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Some remarks on the population endocrinology of the Pied Flycatcher (Ficedula hypoleuca)

Bengt Silverin

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The paper summarizes some of the work that has been done on the population endocrinology of the Pied Flycatcher. Emphasis is given to polyterritoriality and testosterone levels in monoterritorial and polyterritorial males, the time of gonadal regression and the ending of incubation and its relation to prolactin secretion. The importance of knowing the exact ecological status of the individual when doing endocrine studies on free-living birds is also stressed.

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1. Introduction

The Pied Flycatcher is one of the most extensively studied bird species, and its breeding ecology and behaviour is well known (e.g. Askenmo 1977). However, no studies on the endocrinology of the Pied Flycatcher had been performed until I started my studies about 15 years ago. The term "*Population endocrinology*" was used for these studies and it is defined as 'the study of the endocrine status and dynamics of organisms in free-living populations'. Its ultimate aim is to contribute to the solution of problems in population ecology by obtaining information from the endocrine processes underlying those responses to environmental stimuli which are manifested by various behavioural reactions as well as certain phenotypic modifications of important biological parameters of the population. These studies have been reviewed extensively in the endocrinological litterature by Silverin (1983a, b). In the following I present a few of my results.

2. Material and methods

The study sites were east of Gothenburg (Rävlanda 57° 40′ N), south-west Sweden, and for a few studies at Ammarnäs (65° 58′ N), northern Sweden. Flycatchers were, during most years, colour banded as soon as possible after their arrival in the breeding area. Breeding data were collected by regular inspection of nest-boxes and the behaviour of the Pied Flycatchers was followed almost daily by visual observations. Some studies were performed using histological and histochemical techniques. For hormonal assays blood was removed, immediately after capture in the field, from the jugular vein into a heparinised syringe. The syringe was kept on ice and blood samples were centrifuged later the same day. All blood samples were procured between 0700 and 1200 hrs. The plasma was stored at -20° C until analysed. The following hormones have been measured by radioimmunoassay: dihydrotestosterone, testosterone, oestradiol-17 β, corticosterone, LH, FSH and prolactin. For details concerning the methods see Silverin & Wingfield (1982) and Silverin & Goldsmith (1983).

3. Calendar time versus breeding stage

Most endocrine studies on wild birds have been done on individuals whose ecological status has been unknown. Usually a number of birds have been caught at regular intervals and data grouped on a calendar basis. This method is sufficient when studing major changes during e.g. a year, but quite inadequate for studies in population endocrinology. Such studies requires individual recognition of the birds and an exact knowledge of their ecological status. A population breeds more or less asynchronously and a transitory peak in hormonal secretion may be

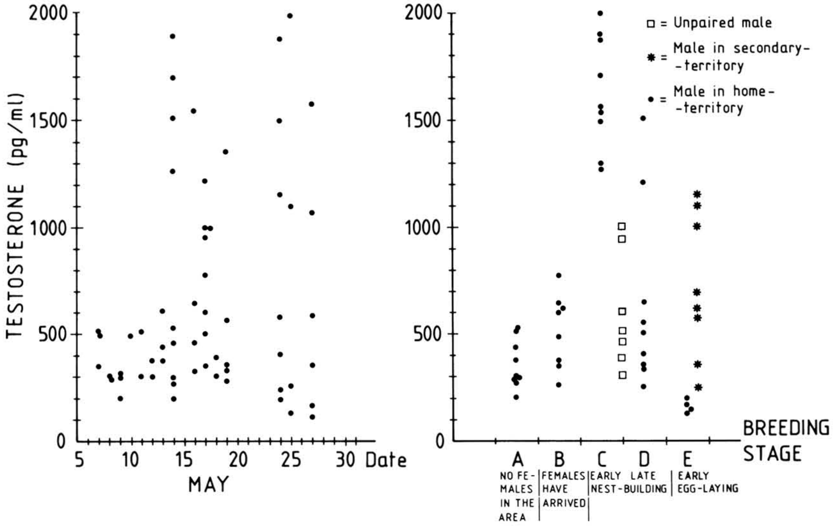

Fig. 1. The figure illustrates the importance of knowing the exact breeding status of the individual. Male plasma levels of testosterone are correlated to the time of capture (left figure) and breeding stage (right figure).

hidden in the standard deviation of the sample if the results are grouped only according to the calendar.

