Asynchronous Hatching, Growth and Survival of Chicks of the Cattle Egret *Bubulcus ibis*

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アマサギ (*Bubulcus ibis*) における非同時孵化と ひなの成長・生残

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Asynchronous hatching is a prevalent phenomenon in altricial or semi-precocial birds. It has been found that in many bird species all eggs but one laid last hatch simultaneously while the last egg hatches a day later (CLARK & WILSON, 1981). Some large birds, e.g. herons, eagles, owls and crows, which have long nestling periods, show much more extended asynchrony in hatching (see CLARK & WILSON, 1981 for a review of asynchrony in hatching). Most of these large birds are piscivorous or carnivorous, with several insectivorous and carrion species. Since LACK's proposal (1947: 324, 1954: 40) asynchronous hatching has generally been interpreted as an adaptation by which brood size can be adjusted to food availability; when food is scarce, the youngest chick in a brood dies of starvation thus avoiding total loss, but when food is plentiful, all chicks are raised (e.g. OWEN, 1960; RICKLEFS, 1965; HAHN, 1981).

According to TRIVERS' (1974) theory, parents and offspring are expected to disagree over the egoistic tendencies of the offspring such as sibling competition for food insofar as these tendencies affect related individuals, i.e. affect inclusive fitness of the parent and offspring. However, there has been a controversy over the existence of parent-offspring conflict during LACK's process of brood reduction, i.e. the partial loss of a brood due to food shortage (O'CONNOR, 1978 vs HAHN, 1981). In this controversy and in other studies of brood reduction in asynchronous hatching birds, it has been postulated tacitly that asynchrony in hatching is manipulated by the parent, despite a dearth of quantitative studies on the process of asynchronous hatching (but see INOUE, 1980). The first aim of this study is to present evidence that asynchrony in hatching in the Cattle Egret *Bubulcus ibis* is determined by the behavior of parents, i.e. the early onset of effective incubation.

Asynchronous hatching apparently results in differential growth and survival rates among siblings under normal or poor food conditions in various bird species (see HAHN, 1981 for a review). The second aim of this paper is to describe general tendencies in growth and survival of Cattle Egret chicks as a function of hatching order. Growth and survival rates of junior chicks are shown to be lower than those of senior siblings and to be much higher in this population than those reported from other populations of Cattle Egrets.

Only growth and survival data are insufficient to elucidate the overall mechanism, significance of asynchronous hatching, and parent-offspring conflict in the Cattle Egret. Feed-

ing behavior, sibling competition and siblicide, which produce these differential growth and survival rates, and an experiment producing even-aged broods will be reported elsewhere with detailed discussion (FUJIOKA, in press, in prep).

STUDY AREA AND METHODS

Breeding biology of Cattle Egrets was studied in a mixed-species heronry at Suzuka City, Mie Prefecture, central Japan (34°50'N, 136°35'E). The data reported here were collected during May to July, 1978 and June to July, 1982. The heronry has been in existence for many years on a small island (50×300 m) in the Ishigaki Pond (ca. 400 m in diameter and 20 m above sea level). Herons nested 2 to 7 m above the ground in crowns and branches of various evergreens, especially Japanese black pines *Pinus thunbergii*, which cover most of the island. The heronry consisted of more than 500 breeding pairs in 1978 and about 250 pairs in 1982 of four species of egrets: Cattle Egrets, Great Egrets *Egretta alba*, Little Egrets *E. garzetta*, and Intermediate Egrets *E. intermedia*, together with many Black-crowned Night Herons *Nycticorax nycticorax*.

Egg-laying and incubation behavior were directly observed from a blind in 1978. The blind was constructed atop of a 3.6 m high scaffold at a distance of 7 to 9 m from observed nests (FUJIOKA & YAMAGISHI, 1981: Fig. 1). Day-time observations usually began just after sunrise and continued until about 30 min after sunset, for a total of 450.5 h in 33 days between 10 May and 20 July 1978 (a total of 751.3 nest-h). Five or fewer nests within a single range of observation were simultaneously observed with the unaided eye or with binoculars (9×35).

