On the development stages of chicks and adult Moorhens *Gallinula chloropus* at the end of a breeding season

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KARHU, S. [Kirstinmäki 6 A 21, SF-02770 Espoo, Finland] 1973. — *On the development stages of chicks and adult Moorhens* Gallinula chloropus *at the end of a breeding season.* Ornis Fenn. 50:1—17.

The growth of the wing, tarsus, bill and weight of Moorhen chicks was studied and used for age estimation. For the age estimation of trapped young a caged brood of six chicks was reared. Wing measurements proved to be the best criterion of age. In estimating the age of trapped young wing measurements alone were used.

The length of the breeding season, obtained by this indirect method, suggests it is possible that some pairs of Moorhen rear three broods a season even in Finland. Two broods per season seem to be quite common.

During the post-breeding moult the weight of adults decreases as long as the new feathers are growing. The study also includes observations concerning timing of autumn migration, fledging success, measurements of the adult birds and size of the Moorhen population.

Introduction

Knowledge of the development of young Moorhens is very sparse. The chicks are difficult to find on account of their concealed life in dense, eutrophic vegetation.

There are, however, some noteworthy studies (STEINBACHER 1939, HOWARD 1940, MILLER 1946, HOEHL 1949, ANFINNSEN 1961, NORDERHAUG 1962 and MUTHORST 1971) about the breeding biology of this nearly cosmopolitan species. TICEHURST (1940) studied the measurements of the Moorhen, while only HEINROTH (1928) has published notes on the development of the young. The moult has been studied very little (GRANT 1914).

Knowledge of the biology of the Moorhen in Finland is scarce, due to its rarity (TOIVARI 1938 and VON HAARTMAN et al. 1963—66). It is, for instance, not known whether the Moorhen raises single or double broods in Finland (VON HAARTMAN et al. 1963—66).

The main purpose of this study was to gain knowledge of the growth of the wing, tarsus, bill and the weight of Moorhen chicks and also to use these measurements in estimating age. By esitmating the age of the young I have tried to determine the number of broods of the Moorhen in Finland. Observations were also made concerning autumn migration, fledging success, measurements of adult birds, and size of the local Moorhen population, which is the only numerically significant one in Finland.

Study area

The study was carried out in Suomenoja Bay in Espoo (60°09′ N, 24°44′ E). The bay is no longer in its original state. In the early 1960's a dam was built around it which broke the connection with the sea and created a pond of approximately 20 hectares, into which the town of Espoo began to discharge sewage, at first untreated but, after 1969, it was mechanically screened.

Because of the nutrients in the sewage the vegetation in the pond has changed greatly. The *Phragmites communis* vegetation that was already dense in the original bay, has increased only slightly, but *Typha latifolia* and *Hippuris vulgaris* in particular have flourished strongly. This has, in my opinion, been the reason why the Moorhen population in the pond has thrived so well.

Rafts of *Typha* serve as principal breeding places for the Moorhens. Some Moorhens breed on those silt beds on which vegetation has accumulated. The silt has built up from the bottom as the water level of the pond rose. *Typha*-rafts, *Hippuris*-rafts and silt beds serve as excellent feeding places for the broods. About one third of the pond's area consists of open water. The depth of the pond is 0.5—2 m. Apparently the sewage has indirectly increased the supply of food for Moorhen broods (see also Fig. 5).

Methods

In order to make estimation of the age of trapped young possible, a brood was reared in the Helsinki Zoo. On 11.8.1972 I took from Suomenoja a clutch of six eggs. They were put into an incubator and hatched shortly afterwards.

The growth of these six young was measured about once every second day, always between 11.00 and 13.00. Wing length was measured from the carpal joint to the tip of the longest primary on the closed wing, the primaries being flattened against a ruler by gentle pressure. The length of the tarsus was measured from the notch on the back of the intertarsal joint to the lower edge of the tarsus with the toes bent backwards. The length of the bill was taken from the back edge of the shield to bill tip. The young were also weighed each time. The young seemed to be in good condition throughout.

95 Moorhens were trapped and banded 1968—72 at Suomenoja (Table 5). 15 wire-net traps were used, of the type used for catching wading and aquatic birds. Only in August—September 1972 was a systematic attempt made to estimate the number of breeding Moorhen pairs. 1—2 traps with food were placed in each assumed territory. The food used was a blend of oats and corn flakes. In previous years no food was used in the traps. The traps were placed on silt beds and in the vegetation. They were examined at 07.00—09.00 and 17.00—20.00.

In 1972 I measured the wing, tarsus, bill and weight of all but one individual, also when retrapping the Moorhens.

The development of the caged brood

Hatching and the main stages of development

The nestlings hatched at intervals of approximately 24 hours (Table 1). Because the eggs are laid at intervals of 24 hours (STEINBACHER 1939, HOWARD 1940, MILLER 1946, WITHERBY et al. 1947, MAKATSCH 1952 and DEMENT'EV et al. 1969) incubation must have begun as soon as the first egg was laid.

TABLE 1. Hatching times of the caged brood. 'Before 08.00' means the time between 16.00 on the day before and 08.00 on the day in question.

Chick No.	Date	Time
1.	13.8	before 08.00
2.	14.8	” ”
3.	15.8	” ”
4.	16.8	” ”
5.	16.8	about 12.00
6.	17.8	” 13.00

Newly hatched nestlings are covered by black down. The feet are black. The tip of bill is yellow. In the place of the shield there is a bright red swelling. Behind it the skin of the head is blue. The crown of the head is pink and naked. HEINROTH (1928) assumes that sexes can be distinguished by the size of the swelling. BOYD & ALLEY (1948) postulate that the brilliant head markings serve to stimulate the adults to feed the young, in a manner analogous to the brightly coloured gape of nestling passerines.

At the age of 20 days the crown of the head was covered in down. The colours of the bill and its base had faded. The first brown feathers appeared on the back and the first light ones on the ventral surface.

Only at the age of 25 days did the first wing feathers begin to appear. At one month the feet began to turn green. The young had fledged by the age of eight weeks, when wing length was about 150 millimetres. According to HEINROTH (1928) the young can fly a little even at seven weeks. The measurements of the brood at birth and full-grown are given in Table 2.

The true shield does not develop at all in the young. Two of the caged young were lighter in colour than the others. Of the two young reared by HEINROTH (1928), the lighter coloured one was a

TABLE 2. Measurements of the caged brood at birth and when full-grown. The full-grown weight is represented by the maximum value (compare with Fig. 2).

Chick No.	1.	2.	3.	4.	5	6.	x̄	±s
At birth								
Wing (mm)	16.0	16.0	16.0	16.0	16.5	16.5	16.2	0.26
Tarsus (mm)	19.0	18.0	19.0	19.0	19.0	19.5	18.9	0.49
Bill (mm)	12.0	12.0	12.0	12.0	12.0	11.5	11.9	0.20
Weight (g)	10	11	13	13	11	10	11.3	1.37
Age (days)	1	0.5	1	0.5	1	1		
Full-grown								
Wing (mm)	176	171	166	158	171	168	168.3	6.09
Age (days)	75	72	64	63	75	71	70.0	5.30
Tarsus (mm)	52.5	51.5	50.0	50.0	52.0	51.0	51.2	1.03
Age (days)	38	42	34	35	42	36	37.8	3.59
Bill (mm)	33.5	34.0	31.5	31.0	32.5	33.0	32.6	1.16
Age (days)	80	79	78	77	76	75	77.5	1.87
Weight (g)	266	270	228	210	263	258	249.2	23.49
Age (days)	61	70	64	58	68	64	64.2	4.40

female, the darker a male. According to STEINBACHER (1939) neither young nor adult Moorhens can be sexed on the basis of their colouring.