An example is given in Fig. 1. The left part of the figure shows male plasma levels of testosterone plotted against the date of sampling. High levels are found in some males during the middle and later part of the month, but it is impossible to draw any conclusions concerning the cause of these high testosterone values. However, when the data are grouped in relation to the exact breeding stage of the individual (right part of Fig. 1) a clear pattern is seen. Pairing is associated with a significant increase in the plasma concentration of testosterone, as well as LH (not shown in the figure). These high values are, however, maintained only for a few days. Thus, the short transitory testosterone peak occuring during the early part of the nest-building period would have been undetected if the exact breeding stage of each individual had not been considered.

The functional significance of this increase is not clear. It seems likely that stimuli from the female, in connection with her choice of mate, induce this rise in male testosterone titers, as testosterone levels in unpaired males remain on "low" levels. Exactly how this rise in testosterone changes the behaviour of the male is not known but, as LH-levels (oestrogen levels are at this time below the level of detectability of the assay system) (Silverin & Wingfield 1982) and the sexual receptivity (willingness to copulate) (von Haartman 1951) increases in females during the later part of the nest-building period, it is likely that there is a reciprocal interaction between female and male behaviour during this breeding phase. The results thus indicate that to become sexually receptive the female first has to stimulate the male so that he, in turn, can stimulate her into nest-building and copulation.

4. Polyterritoriality and testosterone

The polyterritorial and polygamous behaviour of the male Pied Flycatcher is well-known. However, not all males are polyterritorial and the percentage of these males differs with habitat and nest-hole availability (Silverin & Wingfield 1982, Alatalo & Lundberg 1984).

Males establishing secondary territories usually leave their home-territories during the egg-laying period and return before the end of the incubation period (Silverin 1983a, b). In mated males, plasma levels of testosterone have decreased to what I call the territory-establishment level at the end of the nest-building period (Fig. 1). Contrary to males establishing secondary territories, testosterone levels continue to decrease in males not establishing secondary territories and the concentration reaches basal levels during the egg-laying period. In the former group, testosterone levels remain on the territory-establishment level (Fig. 1) and basal levels are not reached until these males have returned to their home-territories. This normally occurs during the end of the incubation period.

It seems likely that high plasma levels of testosterone are necessary for the establishment of the secondary territory. This assumption is supported by the results from an experiment where I treated all males in a population with long-acting testosterone implants (Silverin 1980a). In this population all males established secondary territories and most of them continued to defend secondary territories throughout the breeding season.

Why does the testosterone concentration stay on a territory-establishment level in some males while it reaches basal levels in others? There are three possible explanations. It is well documented that food shortage depresses plasma levels of testosterone (e.g. Wingfield 1980). One could therefore expect a food shortage in those territories where male testosterone concentrations reach basal level during the egg-laying phase. A food shortage would also have increased plasma levels of corticosterone (e.g. Wingfield 1980). Such an increase was, however, not found in monoterritorial Pied Flycatchers (Silverin & Wingfield 1982) and so food shortage can be excluded as a possible cause for the low testosterone values.

None of the two following hypotheses can, however, be excluded. The Pied Flycatcher population is polymorphic and consists of some individuals more or less genetically bound for monogamy and others for polygamy. The first category would attain basal levels of testosterone during the egg-laying period and thus be physiologically unmotivated to establish secondary territories. The second hypothesis assumes that all males are potential polygynists, but that supplementary stimuli are lacking at the end of the nest-building period for some males. Male behaviour during the nest-building period is poorly known as they may wander considerably at this time. It can be speculated that these excursions may have two reasons: 1) to explore the local area for e.g. new breeding facilities; 2) to guard the female in order to avoid being cuckolded. Regardless of the purpose of these excursions, the male may gain supplementary information from the surroundings such as the presence of unmated females or unoccupied nest-holes. Such supplementary information may be necessary to maintain testosterone levels on the territory-establishment level. Lack of such information will result in a decrease in the testosterone concentration to basal levels.

5. Gonadal regression in Pied Flycatchers

Gonadal regression prevents breeding at times when the chances of success are small. Normally testes regress, i.e. sperm-production ceases and testicular size diminishes enormously, at a time when the juveniles leave the nest. This must be looked upon as an adaptation for renesting at a time when the nest may be robbed, i.e. the nestling period. However, in the Pied Flycatcher (Silverin 1975) and the Collared Flycatcher (*Ficedula albicollis*) (Silverin, unpublished data), testes normally regress at the time of hatching and this is independent of both latitude and year (Fig. 2). This implies that a male Pied Flycatcher can not father a new clutch if the nestlings are robbed. Removal experiments have shown that in a normal population renesting can occur till the end of the incubation period, i.e. as long as males produce sperms (Silverin 1980b).