In 1978, 43 nests were inspected every day during the laying and hatching periods, and every 2–7 days during the incubation and nestling periods. Each inspection included counting eggs and/or chicks and measuring chick body weight (to the nearest gram on a Pesola spring-balance) and "tarsus length" (from the junction of the tibiotarsus with the tarsometatarsus including the joint of the former to the junction of the latter with the phalanges, by a caliper accurate to 0.5 mm; after OSAWA, 1968). Inspections continued until chicks were about 2–3 weeks old, when their ability to escape prevented accurate counts. Young Cattle Egrets required about 50–80 days to become independent (FUJIOKA, in press).

In 1982, 50 nests with complete clutches were inspected every 3–5 days to verify the number of eggs and/or chicks. In 12 nests out of the 50, the hatching dates of the chicks were experimentally synchronized. The results of the experiment will be reported elsewhere (FUJIOKA, in prep). To minimize disturbance by the observer, measurement in 38 asynchronously hatching nests (31 unmanipulated nests and 7 nests in which one or two chick(s) were exchanged with one(s) of another nest) was restricted to the tarsus length on the 15th day after the first chick hatched.

Nests were usually visited at sunrise, when regurgitation by chicks was minimal. All the eggs and chicks investigated were marked individually with colored felt-tip pens or with alcohol-based dyes as soon as they were discovered. The chicks were later banded with colored leg-rings when they reached about 10 days old. A total of 77.8 h in 74 days in 1978 and 33.3 h in 52 days in 1982 were spent for such inspection.

Broods (and nests) are named with capitals in 1978 and with Roman numerals in 1982. Laying sequence of eggs and hatching sequence of chicks are denoted in alphabetical order, such as *a*, *b*, and so forth. Brood size is abbreviated to B/3 (broods with three chicks), B/4, and so forth.

RESULTS

(1) Egg-laying

In 1978 the average clutch size was 4.34 in 35 marked nests which were inspected daily throughout the egg-laying period (Table 1). Egg-laying was directly observed only three times: at 0441 and 0515 hours in one nest and at 0554 hours in another. Most egg-laying had occurred already when daily observations from the blind began. Thus it seems that female Cattle Egrets laid eggs mostly in the early morning. By contrast, female Little Egrets have been reported to lay eggs at various times of day at an interval of about 1.5 days (INOUE, 1980). The interval between laying of consecutive eggs (hereafter referred to as "laying interval") for the Cattle Egret in the study area was usually 2 (70.3%) and sometimes 3 days (21.0%) (Table 2).

Table 1. Clutch and brood sizes of Cattle Egrets at Suzuka heronry, central Japan.

Clutch size was obtained by daily visits to nests during the egg-laying period.

Brood size is the number of chicks hatched.

	Number of eggs or chicks							Total	Mean	SD
	1	2	3	4	5	6	7			
Clutch size, 1978		2	6	11	11	4	1	35	4.34	1.16
Brood size, 1978	2	5	12	16	4			39	3.38	1.02
Brood size, 1982	1	8	16	21	3	1		50	3.40	0.97

Table 2. Laying intervals in 1978.

Sequence of egg-laying	Intervals in days						Total	Mean	SD
	1	2	3	4	8	12			
1st-2nd		13	1	2			16	2.3	0.7
2nd-3rd		16	2			1 ¹	19	2.1	0.3
3rd-4th		9	6				15	2.4	0.5
4th-5th	1 ²	6	3				10	2.2	0.6
5th-6th		1	2				3	2.7	0.6
6th-7th					1 ¹		1	—	—
Total	1	45	14	2	1 ¹	1 ¹	64	2.3	0.5

¹ Intervals over five days are excluded from the calculation of mean values. These long intervals may be due to a change of female (pers. obs.; MOCK, pers. comm.).

² This may be because an egg was laid immediately after a nest visit and two days later the next egg was laid immediately before the day's visit.