Wing and weight

The fastest development of wing and weight coincides only partly. The growth of the wing feathers (Figs. 1 and 3) does not begin until about the age of 25 days, when the weight (Figs. 2 and 3) has risen to nearly half its final value. The stages of fastest development of the two are approximately equal in duration. Onward from the half of these fastest growth stages the standard deviations in weight begin to be fairly significantly or significantly greater than the reduced standard deviations in wing length. These standard deviations were reduced to correspond to the standard deviations in weight (Table 3).

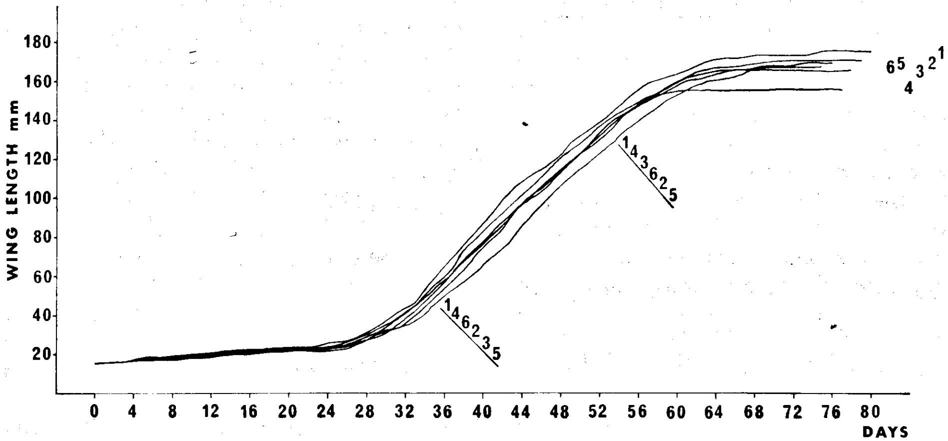

FIG. 1. The curves of wing growth in the caged young. The numbers 1—6 indicate the positions of the growth curves at different stages.

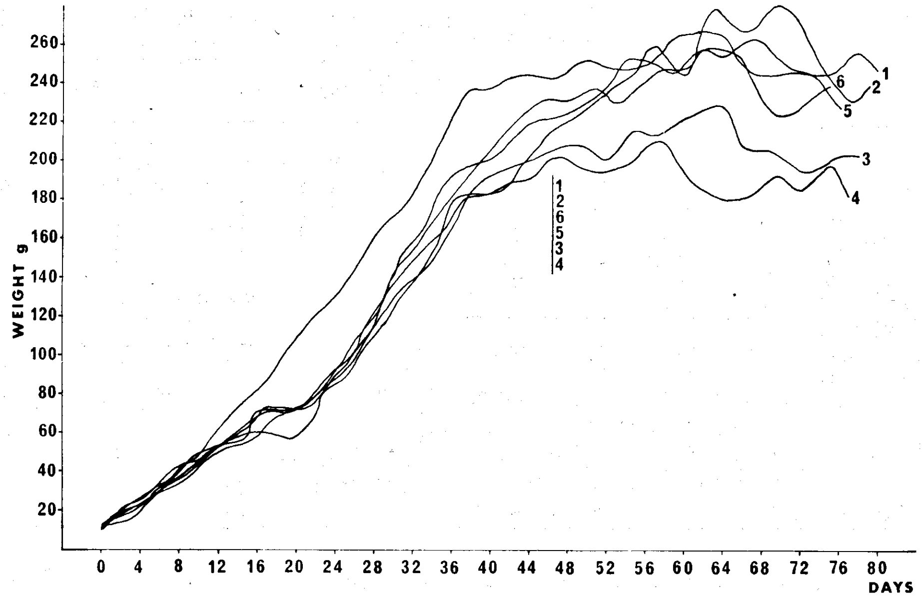

FIG. 2. Weight increase in the caged young. The numbers 1—6 indicate the positions of the growth curves at different stages.

Fig. 2 shows that the weight increase of the young may sometimes be interrupted, or even be reversed. This naturally never occurs with the development of the wing. Also the mean curve of wing development is considerably more regular than the mean curve of weight increase (Fig. 3).

Consequently, wing length may be considered more useful in estimating age than weight. The shorter the ultimate wing lengths of the young, the earlier they are attained (Table 4). Apart from this the rate of wing growth of all young is the same (Fig. 1). Estimating age from wing length becomes less reliable only when the bird is nearly fully grown.

Tarsus and bill

Contrary to wing development, the growth of the tarsus is very rapid (cf. also HEINROTH 1928). By the age of 42 days the tarsi of all caged young had attained their final length (Table 2 and Fig. 4). On the other hand, the growth of the bill is slower than wing development. Even at the age of 75 days the growth of the bill is continuing (Fig. 4), although its fastest growth takes place in the first 35—40 days.

The daily changes in bill length are small so that it is not very accurate for estimating age. The length of the tarsus, however, is a fairly reliable indicator of age.

Discussion

Growth rate — The rapid growth of the hind limbs is very important to the young Moorhen. They seek food from the ground or water independently when only three weeks old. The well developed hind limbs also enable them to escape from predators.

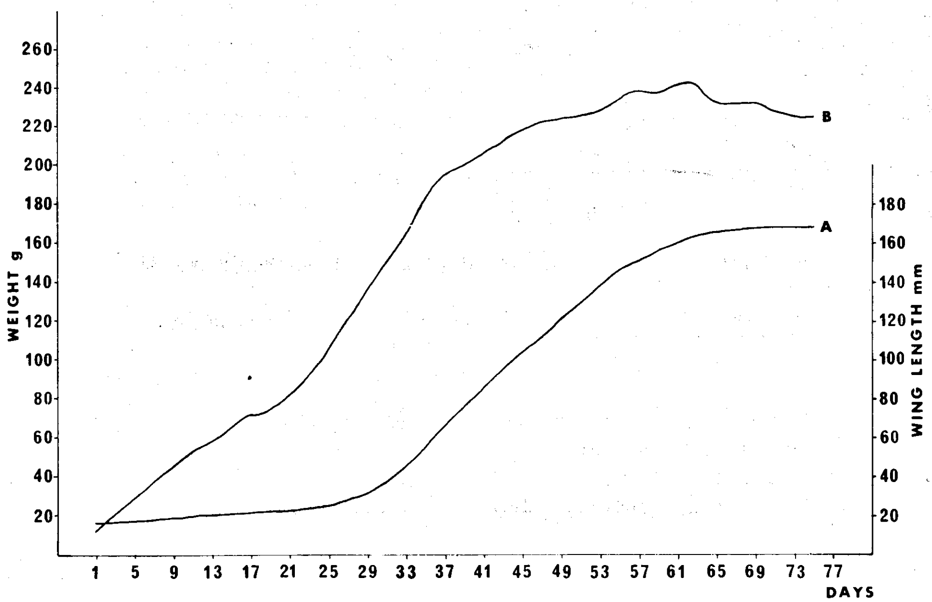

FIG. 3. The mean curves of the wing growth (A) and weight increase (B) of the caged brood.

