

Reproductive organs and breeding behaviour of the male Pied Flycatcher *Ficedula hypoleuca* (Pallas)

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The cycle of the male sex organs in Pied Flycatchers from northern and southern Sweden is described. The results are discussed in relation to the breeding behaviour of the species. The birds were colour banded and watched daily in the field to ascertain the exact breeding situation of every investigated male. The Pied Flycatcher has an extremely early testicular regression, which is well synchronised with the normal hatching time, independent of year and latitude. Once spermatogenesis has been initiated it ceases after a definite time, and no prolongation seems possible. The activity of the Leydig cells declines rapidly immediately after the egg-laying period. This can be correlated with changes in singing activity, and with the aggressive and polygamous behaviour of the species. The sex ratio in the broods was determined; and equal sex ratio, 1:1, was found.

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INTRODUCTION

Most investigations of avian endocrinology are based on birds in captivity. In studies of birds living free, the variation in breeding status of the individuals in one population is not usually considered. The Pied Flycatcher *Ficedula h. hypoleuca* is a rather common bird in Sweden and it readily breeds in nest-boxes. The ecology and ethology of the species have been described by many authors (cf. e.g. von Haartman 1949, 1951a, 1951b, 1954, Creutz 1955, Curio 1959). The purpose of this study was to determine the composition of Pied Flycatcher populations as to sex and breeding status, and to take individuals of an exactly known breeding status for characterization of their endocrinological status. Three categories of males could be distinguished: 1) Unpaired males. 2) Males that mate and stay with the same female during the entire breeding season. 3) Males that mate, but leave their first home territories during the egg-laying phase, and establish second territories in which they sometimes succeed in getting new females to breed.

In this paper the activity of the male sex organs during the breeding season will be described.

MATERIAL AND METHODS

Three study areas were used. One was situated in north Sweden, at Ammarnäs (65°58'N), where the type of vegetation was a subalpine birch forest. The other areas were in southwest Sweden, at Rävlanda (57°40'N), where pine forest dominates, and at Åskloster (57°14'N), an area of broad-leaved forest. Spring migrants were collected at Falsterbo bird station in south Sweden during the first two weeks of May 1972.

The nest-boxes were placed on trees 1.5–2 metres above the ground, and 30 m apart. Since it was necessary for the investigation to mark the whole population during an early stage and then to follow the breeding population in the field, the nest-box areas were, by necessity, relatively small, containing 50 nest-boxes at Ammarnäs, 150 at Rävlanda, and 40 at Åskloster. The birds were caught with

mist-nets during the breeding season, and also with automatic traps in the nest-boxes before the nest-building period and during the feeding period. The birds were marked individually with colour-rings.

The birds were recaptured during different phases of the breeding season to study the sex organs. During the breeding seasons 1971–1973, 100 males were collected. Furthermore, 20 broods were taken to determine the sex ratio of the young. The birds were killed by decapitation, and within a few minutes the organs were preserved in Bouin's fixative for 12 hours. At the laboratory, the testes were weighed on a Mettler precision balance to the nearest $2 \cdot 10^{-2}$ mg, after which they were embedded in paraffin. The testes were cut in 7μ sections and stained with Ehrlich's haematoxylin-eosin and/or Heidenhain's iron haematoxylin.

The different stages in the spermatogenesis were determined using a scale calculated by Bartholomew (1949) and Scott & Middleton (1968). The diameter of 10 transversely cut seminiferous tubules was measured. The amount of free sperms in the tubules was estimated by counting the number of free sperms in 40 tubules. Following Scott & Middleton (op. cit.), the number was considered low if there were 10 or more free sperms in less than 10 tubules, moderate if this was the case for 10–19 tubules, and high if 20 or more contained the above amount of free sperms. To get an index of the number of Leydig cells in the testes, the number of these cells was counted in 50 intertubular areas and then multiplied with the mean weight of the testes (Threadgold 1956). The thickness of the tunica albuginea was measured at 10 places.

The height of the epithelium in the seminal sacs was measured in 10 different tubules.

With the aid of colour marking and daily observations of movements and behaviour of the individual birds, two main categories could be distinguished among the captured males: 1) Males of known breeding status. 2) Males visiting the area, but not breeding within it.