Intervals of three days or longer tended to occur during the latter half of the egg-laying period (Table 2). These intervals accounted for 17.1% ($N=35$) of laying intervals up to the laying of *c*-egg and for 41.4% ($N=29$) after laying of *c*-egg ($\chi^2=4.61$, 1 df, $P<0.05$).

Egg-laying was not investigated in 1982.

(2) Incubation

Both sexes of the Cattle Egret incubated to the same degree, which is typical of ardeids (PALMER, 1962; BLAKER, 1969; JENNI, 1969; INOUE, 1980). Like many other large birds, such as raptors and owls, Cattle Egrets initiated incubation before the clutch was complete, and even before the first egg was laid ("sham incubation"; MILSTEIN *et al.* 1970: 207). Fig. 1 shows the incubation rate, expressed as a percentage of net incubation time in a day

Fig. 1. Daily variation in incubation rates of five pairs in 1978. The rate is the percentage of net incubation time by both parents per observation time for the pair in a day (after INOUE, 1980). See FUJIOKA & YAMAGISHI (1981) for the description of the pairs.

(after INOUE, 1980). In the Cattle Egret, full time incubation, which is defined as about more than 80% of incubation rate, began just before or with the laying of the first egg. The average incubation period for a single egg (including the laying day and excluding the hatching day) in 1978 was 24.1 ± 0.9 SD days with a range of from 22 to 27 days ($N=49$ eggs).

(3) Hatching

Eggs always hatched in the same order as they were laid. Two day intervals were the most common (54.4%) in hatching of consecutive eggs in 1978 (Fig. 2). As with laying, hatching intervals of three days or longer tended to appear during the latter half of the brood's hatching period. These intervals accounted for 7.7% ($N=52$) of the intervals up to the hatching of *c*-egg and for 37.0% ($N=27$) after then ($\chi^2=8.58$, 1 df, $P<0.01$). In

Fig. 2. Time intervals between hatching of consecutive eggs in 1978 (left bar) and those of consecutive chicks in 1982 (right bar). White parts=intervals between *a-b* and *b-c*. Shaded parts=*c-d*, *d-e*, and *e-f*.

Fig. 3. Comparison between egg-laying and egg-hatching intervals in 1978. Mean values of hatching intervals minus laying ones of the two same consecutive eggs are compared with $\pm$ SD and $\pm$ SE.

1982, hatching intervals between two consecutively hatched chicks, not between hatching of consecutively laid eggs, were investigated (Fig. 2). The distribution of hatching intervals in 1982 was similar to that in 1978. Three-day-or-longer intervals accounted for 18.7% ($N=19$) of intervals up to the hatching of *c*-chick and 45.8% ($N=24$) after then ($\chi^2=7.60$, 1 df, $P<0.01$). As mentioned above, these tendencies coincide with those in the egg-laying intervals.

Hatching intervals tended to be slightly shorter than egg-laying intervals in "senior" (*a-c*) eggs and to be similar to egg-laying intervals in "junior" (*d-f*) eggs (Fig. 3). Such a tendency may be due to a gradual increase in time spent on incubation, as shown in Fig. 1.

Brood size is defined as the number of all chicks hatched in a brood. The average brood sizes were 3.38 in 39 nests which had at least one chick in 1978 and 3.40 in 50 nests in 1982 (Table 1). It took 6.3 days on an average for an entire brood to hatch, with a maximum of 16 days (Table 3).

Table 3. Hatching spread in relation to brood size. Data for 1978 and 1982 are combined.

Brood size	Hatching spread in days										Total	Mean	SD
	1	2	3	4	5	6	7	8	9	10+			
1	2										2	1.0	—
2	1	2	2	1		1					7	3.0	1.6
3			1	5	8	5	3	1	1	1	25	5.9	2.5
4					3	9	14	4		2	32	7.0	1.8
5								2	1	3	6	10.5	3.0
Total	3	2	3	6	11	15	17	7	2	6	72	6.3	2.8