TABLE 3. Comparison between the standard deviations in fastest stages of wing growth and weight increase. To obtain the F-value the standard deviations of wing, which were reduced to correspond with the standard deviations of weight (±s red.), are compared with the standard deviations of weight. The number of measurements is six in each case.

	Wing (mm)			Weight (g)				
Age (days)	$\bar{x}$	±s	±s red.	Age (days)	$\bar{x}$	±s	F	Risk-%
27—29	27.9	2.58	1.65	0—2	11.3	1.37	1.45	>10
29—31	31.3	3.08	2.49	2—4	20.2	2.18	1.30	>10
31—33	36.8	3.68	3.12	4—6	27.0	2.96	1.11	>10
33—35	44.2	4.95	4.57	6—8	35.7	4.36	1.09	>10
35—37	55.7	5.67	4.83	8—10	43.0	4.61	1.14	>10
37—39	66.0	7.31	6.50	10—12	52.3	5.05	1.65	>10
39—41	75.8	9.35	7.56	12—14	58.3	5.98	1.59	>10
41—43	86.2	8.48	7.30	14—16	65.8	8.04	1.21	>10
43—45	95.0	9.23	8.34	16—18	71.3	8.56	1.05	>10
45—47	103.8	5.62	4.72	18—20	73.6	13.68	8.42	<5
47—49	110.7	6.04	5.16	20—22	81.3	19.92	15.00	<2
49—51	121.0	6.93	6.03	22—24	91.8	17.66	8.57	<5
51—53	129.3	6.28	5.62	24—26	103.1	20.17	12.78	<2
53—55	137.8	7.45	7.25	26—28	120.7	18.71	6.66	<10
55—57	145.8	6.06	5.86	28—30	136.7	18.68	10.17	<5
57—59	151.3	5.32	5.25	30—32	150.0	14.33	7.49	<5
59—61	156.0	3.52	3.59	32—34	162.8	15.56	18.88	<2
61—63	160.0	3.35	3.58	34—36	182.3	21.74	36.83	<0.2
63—65	164.5	5.32	5.61	36—38	195.2	21.46	14.68	<2

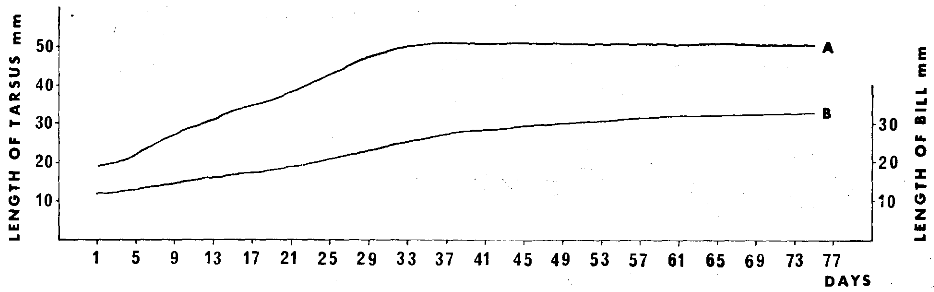

FIG. 4. The mean curve of the growth of tarsus (A) and bill (B) of the caged brood.

On the other hand, early development of wing feathers is not necessary. Even adult Moorhens seldom flee in case of danger by flying and, generally, they seek food by walking.

The early and rapid weight increase is necessary to ensure a sufficient basis for the growth of feathers. Apparently the growth of wing feathers occurs independently of the weight increase, but if the chick is undernourished the growth of feathers is obviously retarded. LACK's (1951) note that wing growth in young Swifts *Apus apus* is greatly retarded by undernourishment, is a proof of the fact. Earlier development of the wing feathers in the Moorhen would apparently require too much energy. Then periods of undernourishment might easily be repeated and mortality increase.

The composition of the food of the young Moorhen is probably such that more rapid development of the bill is not necessary. The long time taken for the bill to develop may also be a consequence of the method of measurement because the shield grows very slowly.

The reliability of the age criteria — A few earlier studies have demonstrated that wing measurements are better criteria of age than weight. According to LACK & SILVA (1949) the weight of the nestling Robin *Erithacus rubecula*

TABLE 4. The correlation between final wing length and the time at which it was attained. The numbers 1—6 indicate the birth order of the young.

	Wing length (mm)	Age (days)
4.	158	63
3.	166	64
6.	168	71
2.	171	72
5.	171	75
1.	176	75
	$r = 0.87$ ($t = 3.55$, $p < 0.025$)	

TABLE 5. Numbers of banded Moorhens, classified by age, and trapped adults and the estimated numbers of the pairs in 1968—72. Two young which later drowned in traps in 1971 and one chick killed by *Cirgus aeruginosus* in 1972 are included. The number of the trapped adults differs from the number of the banded ones because one young banded in 1970 was retrapped in 1971 and 1972.

	Banded			Trapped Adult	Number of pairs
	Adult	Young	Total		
1968	1	1	2	1	1—2
1969	—	3	3	—	1—2
1970	2	7	9	2	3—5
1971	2	23	25	3	6—8
1972	15	41	56	16	9—11
Total	20	75	95	22	

has scarcely any influence on the rate of feather development. HUDEC & FOLK (1961) have shown that in young Starlings *Sturnus vulgaris* the variation in wing length is much less than the variation in body weight. It is the same in the Moorhen (Table 3). According to MURTON et al. (1963) feather growth seems to be independent of body weight in young Wood Pigeons *Columba palumbus*.

In estimating age I have used only wing measurement, being the most reliable age criterion. As the daily growth of the tarsus is much smaller than that of the wing feathers age estimation on the basis of the former is more inaccurate. The least accurate method of estimating age is from the bill.

The size of the population

The Moorhen population in the study area has greatly increased since 1968 (Table 5). The number of pairs in 1968—71 was estimated so that every place where an adult Moorhen was seen or heard during the breeding season was assumed to lodge a pair. KLEMETSEN (1970) used approximately the same method, when estimating the Moorhen population of Östensjövann in Norway. The accuracy of my estimation was checked by trapping. Since 1968 I have spent more than two months each summer in the study area. During these periods I have also checked many times the sites of Moorhen territories. The numbers of ringed Moorhens in 1968—71 also give a good picture of the development of the population (Table 5). Trapping efficiency was approximately the same in these years.

Trapping was considerably more effective in 1972 than in previous years. The estimate of the number of pairs in 1972 is the most accurate of all because it is based on systematic trapping. If a trap in an assumed territory did not contain a Moorhen on five, successive days, it was transferred to another place. In this way I think I probably found nearly all territories.

TABLE 6. Numbers of trapped young and adults from separate territories and the numbers of pairs in 1972.

Territories	Young	Adult	Minimum number of pairs	Probable number of pairs
1—4	14	7	4	4
5—6	2	2	1	2
7	6	2	1	1
8—10	15	4	2	3
11	4	1	1	1
Total	41	16	9	11

Trapping efficiency improved considerably in 1972 when food was used to attract the birds. Particularly when trapping adult Moorhens it improved so much that the 16 trapped adults (in two territories at least, only one of the adults was caught) may be considered a reliable indication of the existence of a minimum of nine pairs (Table 6). In 1968—71 the trapping of adults was a great problem. For example in 1971 only three adult Moorhens went into traps, although at the beginning of May there were at least 7 adults in the area.