RESULTS

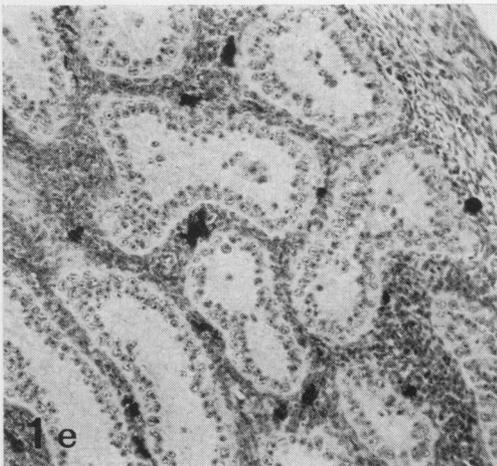
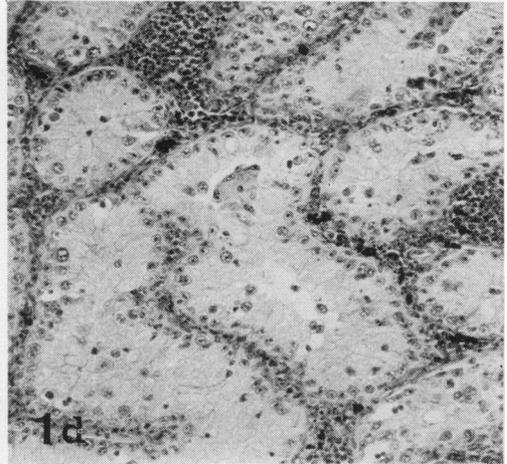
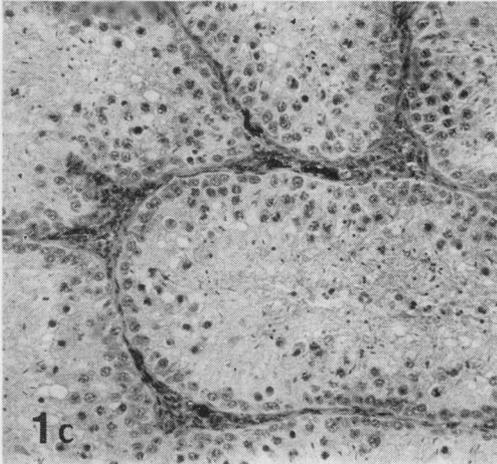
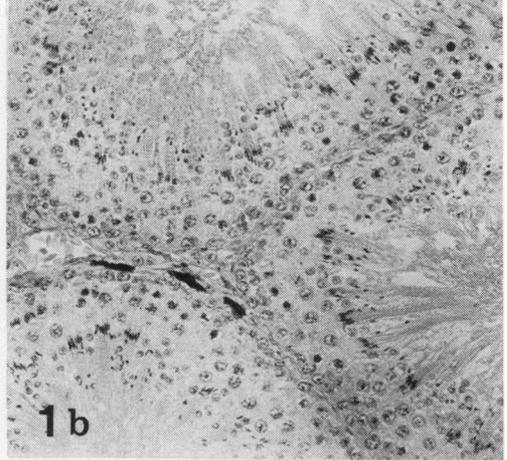
The weight and histological cycles of the testes

The Pied Flycatcher arrives in Sweden in the beginning of May. At this time, every individual has testes which are rapidly progressing towards full breeding condition. Not all of them have reached the final stage in spermatogenesis, but approximately half are in stage 5 (for description of the stage, see below). At the time of nest building all the males have reached the culmination phase of the testes development, stage 6 (Table III). Unfortunately it is not possible to distinguish, by external or internal characters, a one-year-old male from a male more than one year old, the latter in the following text referred to as adult males.

Both testes were examined and no significant histological differences between the right and the left testis were observed. However, there was often a distinct size difference between them. In all cases examined but one, the left testis was heavier than the right one. The weight of the right testis was, on average, only 82 percent of that of the left testis. There were no differences in the histology between the anterior, central, and posterior parts of the testis.

Marked changes in the histology of the

Fig. 1. The different histological stages of the testes of the Pied Flycatcher during the breeding season. Staining: Erlich's haematoxylin-eosin. Magnification of Figs. 1a–e, according to the scale. a. Stage 5. Only a few sperms are present in the tubules. Half of the males from the spring migration are in this stage when they arrive in Sweden. b. Stage 6. The lumen is lined with bundles of sperms and spermatids. This is the appearance of the seminiferous tubules during the height of the breeding season. c. Stage 7. Free sperms in the lumen, but no bundles of sperms lining it. The interstitium has started to regenerate. The testes reach this stage around hatching time. d. Stage 8. No sperms are left in the lumen, but there can still be sperms in the seminal sacs. e. Stage 9. This stage has a very thick interstitium, in which the pigment cells are very conspicuous. Notice that a new tunica albuginea is being formed under the old one. This is the typical appearance of a testis from the nestling period.