(4) Growth

On hatching day (day 0) chicks weighed a mean of $21.1 \text{ g} \pm 3.0 \text{ SD}$ ($N=70$) and their tarsus lengths measured a mean of $18.94 \text{ mm} \pm 0.92 \text{ SD}$ ($N=69$) in 1978. Hereafter, tarsus length rather than body weight is used as an index of growth because body weight tended to vary

Fig. 4. Growth of chicks in 1978 (a solid broad line) and 1982 (symbols). In 1982 measurements were made only once at 15 days old of *a*-chick in each brood. Two regression lines are shown; the thin line is for the last chicks in B/3 and B/4 in 1978 and the broken line is for those in 1982.

within a day. Chicks grew rapidly during the first 20 days after hatching (Fig. 4). In average broods, *a*-chick had already grown to about 35 mm in tarsus length and 70 g in body weight when the last chick hatched.

In 1978, chick growth described a nearly straight line during the measurement period, i.e. the first 20 days of the whole 50–80 days nestling period (Fig. 4). Thus growth rates could be represented by the linear regression formula in relation to brood size and hatching sequence (Table 4). The senior chicks grew almost equally, irrespective of brood size. The growth rates of the youngest chicks in B/2 and B/3 were identical with those of *a*-

Table 4. Growth rates¹ of chicks in 1978 in relation to brood size and hatching sequence.

Chicks	Brood size				
	1	2	3	4	5
<i>a</i>	3.17 (16)	3.30 (37)	3.18 (58)	3.19 (97)	3.23 (32)
<i>b</i>	—	3.12 (38)	3.34 (56)	3.02 (96)	3.29 (31)
<i>c</i>	—	—	3.28 (50)	3.02 (74)	3.38 (30)
<i>d</i>	—	—	—	2.63 (67)	3.39 (15)
<i>e</i>	—	—	—	—	2.53 (15)
No. brood	2	5	11	16	4

¹ Since the growth of chicks was linear during the 1978 measurement period, the rate is shown as the value of *B* in the formula $Y=A+BX$, where *X* is an age in days and *Y* is tarsus length in mm on the day. The numbers of measurements are expressed in parentheses. Total: $Y=16.82+3.18 X (N=717)$.

chicks, whereas the growth rates of the youngest chicks in B/4 and B/5 were conspicuously lower. Intermediate chicks grew at almost the same rate as *a*-chicks. The cause of the unexpectedly large overall growth values in B/5 was unclear. In one B/5 three adults supplied the chicks with food (FUJIOKA, in press).

All 4 *e*-chicks in B/5 showed low growth rates; the correlation coefficient in the linear regression was high (0.977). By contrast, the growth rate of *d*-chicks in B/4 varied, with a coefficient (0.936) smaller than the range of coefficients for the other 13 categories (0.972–0.995). Fig. 5 shows 4 typical examples of growth curves for B/4, in which the chicks were frequently measured. All chicks fledged in broods T and iii. In brood W, *d*-chick was killed by older siblings (sibicide) at the age of about 26 days (FUJIOKA, in press). *D*-chick in brood xiii was dead in the nest on the 4th day from hatching and *c*-chick disappeared at the age of 8 days.

Fig. 5. Growth curves in four typical broods of four chicks. Italics mean the hatching order of the chick. Solid circles indicate the date of hatching.

In 1982, the mean tarsus length of *a*-chicks was almost identical with that of all chicks in 1978 at 15 days old (Fig. 4), while the youngest chicks in B/3 and B/4 in 1982 tended to grow more slowly than those youngest chicks in 1978 (Fig. 4). The growth rate per day of these last chicks, calculated from the linear regression formula, was 2.67 mm with a correlation coefficient of 0.85 ($N=25$), which indicates both a low growth rate and a large individual variation.

(5) Survival

Table 5 gives survival rates of chicks to the age of 14 days in relation to brood size and hatching sequence in 1978. Survival rates of chicks could not be determined precisely by nest inspection, because all chicks older than about 10 days scrambled out of their nests on

Table 5. Numbers of survivors and survival rates (% in parentheses) of chicks before 15 days old in 1978.