At a conservative estimate, more than 80 % of the Moorhens living in the area during the trapping season were trapped in 1972. This is supported by the fact that I retrapped young 60 times (including 7 controls on the same days) and adults 11 times.

The territories in 1972 are shown in Fig. 5. These sites are those in which Moorhens were caught. I have assumed that a bird comes from the territory in which it was first caught. When the young had fledged some were recaught on the opposite side of the bay.

The probable number of pairs in 1972 was 11 because the trapping of all adults apparently was not fully successful. On the other hand, it is possible that there

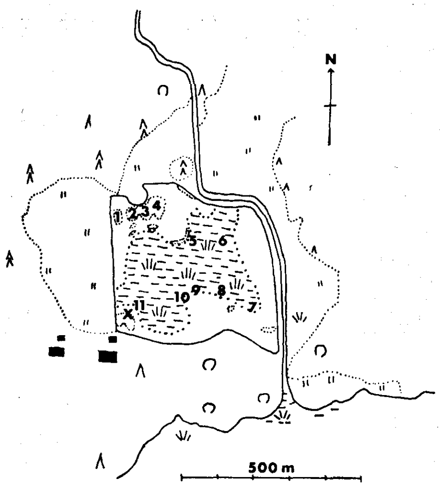

FIG. 5. The sites of the territories as indicated by trapping. X beside territory 11 indicates the place of the nest from which I took the eggs for rearing the caged brood. The study area is surrounded by a dam. In the middle of the area there is dense *Phragmites*-vegetation on the edge of which territories 5—11 are situated. There is open water between the dam and the *Phragmites*-vegetation, in which there are some large *Typha*-rafts, for instance territories 1—4. The black squares indicate the sewage treatment plant.

were Moorhens without mates, although MILLER (1946) considers this unusual, at least in the American subspecies *Gallinula chloropus cachinnans* (Bangs).

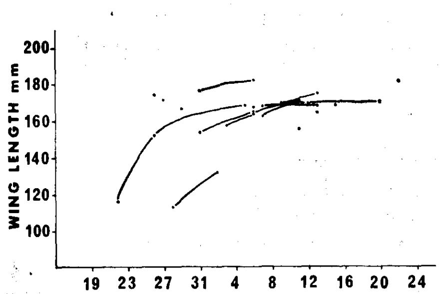

FIG. 6. Wing development in adults. Measurements taken from the same bird (dots) are connected by lines.

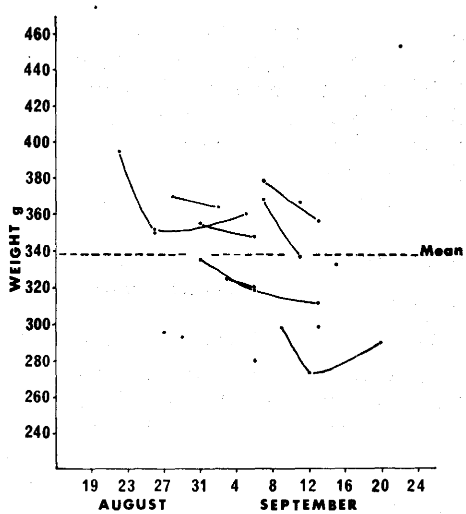

FIG. 7. Weight development in adults. Measurements taken from the same bird (dots) are connected by lines.

The development stages in nature

The adults

Moult and weight development — Many of the trapped adult Moorhens were in the moulting stage. It appears from the control measurements that the wings of six birds grew compared to their former measurements and the wings of only two birds remained unchanged (Fig. 6). The time of the moult is approximately the same as in Central Europe, where it takes place in July—October (GRANT 1914, NIETHAMMER 1942, WITHERBY et al. 1947 and STRESEMANN 1966). Also according to Russian findings the moult falls between these limits (DEMENT'EV et al. 1969). The weights of those six Moorhens, the wings of which had grown, had decreased on nearly every occasion that they were retrapped (Fig. 7 and Table 7). There is a clear negative correlation between the developments of the wing and weight; $r = -0.63$ ($t = 2.81, p < 0.025$). Near-

TABLE 7. The development of wing length and weight in the six controlled adults.

	Wing length (mm)	Weight (g)	Date	Time
1.	116	395	22.8	19.30
	152	352	26.8	18.00
	168	360	5.9	07.00
2.	113	370	28.8	19.00
	132	364	2.9	19.00
3.	176	355	31.8	18.00
	182	348	6.9	18.30
4.	153	336	31.8	18.00
	164	319	6.9	08.00
	174	312	13.9	18.30
5.	157	326	3.9	20.00
	163	320	6.9	19.00
6.	162	368	7.9	18.30
	170	337	11.9	08.00

$r = -0.63$ ($t = 2.81$, $p < 0.025$)

TABLE 8. The wing length and weight of adults. Because many adults were moulting, the mean of wing length has not been calculated. Two weight means are given, of the first time of weighing (1) and of all (2) the weighings.

	N	$\bar{x}$	$\pm s$	Range
Wing (mm)	27	—	—	113—182
Weight (1) (g)	16	343.0	37.76	280—453
Weight (2) (g)	27	337.8	40.45	274—453

ly all the weighing on which Table 7 is based was done in the evening, so that the time of the day cannot have caused apparent weight changes.

On the other hand, the time the bird spent in the trap, which is unknown, might have caused a certain reduction in weight. The wing length and weight of the adults are given in Table 8.

Tarsus and bill — These two measurements vary considerably (Tables 9 and 10). The tarsus observations are quite uniformly spread. The difference between minimum and maximum is 14 millimetres, which seems unexpectedly large bearing in mind the total length of the tarsus.

The bill observations are only slightly concentrated round a mode. The difference between minimum and maximum is 6 millimetres.

Discussion — The moult begins at the end of the breeding season (DEMENT'EV et al. 1969). Moorhens drop all their wing feathers simultaneously (GRANT 1914, WITHERBY et al. 1947 and DEMENT'EV et al. 1969). Because the growth of the new feathers also takes place simultaneously, the energy needed is undoubtedly great. Obviously for this reason weight decreases when the wing feathers are growing. Meinertzhagen (TICEHURST 1940) observed that Moorhens are lighter during the moulting period than later in winter and spring. The weights in autumn of six adult cocks were 342—404 grams and six adult hens were 288—354 grams (Meinertzhagen).

TABLE 9. Length of tarsus in adults.

Length (mm)	45—46	47—48	49—50	51—52	53—54	55—56	57—58	59—60	$\bar{x}$	$\pm s$	Range
Number of birds	1	2	4	2	1	3	1	2	52.3	4.29	45—59

TABLE 10. Length of bill in adults.

Length (mm)	33	34	35	36	37	38	39	$\bar{x}$	$\pm s$	Range
Number of birds	2	2	3	4	2	—	3	35.9	1.97	33—39

I was not able to sex the Moorhens which I measured because the shield in most of them had already become reduced and dark. By comparing the weights which I obtained (Fig. 7) with the results of Meinertzhagen, we may conclude that about half of my adults were cocks.