0.1 mm

Table I. Mean values \pm S. E. for the estimates of some parameters in the different stages of the testes of the Pied Flycatcher during the breeding season

Stage	Number of birds	Mean testicular weight (mg)	Diameter of the seminiferous tubule (μ)	Thickness of the tunica albuginea (μ)
5	10	22.65 \pm 3.21	209.95 \pm 6.92	15.95 \pm 0.75
6	49	33.33 \pm 2.15	240.71 \pm 4.52	14.55 \pm 0.86
7	12	8.45 \pm 1.32	157.20 \pm 11.77	26.32 \pm 2.29
8	11	4.17 \pm 0.17	122.96 \pm 8.03	34.19 \pm 3.53
9	18	1.55 \pm 0.17	76.14 \pm 4.17	43.48 \pm 1.79

testes appear towards the end of the incubation period. The different stages of the testes from the time the birds arrive in Sweden until the juvenile birds leave the nests can be described as follows (see also Table I and Fig. 1a–e).

Stage 5. The seminiferous tubules contain 1–2 layers of spermatogonia, 2–4 layers of primary spermatocytes, and 2–4 layers of secondary spermatocytes. This stage is above all characterized by the layer of spermatids that line the lumen, and by the presence of very few sperms or none. There are mature Leydig cells in the interstitium, which is very thin.

Stage 6. Full spermatogenesis is going on. A layer with spermatids mixed with bundles of mature sperms lines the lumen, which has been enlarged. The interstitium is as in stage 5.

Stage 7. No bundles of sperms line the lumen, which contains large numbers of free sperms and cellular debris from a degenerating germinal epithelium. There are plenty of vacuoles in the epithelium. The interstitium has started to regenerate. There are no mature Leydig cells.

Stage 8. The germinal epithelium shows varying regression, 1–2 layers of spermatogonia, and a few scattered spermatocytes and no sperms. The interstitium is regenerating vigorously.

Stage 9. The testes are very small with no spermatocytes and 1–2 layers of spermatogonia. Some tubules have a small lumen left, containing some cellular debris. The interstitium is very thick. Pigment cells are common. These give the testes a somewhat grey-green colour.

Contrary to Scott & Middleton (1968), I have found no reason to divide stage 7 into two substages 7a and 7b. In the Cowbird *Molothrus*

ater, substage 7a is characterized by cellular debris and great numbers of free sperms in the tubular lumen, and 7b by small amounts of cellular debris in the very much enlarged lumen. In the Pied Flycatcher there is a smooth transition from stage 7a to 8.

The changes in the mean weight of the testes during the breeding season are shown in Table II. The maximum weight is attained around the egg-laying period. There is, however, a sharp rise in weight immediately after arrival in Sweden. During the incubation period there is a clear decrease in testicular weight, and around hatching time the weight decreases very rapidly. A couple of days later the testicular weight is approximately 20 percent of the maximum weight. The testes then continue to decrease slowly in size and weight.

These changes are accompanied by changes in histology. The size variation in the seminiferous tubule parallels that of the testicular weight (Table II). There are no changes in the thickness of the tunica albuginea until the end of the incubation period, when a new tunica replaces the old one from beneath (Fig. 1e). Fig. 3 shows the variations in the testicular weight at different stages. Obviously the weights are of limited value as criteria of the histological stages of the testes in this species.

When the testes are in full spermatogenesis (stage 6) free sperms may be found in the lumen of the seminiferous tubule. The sperms are then stored in the seminal sacs. There is no direct correlation between the amount of free sperms in the tubules of the testes of stage 6 and in the tubules of the seminal sacs. No less than 35 out of 44 testes at stage 6 had empty lumina, although the seminal sacs contained

Table II. Changes in the reproductive organs of the male Pied Flycatcher during the breeding season. All values are given as mean \pm S. E.

