary | | | | Secondary | | | | Monogamous | | | |
| | | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x | No. | No. lost | % lost | L_x |
| Egg | | 86 | | | 100.0 | 71 | | | 100.0 | 62 | | | 100.0 |
| | unhatched | | 2 | 2.3 | | | — | — | | | — | — | |
| | predation | | 20 | 23.3 | | | 17 | 23.9 | | | 15 | 24.2 | |
| | cuckoo | | — | — | | | 4 | 5.6 | | | — | — | |
| | weather | | 3 | 3.5 | | | 5 | 7.0 | | | — | — | |
| | desertion | | — | — | | | 2 | 2.8 | | | — | — | |
| | unknown | | 5 | 5.8 | | | 3 | 4.2 | | | 2 | 3.2 | |
| | total | | 30 | 34.9 | | | 31 | 43.7 | | | 17 | 27.4 | |
| Egg hatched | | 56 | | | 65.1 | 40 | | | 56.3 | 45 | | | 72.6 |
| | predation | | 16 | 28.6 | | | 18 | 45.0 | | | 21 | 46.6 | |
| | weather | | 8 | 14.3 | | | — | — | | | — | — | |
| | unknown | | 4 | 7.1 | | | 5 | 12.5 | | | 9 | 20.0 | |
| | total | | 28 | 50.0 | | | 23 | 57.5 | | | 30 | 66.7 | |
| Young on day 9 | | 28 | | | 32.6 | 17 | | | 23.9 | 15 | | | 24.2 |