Chicks	Brood size					Total
	1	2	3	4	5	
<i>a</i>	2 (100.0)	5 (100.0)	10 (83.3)	13 (86.7)	4 (100.0)	34 (89.5)
<i>b</i>	—	5 (100.0)	12 (100.0)	14 (93.3)	4 (100.0)	35 (97.2)
<i>c</i>	—	—	11 (91.7)	12 (80.0)	4 (100.0)	27 (87.1)
<i>d</i>	—	—	—	12 (80.0)	3 (75.0)	15 (78.9)
<i>e</i>	—	—	—	—	2 (50.0)	2 (50.0)
No. of brood	2	5	12	15 ¹	4	38
Total no. of survivors	2 (100.0)	10 (100.0)	33 (91.7)	51 (85.0)	17 (85.0)	113 (88.3)
Survivors per nest	1.0	2.0	2.8	3.4	4.3	3.0

¹ One total brood failure owing to predation is excluded.

the approach of a human. One brood (D) with four chicks was excluded from Table 5 since it was completely destroyed by a predator (probably by a snake *Elaphe climacophora*, which I saw several times in the vicinity). The survival rate of Cattle Egret chicks in the study area (mean=88.3%) was relatively high compared with the reported survival rates in earlier studies, in which most junior chicks died of starvation during the early stage of the nestling period (SKEAD, 1966; BLAKER, 1969 and Siegfried 1972 for the Cattle Egret; OWEN, 1960 for the Grey Heron).

In this study deaths amongst *d*- and *e*-chicks were more frequent than amongst older chicks (Table 5). Most of the senior chicks which died probably did so after falling from the nest, either because of the inability to climb back to it (WERSCHKUL, 1979), or because of lethal harassment by unrelated adults of several species in the colony (BLAKER, 1969: 121), usually during nest visits by the author. The number of survivors per nest was highest for B/5. However, it should be noted that examination of the survival rate was restricted to only 14 days of the nestling period, which lasted 50 to 80 days. Junior chicks in B/4 or B/5 were more likely to die owing to siblicide after the measurement period (FUJIOKA, in press).

The survival rate for 1982 nests was calculated differently from that for 1978 ones because nests were visited for measurements only once, when *a*-chick was 15 days old but the last sibling was much younger. Color-ringed chicks known to have survived more than 40 days were categorized as "survivors" and chicks found dead in the nest or on the ground in the heronry were categorized as "fatalities." All others were "missing." Table 6 gives the number of survivors, fatalities, and missing chicks, together with survival rates (the percentage of survivors to chicks known whether survived or not) in relation to brood size and hatching sequence. The total survival rate (85.9%) was relatively high compared with other reports but agreed closely with my 1978 data from this heronry. However, missing chicks probably included dead chicks more than known chicks because survivors were found more easily than fatalities. The minimum survival rate, i.e. the number of survivors per all hatched chicks was 60.3%.

In B/3 and B/4, the youngest chicks appear to show high survival rates, but there were more missing chicks among them than among older chicks. In B/5 or B/6, all of the dead or mis-

Table 6. Numbers of survivors, fatalities, and missing chicks with survival rates¹ (% in parentheses) in 1982.

Chicks	Brood size						Total
	1	2	3	4	5	6	
<i>a</i>	0-1-0 (0.0)	3-1-1 (75.0)	9-0-3 (100.0)	10-1-6 (90.9)	2-0-0 (100.0)	1-0-0 (100.0)	25-3-10 (89.3)
<i>b</i>	—	2-0-3 (100.0)	9-1-2 (90.0)	10-1-6 (90.9)	2-0-0 (100.0)	1-0-0 (100.0)	24-2-11 (92.3)
<i>c</i>	—	—	5-2-5 (71.4)	11-1-5 (91.7)	2-0-0 (100.0)	1-0-0 (100.0)	19-3-10 (86.4)
<i>d</i>	—	—	—	7-3-7 (70.0)	2-0-0 (100.0)	1-0-0 (100.0)	10-3-7 (76.9)
<i>e</i>	—	—	—	—	0-1-1 (0.0)	1-0-0 (100.0)	1-1-1 (50.0)
<i>f</i>	—	—	—	—	—	0-1-0 (0.0)	0-1-0 (0.0)
No. brood	1	5	12	17	2	1	38
Total	0-1-0 (0.0)	5-1-4 (83.3)	23-3-10 (88.5)	38-6-24 (86.4)	8-1-1 (88.9)	5-1-0 (83.3)	79-13-39 (85.9)

¹ Survival rates=survivors/(survivors+fatalities) at the age of more than 40 days after hatching.

sing chicks were the youngest.