	Number of birds	Average weight of both testes (mg)	Diameter of the seminiferous tubule (μ)	Thickness of tunica albuginea (μ)	Index number of Leydig cells	The height of the epithelium in the tubule of the seminal vesicle (μ)
Spring migration	17	23.14 \pm 1.60	212.53 \pm 5.14	15.88 \pm 0.48	33.29 \pm 4.23	11.20 \pm 0.80
Nest-building	11	33.66 \pm 2.54	247.27 \pm 6.21	14.05 \pm 0.92	77.15 \pm 10.75	15.97 \pm 1.36
Egg-laying	6	36.67 \pm 1.11	275.50 \pm 2.49	13.83 \pm 0.70	116.71 \pm 29.09	18.83 \pm 0.87
Incubation (4-14 days)	16	22.48 \pm 2.89	221.64 \pm 12.76	18.72 \pm 1.79	14.29 \pm 4.84	14.62 \pm 1.01
Nestling						
1-3 days	16	6.97 \pm 2.01	131.69 \pm 14.27	33.07 \pm 2.93	1.92 \pm 0.94	9.55 \pm 0.76
4-6 days	10	8.60 \pm 3.98	119.00 \pm 22.92	38.70 \pm 5.36	5.85 \pm 3.65	10.13 \pm 1.13
7- days	9	2.93 \pm 1.20	80.13 \pm 15.96	37.91 \pm 3.93	0	6.32 \pm 0.87

large amounts of free sperms (Fig. 2a). This supports the theory that the release of sperms is cyclic. The appearance of sperms in the seminiferous tubules could not be related to a certain stage of breeding.

The interstitium

The interstitium of the testis in the Pied Flycatcher passes through distinct changes during the breeding season, both quantitatively and qualitatively. When the testis is in stage 5 and 6 the interstitium is very thin and consists mainly of strands of fibroblasts and blood vessels. Leydig cells are concentrated in the triangular profiles of the intertubular spaces.

The following cells can be distinguished in the interstitium (apart from the cells in the blood vessels):

1. Fibroblasts
2. Pigment cells
3. Mature Leydig cells. Histochemical investigations concerning their cytology have not yet been made.
4. Juvenile cells.

The Leydig cells, which produce testosterone, undergo a seasonal secretory cycle. The nuclei attain their maximum diameter during the secretory phase of the cycle and the cells are then called mature Leydig cells. As shown in

Table II, the maximum number of these cells occurs at the time of nest-building and egg-laying. The cells have a maximum size of about $10 \times 17 \mu$ and the diameter of the nucleus is approximately 5μ . The number and size of the Leydig cells decrease very rapidly during the incubation period, and when the eggs are hatched there are no mature Leydig cells left, except in those individuals that are still in stage 6. During the incubation period the number of fibroblasts increases rapidly, and cells that resemble the juvenile cells, described by Marshall (1949), appear. They are smaller than the mature Leydig cells and have a round nucleus with a diameter of from 2 to 3μ .

The more regressed the testes are, the more prominent are the pigment cells, which have a very irregular form.

Accessory sex organs

The seminal sacs were examined in most individuals. The different components of the reproductive ducts are usually active at the same time (Bailey 1953, Johnston 1956), while the seminal sacs may also reflect the activity of the other ducts. The height of the epithelial cells in the tubules were used as an activity index. The variation of this index during the breeding season is shown in Table II.

When the birds arrive in Sweden the tubules of the seminal sacs are surrounded with a thick layer of muscles, consisting of an inner circular layer of smooth muscles and an outer longitudinal layer. The lumen is uneven and lined with a stratified epithelium of more or less cuboidal cells. During the nest-building period the seminal sacs are enlarged, due to the tubules which increase in number and diameter. The lumen is greatly distended and smooth, and lined with a simple ciliated columnar epithelium (Fig. 2a). The lumen is usually filled with sperms, but sometimes it also contains great amounts of secretions. In these tubules the sperms are much less numerous. The proportion between the number of tubules containing sperms only and tubules containing sperms and secretions varies greatly. In parallel with the enlargement of the lumen, the muscle layers diminish in volume, especially the inner layer. The regression of the seminal sacs starts early in the breeding season (Table II). The height of the epithelial cells is reduced and they also become stratified. The lumen becomes uneven but is still rather large. Sperms are present in the seminal sacs during stage 7, and sometimes also in stage 8. When the testes have started to regress, varying amounts of

cellular debris appear in the tubules of the seminal sacs. At stage 9 the regression of the seminal sacs is complete. Its lumen is now narrow, and its epithelium is stratified and surrounded by muscular layers (Fig. 2b). The lumen contains no sperms and very little cellular debris.

The histology of 25 vasa deferentia, from stage 6, was examined. They had a columnar epithelium of approximately the same height as the epithelium in the tubules of the seminal sacs (mean values 13,6 μ and 15,7 μ respectively). The ducts were mostly empty and contained large amounts of sperm in only eight cases. These latter individuals also had a large amount of free sperms in the seminiferous tubules. When there were no sperms in vas deferens the amount of free sperms in the testis was also low. This is an additional indication that the sperms are not released continuously.