The standard deviations of tarsus and bill in the adult Moorhens I measured were unexpectedly great. They are much greater than might have been expected from earlier references. The length of the tarsus according to NAUMANN (1899) is 47 mm, according to WITHERBY et al. (1947) 48—53 mm and according to HEINROTH (1928) 51—54 mm; the numbers of measurements were not given. According to TICEHURST (1940) the bills of eight adults in winter were 36—38 millimetres. The measurements were carried out in the same way as mine. The upper limit of my measurements is only a little higher and can be explained by the fact that the shields of some of my adults were still somewhat enlarged. On the other hand the lower limit of my measurements is considerably lower. The great variation in my observations can hardly be due to mismeasurements because the results did not change on retrapping.

Wrong ageing could be one reason for the small bill measurements of my birds. However, this is out of the question because adults and young differ clearly from each other in colouring and all the adults which I measured had a crimson iris. According to WITHERBY et al. (1947) the iris is greybrown in the juvenile. The colour of iris in one of the young that I banded had, it is true, changed 5.9—12.9 from greybrown to somewhat reddish, but the colour of the iris and plumage of the young diverged nevertheless so much from that of the adults that wrong ageing was out of the question.

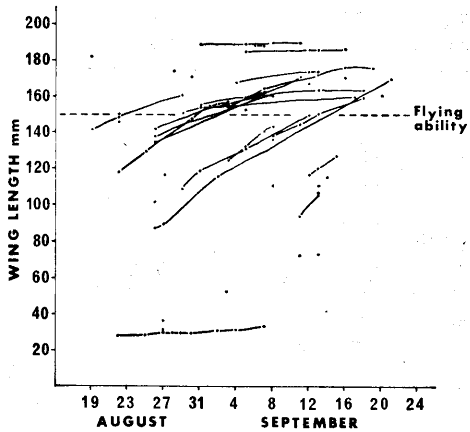

FIG. 8. Increase in wing length in young. Measurements taken from the same bird (dots) are connected by lines.

Apparently the reason for the great variation of tarsus and bill are differences between sexes.

The young

Development stages during trapping period — From the measurements of wing length, weight, tarsus and bill (Figs. 8, 9 and 10) it may be concluded that in the study area there were at the same time young of different stages of development. In the smallest young the wing feathers had hardly begun to appear while the wing feathers of the largest young had already finished growing (Fig. 8).

Most of the young seem to attain flying ability before the end of September. The caged young were last in attaining flying ability. This happened 7—13.10.

Weight in most of the young remains below the minimum weight of adults, at least until migration commences (Fig. 9). Only one juvenile attained the mean adult weight. According to TICEHURST (1940) young remain lighter in winter

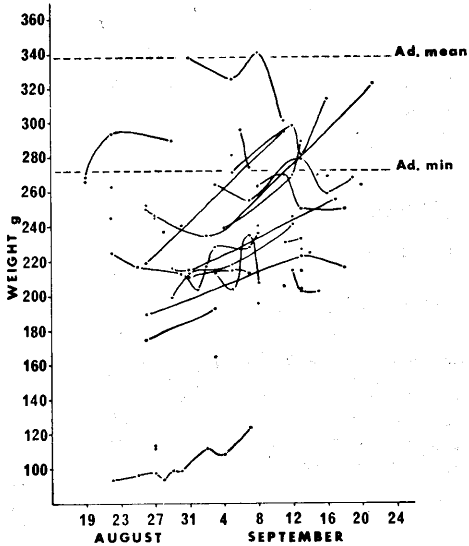

FIG. 9. Weight development in young. Measurements taken from the same bird (dots) are connected by lines.

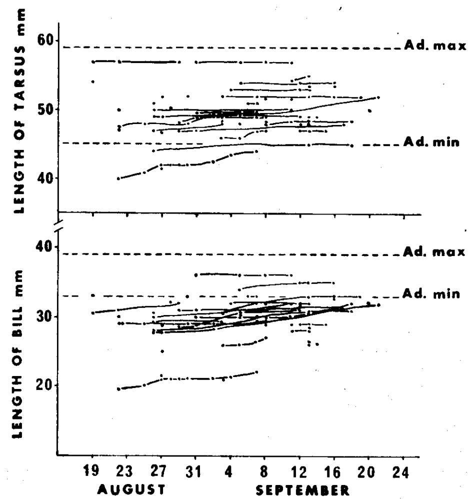

FIG. 10. Development of tarsus and bill in young. Measurements taken from the same bird (dots) are connected by lines.

than adults. The weight of some young varied greatly, but this may have been caused by measurements taken at different times of the day. Certainly the weights of the caged brood (Fig. 2) also varied considerably although weighing was carried out at the same time each day. The length of time spent by the birds in the trap may have influenced the weight.

The length of the tarsus (Fig. 10) of almost all young was above the minimum of the adults. Only in a few downy chicks were the tarsi still growing. The tarsal length of the largest young was only two millimetres below the maximum of adults. This also proves that the exceptionally long tarsi of the adults were not due to mismeasurement, but to individual differences between different Moorhens.

Nearly all lengths of the bill of the young were below the minimum of the adults (Fig. 10). This is caused by the fact that their shields were just beginning to grow.

Hatching times — The age of trapped young has been determined by comparing their wing length (Fig. 8) with that of the caged brood (Fig. 3). The date of hatching has also been determined in a similar way (Fig. 11). The incubation period was assumed to be 20 days, as most authors give 19—22 days (NAUMANN 1899, STEINBACHER 1939, NIETHAMMER 1942, BROWN 1944, MILLER 1946, WITHERBY et al. 1947 and DEMENT'EV et al. 1969).

The caged brood clearly hatched latest, nearly 2.5 months after the first young hatched in the study area (Fig. 11). The true difference is probably even greater because wing lengths of the six earliest hatched young were greater at the time of measurement than the highest values of the mean curve (Fig. 3). I estimated their age as 75 days, but they were probably older. HUOKUNA'S (VON HAARTMAN et al 1963—66) observations of three nests (3+5+6 eggs) 3.5.1953 indicate that breeding may take place earlier than

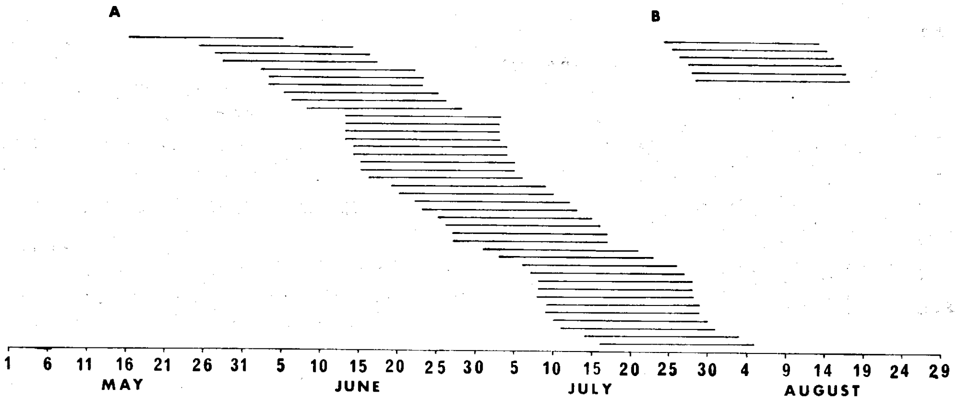

FIG. 11. Commencement of incubation and hatching of 40 trapped young (A) and of the caged young (B). Each line indicates one chick; the line begins at the date when incubation started and ends with hatching. Incubation time was estimated to be 20 days.

indicated in Fig. 11. The clutches found by HUOKUNA may have been incomplete, but even so incubation probably began in the course of 2—3 days.