(6) Mortality causes

Of 128 chicks from 38 broods in 1978, 15 died before day 15. One chick fell out of the nest at the time of nest inspection and then disappeared. In two cases (*d*-chicks in B/5 and B/4), their remains were found in the nest on day 4; the probable cause of their death was starvation. Of the other 12 chicks, seven disappeared before day 9 when they could not walk out of the nest at all, and five disappeared between days 10 and 14. The former were likely to have died of starvation and to have been carried out of the nest by the parent (three practical scenes were observed for Little Egrets). The latter five chicks seemed to have died from falling out of the nest. However, the possibility that they were killed by snakes or crows could not be eliminated.

In 1982, a total of 13 fatalities out of 131 chicks in 38 asynchronously hatching broods were found. Of these 13 mortalities, five were due to falling from the nest at nest inspection. The other eight chicks died of natural causes; six of starvation, one of desertion by its parents, and one showed signs of sickness about its eyes. Out of the six starved chicks, *b*- and *c*-chicks in a brood died after a typhoon and four were the youngest chick in each of B/4, B/5 and B/6.

DISCUSSION

(1) Asynchronous hatching

The hatching interval in the Cattle Egret appears to depend on both the egg-laying interval and the pattern of starting incubation (Table 2, Figs. 1 to 3). In the Little Egret 1.5 day-intervals of egg-laying and later onset of incubation result in a short hatching period (1-6 days) (INOUE, 1980). In the Cattle Egret, at least 2 day-intervals of egg-laying (Table 2) and the commencement of full incubation at the time of the first laying (Fig. 1) yielded a long hatching period, averaging 6.3 days (152 h) with a maximum of 16 days (Table 3). Thus this species shows one of the most extreme asynchronous hatching patterns

known for birds (see CLARK & WILSON, 1981 for a review of hatching spread). Furthermore, egg-laying intervals and, as a result, hatching intervals tended to elongate in order of laying or hatching (Table 2; Figs. 2 and 3). This tendency is more conspicuous in the Little Egret (INOUE, 1980). It is possible that such a hatching pattern facilitates the death of junior chicks and reduces the death of senior chicks.

(2) Growth and survival

As a result of such asynchronous hatching, the growth and survival rates of junior chicks in large broods (four chicks or more) were lower than those of senior siblings (Tables 4 to 6, Figs. 4 & 5). Presumably most of the natural mortality causes were starvation (excluding causes such as falling from the nest, which were influenced by human disturbance). All deaths from starvation and siblicide occurred amongst the youngest chicks in large broods.

In this study, however, both the first and intermediate chicks grew and survived favorably (Tables 4-6, Fig. 4). Even *d*-chicks usually survived to two weeks old (Table 5). On the contrary, SKEAD (1966), BLAKER (1969) and SIEGFRIED (1972) reported that the great majority of junior chicks of African Cattle Egrets died of starvation before reaching 15 days old. Therefore, the condition of food resources around the study area seems likely to have been highly favorable, at least during the two breeding seasons studied.

The large clutch size in this heronry may also imply the availability of a good food supply in the surrounding area for several recent years. The average clutch size in 1978 (4.31) is considerably larger than that for the Cattle Egret reported by other authors: 3.67 (VALENTINE, 1958), 3.5 (JENNI, 1969), 2.42 (DUSI & DUSI, 1970), 2.86 (WEBER, 1975), and 3.0 (MAXWELL & KALE, 1977) in various regions of the southern USA; 2.6 in Ghana (BOWEN *et al.*, 1962), and 2.86 in South Africa (BLAKER, 1969). However, it should also be noted that the clutch size of many birds tends to be large both at higher latitudes (LACK, 1947, 1968) and in colonizing areas (see JENNI, 1969 for further discussion on regional variation in clutch size of the Cattle Egret).