Variation in testicular activity

The variation in testicular activity among confirmed breeding males is apparent in Table II. A few individuals were still in stage 6 when the eggs were hatched (Table III). One of these was an adult male (known by banding).

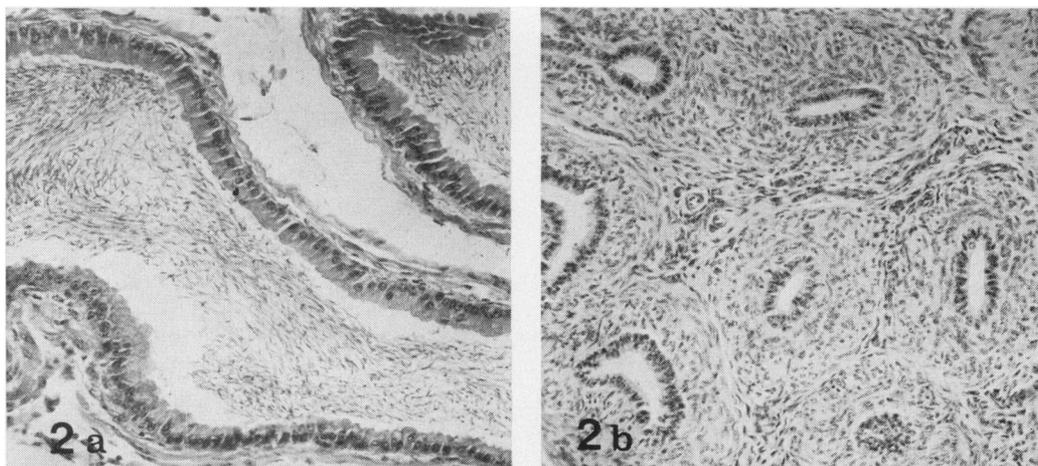


Fig. 2. The histological appearance of the seminal sacs in an active stage, Fig. 2a, and an inactive stage, Fig. 2b. Staining: Erlich's haematoxylin-eosin. The magnification is the same as in Fig. 1. a. The tubules of the seminal sacs are filled with sperms, and the muscle layers are very thin. The epithelial cells are columnar. b. No sperms in the lumen of the tubules. The muscle layers are very thick and the epithelial cells are low and stratified.

Table III. Number of male Pied Flycatchers examined in different stages of testicular activity during the different phases of the breeding season

Stage of testicular activity	Spring migration	Nest-building	Day of egg-laying		Day of incubation				Day of nestling		
			1-3	4-7	1-3	4-6	7-9	10-14	1-3	4-6	7-
5	10	-	-	-	-	-	-	-	-	-	-
6	7	11	3	3	-	-	4	6	1	2	-
7	-	-	-	-	-	2	1	1	5	1	1
8	-	-	-	-	-	-	2	-	4	1	-
9	-	-	-	-	-	-	-	-	6	6	8

Another adult male, taken when the juveniles were two days old, was in stage 9. One male, at least three years old, taken during the eighth incubation day, was in stage 6. Six males taken during the incubation period had testes that

were already in a regression phase. For two of these males it took a long time to attract a female, in spite of their eager singing during many days. In these cases the clutches were laid about two weeks after the average laying date for the population. The first clutches of the other four males were robbed, but they succeeded in producing new clutches, approximately eight days after the first clutch was robbed. Apart from the above individuals, the variation in testicular activity during the different breeding phases was very low, in spite of the fact that regression varied between different latitudes (Fig. 4). It did not vary much between the different years (Fig. 4).

A number of males that do not breed in the area appeared. These individuals could of course breed outside the study areas, but they could also be unmated males. An occupied nest-box was usually visited by many different males during the breeding period, and even during the same day. Also, empty nest-boxes were often visited with territory establishment as a consequence. A comparison of the testes from these males with those from the males breeding with certainty shows no differences (Fig. 5). However, it should be pointed out that two males that had been singing around empty nest-boxes during a time when the eggs were hatching in the breeding population (and were therefore probably unpaired males) were in stage 6.