A seventh chick whose wing length when first trapped was higher than the maximum of the mean curve was not trapped until 16.9, so that it need not necessarily have been among the first young hatched.

The number of broods

Because there are clutches from April—May to August it is reasonable to suppose that the Moorhen lays more than one clutch during the summer in Finland.

Two broods is the rule in Western and Central Europe (HOWARD 1940, NIETHAMMER 1942, WITHERBY et al. 1947, MAKATSCH 1952 and MUTHORST 1971), in the United States (MILLER 1946), in the Soviet Union (DEMENT'EV et al. 1969) and in Norway (NORDERHAUG 1962). In Germany STEINBACHER (1939), however, noted among nine pairs kept under observation only two which bred a second time. Three successive broods are fairly usual in Great Britain (BROWN 1944 and WITHERBY et al. 1947). Both LENZ (1967) and MUTHORST (1971) observed single pairs with three broods in Germany. It is possible that the Moorhen lays three successive clutches also in the United States (MILLER 1946) and in Norway (NORDERHAUG 1962). According to HOEHL's (1949) observations three successive clutches is almost the rule in Germany. He also noted a pair laying four clutches after a warm winter, none of which was a replacement clutch. There is also one observation of four separate nestings in Great Britain (BENTHAM 1931).

According to HOWARD (1940) the hatching interval between two successive clutches is 44 days, and according to HOEHL (1949) 26—56 days, the average being 44 days (calculated from HOEHL's diagram). From HOEHL's (1949) diagram it is also possible to see that the incubation season (interval between the first incubated egg and last hatching in a season) is 99—115 days in the case of three broods and 140 days in the case of four broods.

The interval between the first and last hatching in my area was 73 days according to Fig. 11. This means that the incubation season is 93 days. Referring to what has been said above about the probably earlier hatching of the six oldest young and about HUOKUNA's observations of clutches on 3.5.1953 the incubation season lasts 100—110 days in Finland. This suggests three successive clutches according to HOEHL (1949). Thus it is possible that at least some Moorhens rear three broods in one season in Finland. Two broods seem to be quite common.

Because the proof is indirect and not based on the behaviour of ringed pairs, I cannot exclude the possibility of error caused by replacement of destroyed clutches.

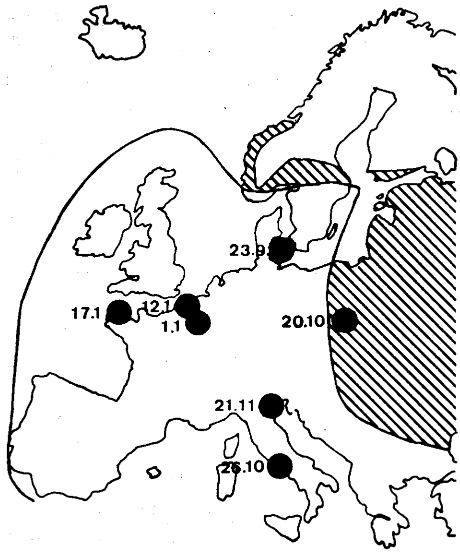

FIG. 12. Foreign recoveries of Moorhens banded in the study area (= all foreign recoveries of Moorhens banded in Finland). Recovery dates are marked on the map. Moorhens breed in the shaded area but do not winter in large numbers there. South of this area they both breed and winter. (Distribution boundaries according to PETERSON et al. 1954.)

The time of autumn migration

I finished the trapping of Moorhens in 1972 on 23.9. Trapping was noticeably less successful 20—23.9. This gave reason to suppose that a large part of the population had started to migrate. A Moorhen, found on 23.9.1971 in Denmark and banded by me as a chick in July of the same year, supports this conclusion. The Moorhen found in Denmark was probably still migrating. The real wintering area of Finnish Moorhens seems to be in southern and western Europe (Fig. 12).

The wings in most of the young have reached a stage which makes migration possible before the end of September (Fig. 8). Also the new wing feathers of adults grow to their final length before the end of September (Fig. 6). The main migration of both adults and young may, thus, start at approximately the same time.

Some of the young Moorhens do not, however, attain flying ability before the end of September (Fig. 8), so that they do not migrate until October. The migration of the caged brood would have taken place about the end of October.

The majority of Moorhens seem to migrate from Finland before the weather gets cold. NORDERHAUG (1962) reports the same from southern Norway. There are also a few winter records from Finland (VON HAARTMAN et al. 1963—66). However, I assume that these birds had been injured and were therefore unable to migrate. Quite a number of Moorhens winter in western Norway and, when the lakes freeze, they find refuge along the seashore (ANFINNSEN 1961).

The migration of the Moorhen continues in my opinion throughout the autumn but with a clear peak at the end of September. The last to migrate are probably the parents and the young of the third brood. The observation of SAAREOKSA (VON HAARTMAN et al. 1963—66) of a Moorhen flying southwards at night 31.7.1960 can indicate early migration as VON HAARTMAN et al. (1963—66) assume but it may have been a wandering unmated bird.

Hitherto only one banded Moorhen has returned to its breeding place. It was banded on 9.8.1970 as a chick and was retrapped on 28.7.1971, 7.9.1972 and 11.9.1972.

Fledging success

There were 4.6—5.1 young per pair of Moorhens in the study area (Table 11). Assuming (as TICEHURST 1940) that the mean clutch size is 8 and there are two broods, the survival rate was 28.7—32 %. In Norway the mean of 15 clutches was 8.6 eggs (ANFINNSEN 1961). As some of the banded young must have died before fedging, I estimate final breeding success to be 20—25 %.

On 27 January, 1940, TICEHURST (1940) collected from a single dyke in Great Britain 45 Moorhens which had succumbed to cold and starvation, representing the entire population over a considerable area. If the young of the population had lived to breed in 1940 it gives an ultimate survival rate of 20 % as a maximum (TICEHURST 1940) These results coincide approximately with mine, assuming that the mortality rate does not increase to any great degree after fledging. My estimation also corresponds with the fledging success of 23,1 % (ALLEY & BOYD 1947) and 20.7 % (SAGE 1969) in the Coot *Fulica atra,* and the fledging success of 26 % (GULLION 1954) in the American Coot *Fulica americana.* On the other hand, ASKANER (1959) has estimated a fledging success of 15.4 % for the Coot in one area, and 92.1 % in another. These differences were caused by the large differences in the supply of food.

TABLE 11. The number of young per half of adults and per minimum number of pairs. The calculation is based on the figures in Table 6.

Territories	Number of young per half of adults	Number of young per minimum number of pairs
1—4	4	3.5
5—6	2	2
7	6	6
8—10	7.5	7.5
11	8	4
Mean	5.1	4.6

Discussion

Reproduction and the balance of population

Although the growth of Moorhen young takes over two months, because of the early independence of its young it can rear 2—3 broods even in Finland. The members of the caged brood were able to feed independently when only three weeks old. At this age they did not come to take food from the hand any more. The weight increase in these young was interrupted at the age of approximately three weeks (Figs. 2 and 3), probably as a consequence of the change in their behaviour. Also PITT (WITHERBY et al. 1947) found that the young can feed themselves at the age of three weeks, but depend on their parents for about five weeks. The young reared by HEINROTH (1928) became independent at the age of one month. According to HOWARD (1940) the parents begin to drive away 21-day-old young. As the hatching interval between successive clutches of the Moorhen is only 44 days (HOWARD 1940 and HOEHL 1949), the new clutch is commenced when the earlier young are still covered in down.