The greater mortality and/or the delayed growth of junior chicks have been reported for many asynchronously hatching species (see HAHN, 1981 for a review; OWEN, 1960; BLAKER, 1969; JENNI, 1969; SIEGFRIED, 1972; WERSCHKUL, 1979, and INOUE, 1981 for herons; NISBET & COHEN, 1975 for terns; PARSONS, 1975, and HAHN, 1981 for gulls; LOCKIE, 1955; SELANDER, 1960; RICKLEFS, 1965; SEEL, 1970; DYRCZ, 1974; BALPH, 1975, and HOWE, 1976 for passerines). This phenomenon has generally been explained as a mechanism for brood reduction in habitat with unpredictable food resources ("the brood reduction hypothesis," LACK, 1947, 1954; O'CONNOR, 1978).

Population densities of grasshoppers (the most important food of Cattle Egrets) vary greatly geographically (e.g. EDWARDS, 1964). In the study area, however, Cattle Egrets foraged on grasshoppers and frogs mostly in paddy fields, which are created suddenly at the start of the breeding season (pers. obs.) and which provide an artificially stable habitat throughout the breeding season. This unnatural condition may result in the large clutch size and the high growth and survival rates in this study area.

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SUMMARY

(1) Asynchronous hatching, growth and survival of chicks in the Cattle Egret *Bubulcus ibis* were studied at a heronry in central Japan in 1978 and 1982.

(2) The average clutch size was 4.34 in 35 marked nests (studied only in 1978). Eggs were laid in the early morning at an interval of two days (70.3%) or more, averaging 2.27 days.

(3) Incubation behavior by both sexes started gradually a few days before first egg-laying. The average hatching interval was 1.88 days in 1978 and 1.93 in 1982.

(4) Both laying and hatching intervals tended to be prolonged in the latter half of the laying and hatching periods, respectively.

(5) The average hatching spread (data combined from the two years) was 6.3 days ($N=72$) with a maximum of 16 days (three instances).

(6) The first and intermediate chicks grew equally irrespective of their own brood size. Growth rates of the youngest chicks in B/4 and B/5 in 1978, as well as in B/3 and B/4 in 1982, were lower than older siblings.

(7) More deaths were recorded amongst *d*- and *e*-chicks in B/4 and B/5 than amongst *a*-, *b*- and *c*-chicks. It was likely that the former died of starvation or siblicide, whereas the latter died of various accidents.

摘 要

(1) 1978 年と 1982 年に三重県鈴鹿市のサギ類集団繁殖地でアマサギ (*Bubulcus ibis*) における非同時孵化と雛の成長・生残について調査した。

(2) 35 巣での平均一腹産卵数は 4.34 であった (1978 年のみ調査)。卵は 2 日以上、平均 2.27 日の間隔で早朝に産まれた。

(3) 初卵産下日の数日前より両親とも次第に抱卵行動を始めた。平均孵化間隔は 1978 年には 1.88 日、1982 年には 1.93 日であった。

(4) 産卵間隔および孵化間隔はそれぞれ産卵期、孵化期の後半に長くなる傾向があった。

(5) 2 年分の平均孵化期間は 6.3 日 ($N=72$) で、最長は 16 日に及んだ (3 例)。

(6) 第 1 子と中間の雛はその巣の雛数にかかわらず同様に成長したが、1978 年の雛数 4 と 5 の巣および 1982 年の雛数 3 と 4 の巣の末子の成長率は早うまれの兄弟より低かった。

(7) 雛数 4 と 5 の巣の第 4 子と第 5 子は第 1~3 子より多く死亡した。後者が様々な事故で死亡したのとは対照的に、前者の死亡原因は餓死や兄弟殺しであった。

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