Mean testicular weight (mg)

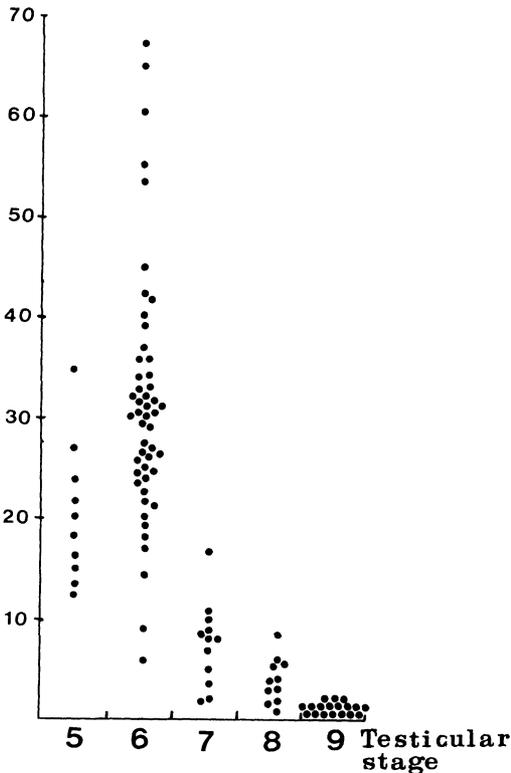


Fig. 3. The variation in the mean weight of the testes during the different stages. Notice that one cannot with certainty put the weight (size) of the testes in relation to their activity.

Second broods

The Pied Flycatcher can lay a new clutch if the first one is destroyed, but second broods

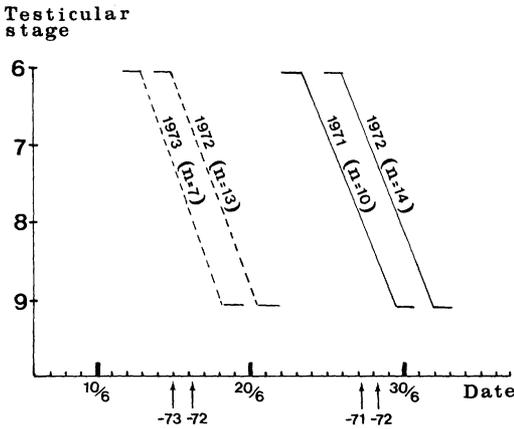


Fig. 4. The diagram illustrates the time of testicular regression during different years and at different latitudes in Sweden. The continuous lines represent Ammarnäs (65°58') and the broken lines represent Rävlanda (57°40'). The arrows indicate the average hatching time of the populations. The number of males examined, from the time covered by the lines, is given in parenthesis.

have never been found in western Europe (Creutz 1955). In my areas, re-laying always took place in a new nest-box, and usually with a new male.

In 1971 one third of the clutches at Ammarnäs were robbed during the egg-laying period by weasels and a pair of Wrynecks *Jynx torquilla*. In one of the study areas in the southwest of Sweden many clutches were destroyed by the Great Spotted Woodpecker *Dendrocopos major* in 1973. In these cases four and two re-layings, respectively, were observed. In only one case did the female breed with the same male again. The males were collected during the incubation period. The testes were examined, and found not to differ in activity from the average values of the population for that time (Fig. 5), but in two cases the testes were in a regression stage, when all other males are in stage 6. Thus, spermatogenesis in the late-breeding males does not seem to be prolonged by stimuli from breeding itself. One polygynous male was examined showing no prolongation of spermatogenesis.

Experimental removal of broods

In the two investigation areas at Rävlanda in

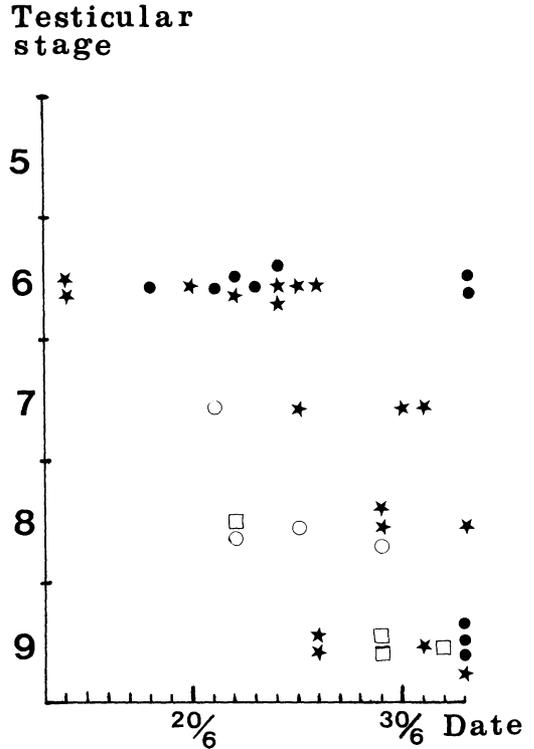


Fig. 5. The stage of testicular activity in different types of males from Ammarnäs 1971 and 1972. * = Testes from breeding males with an exactly known breeding status. ○ = Testes from rebreeding males. □ = Testes from males visiting an occupied nest-box. ● = Testes from males visiting an empty nest-box.