The Moorhen has achieved the greatest possible production of young by breeding many times and by laying relatively large clutches. Because the Moorhen feeds its young about three weeks it would hardly be able to rear more chicks per one brood.

Mortality in the young seems quite heavy. In order to maintain a stable breeding population the Moorhen apparently requires two broods a season. ANFINNSEN (1961) estimates that the chance of a single egg developing into a mature Moorhen is between 6 and 12 %, the correct percentage probably being closer to the lower than the upper limit. The Moorhen attains maturity as early as the age of one year (LACK 1968 and DEMENT'EV et al. 1969).

Among other Rallidae the Coot rears two, sometimes even three broods (WITHERBY et al. 1947), but according to ALLEY & BOYD (1947), KORNOWSKI (1957), ASKANER (1959) and SAGE (1969) second broods seem to be uncommon. Second broods are hardly possible in Finland (VON HAARTMAN et al. 1963—66). The number of broods in the American Coot is regularly two (GULLION 1954). Among the smaller Rallidae two broods are reared by *Rallus aquaticus* (DEMENT'EV et al. 1969), by *Crex crex* (MORRIS 1892 and DEMENT'EV et al. 1969), by *Porzana parva* (WITHERBY et al. 1947 and DEMENT'EV et al. 1969) and probably by *Porzana porzana* (WITHERBY et al. 1947). The average clutch size of all the mentioned Rallidae is 7—10.

The reason for large reproduction in Rallidae is apparently caused by their habitats, in most cases eutrophic lakes, rich in food, which enable the birds to rear large broods. On the other hand, there are numerous enemies which lead to a high mortality rate. For instance, the American subspecies of the Moorhen has at least 16 enemies (MILLER 1946).

The growth of the study population

The strong increase in numbers of Moorhens in my study area must have been caused either by the population's own production or by immigration. Only one ringed Moorhen has so far returned to its birth area. The growth of the population seems therefore to have been caused by immigration from elsewhere. The cause of this development may be the habitat which has become exceptionally advantageous. The fact, however, that most pairs seem to rear two broods would indicate the 'self-sufficiency' of the population.

Acknowledgements

Special thanks are due to Dr. Ilkka Koivisto, director of the Helsinki Zoo, who kindly arranged for the rearing of the caged brood. I am most grateful to Mrs. Raija Kettunen, Mr. Pertti Muuronen, Miss Tuula Savolainen and Mrs. Ritva Stüwe, the zookeepers, who reared the caged brood and to Mr. Reijo Purasmaa M.Sc. and Mr. Timo Tallgren for participating in the ringing of Moorhens in 1968—70.

Mr. Gerhard Stüwe, the directorial assistant of the Helsinki Zoo, gave valuable advice for rearing the brood and helped in the translation. Professor Ernst Palmén, Dr. Göran Bergman, Dr. Ilkka Koivisto and Dr. Lasse Sammalisto kindly read the manuscript.

Selostus: **Liejukanan *Gallinula chloropus* poikas- ja aikuisvaiheiden kehityksestä pesintäkauden lopulla**

1. Olen selvittänyt liejukanan poikasten siiven, nilkan, nokan ja painon kasvunopeutta ja niiden käyttöä iänmäärityksessä. Niiden avulla olen epäsuorasti määrittänyt pesintäkauden pituuden ja pesintäkertojen määrän. Aineisto antaa myös kuvan poikastuotosta, syysmuuton ajankohdasta, aikuisten lintujen pesinnän jälkeisestä tilasta sekä tutkitun populaation koosta. Tutkimusalueena on ollut Espoon Suomenojanlahti (60°09′ N, 24°44′ E).

2. 1968—72 on Suomenojanlahdelta pyydystetty ja rengastettu 95 liejukanaa. Olen mitannut 1972 pyydystettyjen 40 poikasen ja 16 aikuisen linnun siiven, nilkan, nokan ja

painon. 1972 pyydystettyjen liejukanojen lukumäärän ja saantipaikkojen mukaan osoittautui populaation vähimmäisparimääräksi 9 ja todennäköiseksi parimääräksi 11.

3. Mainittujen 40 poikasen iänmääritystä varten kasvatettiin Korkeasaaren eläintarhassa kuuden yksilön vertailupoikue. Myös siitä suoritin edellä mainitut mittaukset. Vertailupoikueen kasvattamista varten otin Suomenojanlahdelta myöhäisen munapesyeen. Poikaset kuoriutuivat suunnilleen vuorokauden välein.

4. Vertailupoikueen nilkan ja painon kasvu tapahtui nopeimmin, siiven ja nokan hitaimmin. Liejukanan poikaselle on tärkeätä jalkojen nopea kehitys. Poikanenhan etsii itse ravintonsa jo kolmen viikon ikäisenä. Hyvin kehittyneet jalat auttavat myös pakenemaan ja piiloutumaan nopeasti vihollisilta. Painon aikainen kasvu taas on välttämätöntä taatakseen myöhemmin kasvunsa aloittavien sulkien ja höyhenten nopealle kehitykselle riittävän pohjan, jottei poikanen joutuisi liian helposti aliravitsemustiloihin. Siipien aikainen kasvu ei ole tarpeellista, koska poikanen tarvitsee niitä vasta muuttoa varten.

5. Siiven mitta osoittautui parhaaksi ikäkriteeriksi. Painoa edullisempi se on siksi, että sen nopeimman kasvukauden hajonnat ovat painon vastaavan kauden hajontoja pienemmät. Siiven kasvu tapahtui myös ilman painon kasvussa ilmenneitä keskeytyksiä. Siiven nopeimman kasvukauden päivittäinen pituuskasvu on nilkan kasvua suurempi, joten siiven mitasta määritetty ikä on myös nilkasta määritettyä ikää tarkempi. Nokan päivittäinen kasvu on niin vähäistä, että sen kasvukäyrästä määritettyä ikää voidaan pitää vain suuntaa antavana. Pyydystettyjen poikasten iät on määritetty pelkästään siiven mitasta.

6. Aikuisten lintujen pesinnän jälkeisessä sulkasatovaiheessa niiden paino laskee uusien sulkien kasvaessa. Aikuisten lintujen nilkan ja nokan pituuksien suuret hajonnat johtuvat todennäköisesti sukupuolten välisistä eroista.

7. Luonnosta pyydystetyt poikaset edustivat kaikkia kehitysvaiheita untuvikosta täysikasvuiseen. Pyydystettyjen poikasten ikä on määritetty vertaamalla niiden siiven pituutta vertailupoikueen siiven kehityksestä piirrettyyn keskiarvokäyrään. Näin on voitu määrittää niiden kuoriutumishetki. Ensimmäinen kuoriutuminen oli tapahtunut ennen 5.6. Viimeisenä kuoriutui vertailupoikue.