1973, all the juveniles (27 broods) were taken when they were one day old. In one area also all the males were removed. In this forest there were, besides my two areas, additional areas with approximately 350 nest-boxes, where a relatively effective follow-up of re-nesting birds could be done. The distances between the areas ranged from 0.5 to 2.5 km. No re-nesting was found.

During two days of the nest-building period every male and female Pied Flycatcher was removed from the study area with 40 nest-boxes at Åskloster. New flycatchers appeared immediately in the area and bred in 11 boxes.

Sex ratio

Twenty broods were taken and the juveniles were dissected to determine the sex. Of these, 52 per cent were males. The sex ratio was tested with a binomial test, with the result that the possibility of an equal sex ratio was not refuted ($P > 0.68$).

DISCUSSION

The Pied Flycatcher is usually a polyterritorial and occasionally polygamous single-brooded species. The male usually deserts the female, generally on the day when she lays her first egg, and establishes a second territory where he tries to get a second female to breed. How he succeeds in this varies between different years and places (von Haartman 1951a, own observations).

The breeding times of the populations must be regarded as a result of environmental adaptations. The optimal conditions for producing fledglings occur later in the northern than in the southern parts of Sweden. There must therefore be a timing mechanism for the reproduction to occur at the right time. The initiation of the testicular growth in the Pied Flycatcher might be due to the changes in the photoperiod as in many other migratory birds (e. g. Farner 1964, Wolfson 1965, Farner & Follett 1966, Hamner 1966, Lofts & Murton 1968, Haase 1973), although one must not exclude the possibility of an initiation based on an endogenous rhythm as shown in some *Sylvia* species (Berthold 1971, 1972). When the Pied Flycatchers arrive in Sweden in the beginning of May, about one half of the males do not show maximum spermatogenesis, but are in stage 5. Berthold (1969) showed that northern populations of some passerines have a much later testicular development than southern ones. It is possible, therefore, that the males of stage 5 are transients belonging to northern populations. The possibility should not be excluded that these males might also be one year old. Spermatogenesis is known to start earlier in the following adult males: *Zonotrichia leucophrys nuttali* (Blanchard

1941), *Agelaius phoeniceus* (Wright & Wright 1944), *Pipilo erythrophthalmus* (Davis 1958), *Quiscalus mexicanus* (Selander & Hauser 1965), and *Zonotrichia leucophrys gambelii* (King et al. 1966).

Normally, testicular regression in the Pied Flycatcher occurs at a definite time, around hatching. Spermatogenesis is not prolonged by late breeding or by new clutches laid after the first clutch has been robbed. The duration of spermatogenesis seems to be of a definite time. Although the testicular regression occurs later in the season in the northern populations than in the southern ones, approximately 12 days (Fig. 4), it is unlikely that the northern populations have a longer duration of spermatogenesis activity. It is more probable that they have evolved a higher threshold value for photostimulation and are thereby destined to breed later in the season. That northern populations have a higher threshold value for photostimulation than southern ones has been shown in *Passer domesticus* (Threadgold 1960), *Fringilla coelebs* (Dolnik 1963), and *Zonotrichia leucophrys gambelii* (King et al. 1966). Threadgold (1960) also showed that more northern populations of the House Sparrow have a shorter duration of spermatogenesis.

Even if the number of polygamous males is low, altogether five individuals in my areas, the males are usually polyterritorial. Von Haartman (1956) reported that about 60 per cent of the males at Lemsjöholm tried to establish second territories. The corresponding figure in my areas was 80 per cent. Von Haartman (1969a) also pointed out the importance of polyterritoriality for the development of polygyny. In other investigated one-brooded species, spermatogenesis usually ceases when the juveniles leave the nest, or later. King et al. (1966) and Martin et al. (1972) consider this an important adaptation in case the brood should be robbed. The testicular cycle is therefore also less dependent on the timing with the female gonad cycle, which is more easily influenced by environmental stimuli than the male's. The Pied Flycatcher does not have this adaptation. Among the species examined, there is only one with a testicular regres-

sion at the same time in the breeding cycle as the Pied Flycatcher, namely the Black-billed Magpie *Pica pica* (Erpino 1969).

Breeding must cease before deteriorating conditions arise, to avoid production of young when the chance of survival is reduced. The refractory period therefore prevents breeding during suboptimal conditions. There are some late broods among the Pied Flycatchers. Creutz (1955) reports that the number of juveniles in late broods is 3.9 while the number in the earlier broods is 5.5. Von Haartman (1969b) reports that in Lemsjöholm clutches which were started after 25 May decreased in clutch-size. In clutches hatched after 7 July in Amarnäs very few juveniles leave the nests. From these late broods 25 % of the hatched eggs became fledglings in 1970 ($n=9$), 100 % ($n=1$) in 1971, and 20 % ($n=2$) in 1972. The figures from the period 4–6 July are: 22 % ($n=8$) in 1970, 50 % ($n=2$) in 1971, and 77 % ($n=20$) in 1972. The corresponding figures from earlier broods, during these years, lie approximately between 80–100 % ($n=278$) (Myhrberg & Nyholm, unpublished data). The reason for this great loss in late broods is not known, but it is apparently an advantage for the Pied Flycatcher to lay early broods, and thereby no disadvantage if there is an early ending to sexual activities. On the other hand, it must be a disadvantage not to be able to produce a new clutch if the first one is destroyed after hatching, even if these clutches produce fewer young than the first ones. The male Pied Flycatcher can partly compensate for this incapacity by polygamous behaviour. Von Haartman (1951a) showed that one monogamous male produced 26 juveniles during six years, while one polygamous male produced the same number of juveniles during three years. During one year in Lemsjöholm the average number of fledged broods was 1.35 among polygamous males, while the corresponding figure for monogamous males was 0.76 (von Haartman 1969). Von Haartman also points out that polygyny is more pronounced in some individuals, and that polygamous behaviour may be due to genetic factors. In this connection it should be pointed

out that the three males which after hatching were still in stage 6 (Table III) were males which during the earlier breeding phases had not established second territories.

When considering the adaptive value of polygamous behaviour, it is not enough to find out whether or not there are sperms in the testes and the seminal sacs; one must relate it to the cycle of the Leydig cells, the producer of testosterone, and thereby to much of the sexual behaviour during the breeding period. Benoit (1922) showed that the size of these cells is developed parallel to some secondary sex characters. This has also been shown by Munding (1972) and Haase (1973). Behaviour changes due to androgens have been shown by many authors, e.g. Bennet (1940), Colli (1950), Erickson & Lehrman (1964), Murton et al. (1969b). The number of Leydig cells shows a marked decrease after the egg-laying period (Table II), and around hatching time there are no mature Leydig cells left. Creutz (1955) and Curio (1959) point out that the song of the male Pied Flycatcher, whose function, among other things, is to attract a female, is most intense during the egg-laying period. During the incubation period the song intensity decreases rapidly and when the eggs are hatched only occasional strophes are heard among some males. Von Haartman (1956) mentions that aggressiveness among males is markedly reduced after the females have started to incubate. Aggressive behaviour is a necessity for the establishment of a territory. Both points are very obvious in my populations. Most males that establish a second territory return to their home territory in the middle of the incubation period; thereafter no more attempts are made to establish a second territory. These observations are well correlated with the changes in the cycle of the Leydig cells.

Formerly, one thought that a major reason for polygamy was an unbalanced sex ratio in the broods. This has been proved wrong. The Pied Flycatcher, as other polygamous species (Kluijder et al. 1940, Williams 1940, Selander 1960, Verner 1964, Zimmerman 1966), has a primary sex ratio 1:1. Even if the sex ratio

is equal for juvenile birds, it can be changed due to differential mortality rates between the sexes. The Boat-tailed Grackle *Cassidix mexicanus* (Selander 1960) has a sex ratio 1:3.72 (♂:♀) in adult birds during the breeding season. A skewed distribution between adult sexes does not seem to exist among Pied Flycatchers (von Haartman 1951a). There will still be a somewhat unbalanced sex ratio among breeding birds, to the advantage of the female, as one-year-old males usually do not breed, while one-year-old females do (Trettau & Merkel 1943, von Haartman 1951a, Creutz 1955). Despite this, one-year-old male Pied Flycatchers have testes in spermatogenesis (Salomonsen 1931).

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