8. Ensimmäiseksi kuoriutuneen poikasen haudonnan alkamisen ja viimeisen toteamani kuoriutumisen väli on 93 vuorokautta. Viitaten kuuden vanhimman poikasen todennäköisesti aikaisempaan kuoriutumiseen ja HUOKUNA (VON HAARTMAN et al. 1963—66) toukokuun alun munapesähavaintoihin voidaan laskea haudonnan kestävän Suomessa 100—110 vuorokautta. Se vastaa HOEHLin (1949) havainnoista laskemaani kolmen pesintäkerran vaatimaa haudontakautta. Tämän mukaan on mahdollista, että muutamat liejukanaparit Suomessakin kasvattavat kolme poikuetta kesässä. Kaksi pesintäkertaa lienee aivan tavallista. Koska todistelu on epäsuora, eikä siis perustu varmuudella saman parin munimiin peräkkäisiin pesyeisiin, en tietystikään pysty sulkemaan pois tuhoutuneiden pesyeiden tilalle munittujen uusintapesyeiden aiheuttamaa virhemahdollisuutta.

9. Päämuutto tapahtunee ennen syyskuun loppua, koska suurin osa poikasista saavuttaa lentokyvyn ennen tätä ajankohtaa. Myös aikuisten lintujen uudet sulat ovat silloin saavuttaneet täyden pituutensa. 1972 muuton ajankohta oli 20—23.9. Silloin väheni pyydyksistä saatavien liejukanojen määrä voimakkaasti. Muuton ajankohtaa tukee myös Tanskasta 23.9.1971 löydetty liejukana, jonka oli rengastanut poikasena saman vuoden heinäkuussa. Viimeiset poikaset muuttanevat vasta loka—marraskuun vaihteessa.

10. Populaation poikastuotto oli 28.7—32 % arvioidusta munittujen munien määrästä. Ilmeisesti osa rengastamistani poikasista kuoli ennen lentokyvyn saavuttamista, jonka vuoksi olen arvioinut lopullisen tuoton olleen 20—25 %. Koska kuolleisuus näyttää erittäin suurelta, arvelen että kaksi pesintäkertaa vuodessa on välttämätöntä lajin säilymisen kannalta.

11. Tähän mennessä on vain yksi liejukana varmuudella palannut synnyinpaikalleen. Mahdollisesti populaation kasvu onkin ollut muualta tulleiden lintujen varassa. Toisaalta se, että suurin osa pareista näyttää kasvattavan kaksi poikuetta kesässä viittaisi populaation kasvun 'omavaraisuuteen'.

References

ALLEY, R. & BOYD, H. 1947. The hatching and fledging success of some Coot. Brit. Birds 40:199—203.

ANFINNSEN, M. T. 1961. Sivhøne, *Gallinula chloropus* (L.) i Norge. Utbredelse og rugeforhold. Sterna 4:345—377.

ASKANER, T. 1959. Några iakttagelser över häckningsbeteende och häckningsresultat hos sothönan (*Fulica atra*). Vår Fågelvärld 18:285—310.

BENTHAM, H. 1931. Moorhens rearing four broods. Brit. Birds 25:106.

BOYD, H. & ALLEY, R. 1948. The function of the head-colouration of the nestling Coot and other nestling Rallidae. Ibis 90:582—593.

BROWN, R. H. 1944. Notes on a pair of Moorhens. Brit. Birds 37:202—204.

DEMENT'EV, G. P., GLADKOV, N. A. & SPANGENBERG, E. P. 1969. Birds of the Soviet Union. III. — IPST, Jerusalem.

GRANT, C. H. B. 1914. The moults and plumages of the Common Moorhen (*Gallinula chloropus* Linn.). Ibis 10:298—304.

GULLION, G. W. 1954. The reproductive cycle of American Coots in California. Auk. 71: 366—412.

HAARTMAN, L. VON, HILDÉN, O., LINKOLA, P., SUOMALAINEN, P. & TENOVUO, R. 1963—66. Pohjolan linnut värikuvin. I. — Otava, Helsinki.

HEINROTH, O. & HEINROTH, M. 1928. Die Vögel Mitteleuropas. III. — H. Bermühler Verlag, Berlin.

HOEHL, O. 1949. Wie oft brütet das Teichhuhn? Die Vogelwelt 70:120.

HOWARD, E. 1940. A Waterhen's worlds. — Cambridge Univ. Press, Cambridge.

HUDEC, K. & FOLK, C. 1961. Postnatal development in the Starling (*Sturnus vulgaris* L.) under natural conditions. Zoologicke Listy 10:305—330.

KLEMETSEN, A. 1970. Check method census of Coot, *Fulica atra,* and Moor-Hen, *Gallinula chloropus,* in Östensjövann, South Norway 1967—68. Nytt Mag. Zool. 18:199—207.

KORNOWSKI, G. 1957. Beiträge zur Ethologie des Blesshuhns. J. Orn. 98:318—355.

LACK, D. 1968. Ecological adaptations for breeding in birds. — Methuen, London.

LACK, D. & LACK, E. 1951. The breeding biology of the Swift, *Apus, apus.* Ibis 93: 501—546.

LACK, D. & SILVA, E. T. 1949. The weight of nestling Robins. Ibis 91:64—78.

LENZ, M. 1967. Teichralle (*Gallinula chloropus*) brütet dreimal in einem Jahr. Ornithol. Mitt. 19:219.

MAKATSCH, W. 1952. Der Vogel und sein Ei. Die neue Brehm-Bücherei. Heft 3.

MILLER, R. F. 1946. The Florida Gallinule. Breeding birds of the Philadelphian region (part III). Cassinia 36:1—16.

MORRIS, F. O. 1892. A natural history of the nests and eggs of British birds. III. — London. (Ref. GULLION, G. W. 1954).

MURTON, R. K., ISAACSON, A. J. & WESTWOOD, N. J. 1963. The food and growth of nestling Wood-pigeons in relation to the breeding season. Proc. zool. Soc. Lond. 141:747—781.

MUTHORST, B.-H. 1971. Zur Biologie des Teichhuhns (*Gallinula c. chloropus*) und des Blesshuhns (*Fulica a. atra*) (Aves). Abh. Verh. Naturwiss. Ver. Hamburg NF 15: 107—126.

NAUMANN, J. F. 1899. Naturgeschichte der Vögel Mitteleuropas. VII. — Fr. Eugen Köhler, Gera.

NIETHAMMER, G. 1942. Handbuch der deutschen Vogelkunde. III. — Akadem. Verlagsges., Leipzig.

NORDERHAUG, M. 1962. Fra sivhønas (*Gallinula chloropus*) forekomst og levevis ved Tønsberg. Sterna 5:53—61.

PETERSON, R. T., MOUNTFORT, G. R. & HOLLOM, P. A. D. 1954. A Field Guide to the Birds of Britain and Europe. — Collins, London.

SAGE, B. L. 1969. Breeding biology of the Coot. Brit. Birds. 62:134—143.

STEINBACHER, G. 1939. Zur Brutbiologie des Grünfüssigen Teichhuhns (*Gallinula chloropus* L.). J. Orn. 87:115—135.

STRESEMANN, E. & STRESEMANN, V. 1966. Die Mauser der Vögel. J. Orn. Sonderheft 107:1—445.

TICEHURST, C. B. 1940. Notes on the Moorhen (*Gallinula chloropus chloropus*). Ibis 4: 539—542.

TOIVARI, L. 1938. Liejukana, *Gallinula ch. chloropus* (L.), pesivänä Vanhankaupungin lahdella. Ornis Fenn. 15:117—119.

WITHERBY, H. F., JOURDAIN, C. R., TICEHURST, N. F. & TUCKER, B. W. 1947. The handbook of British birds. V. — H. F. & G. Witherby, London.

Received April 10, 1973.