To test whether the female's inability to renest after hatching time is due to the male's inability to produce sperm, all males within two small populations were given long-acting testosterone implants early in the breeding season. This administration of testosterone resulted in a lack of testicular regression and testes continued to produce sperm as long as the experiment continued. Furthermore, most males did not return to the home-territory but continued to defend secondary-territories where they tried to attract females to breed. In one of the experimental populations all clutches were removed during the later part of the incubation period and in the other population, at a later date, all broods were removed. The same experiment was performed in an untreated control population (Silverin 1980a, b). After removal, testosterone treated males were, in both populations, seen in courtship displays in front of females whose nests had been robbed. But only in the case where

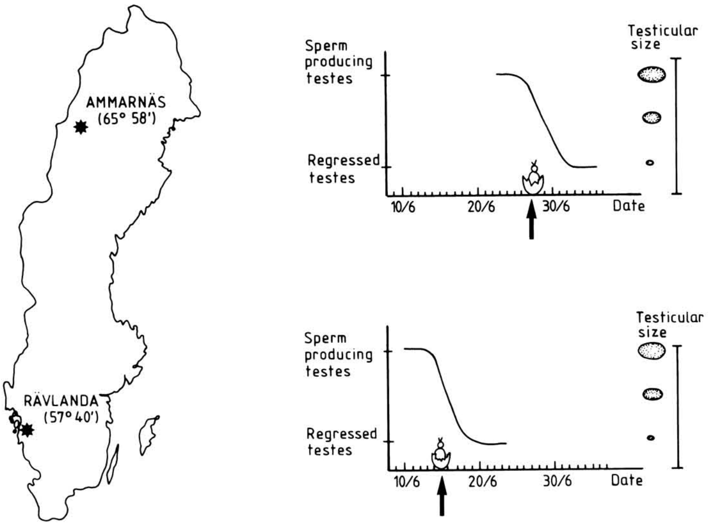

Fig. 2. The time of testicular regression in 1972 in two different populations of Pied flycatchers is illustrated in this figure. The arrows indicate the average hatching time for the populations that year.

clutches had been removed did females lay new clutches. The control population showed the same result. Experiments on caged females, paired as well as unpaired, have shown that under experimental conditions ovary growth can be induced until, but not later than approximately the average hatching date for the population (Silverin 1980b).

Thus, it seems obvious that both male and female Pied Flycatchers enter the so called refractory period around the average hatching time for the population. Why has this early gonadal regression evolved in the Pied Flycatcher? There are at least two adaptive values connected with it. Pied Flycatchers arrive late in spring at the breeding areas (beginning of May) and start migration early in the autumn (late August). The flycatchers seem to be short of time after breeding as many of them, especially the males, start to moult at the end of the nestling period (Ojanen & Orell 1982). At the onset of the autumn migration (approximately 40 days after breeding), the birds have not put on any weight (Silverin 1981) and many are still in moult (Hyytiä & Vikberg 1973). It has been shown in other bird species that renesting results in a second increase in male testosterone levels and that this delays the onset of moult (e.g. Wingfield & Farner 1979). This would probably be the case in the Pied Flycatcher if they had had a "normal" gonadal cycle. As moult is a very energy consuming process, a delay would either postpone the onset of migration or the birds would have to moult most of their feathers while migrating. In both cases an increase in mortality would be expected.

Another important factor to consider is the seasonal decline in clutch size. The Pied Flycatcher shows a very rapid decrease in clutch size (von Haartman 1967) and a higher proportion of young die due to starvation if the clutch is laid late in the season (Källander 1975).

Thus it is suggested that shortness of time and/or the very low success of late breedings have been important factors in the evolution of the early gonadal regression in the Pied Flycatcher. Whether the males' polygamous behaviour evolved prior to the evolution of the early gonadal regression, and thus turned out to be a preadapted behaviour, or evolved afterwards is impossible to tell.

6. Ending of incubation

The female alone incubates the eggs for approximately 14 days. A nest with dead eggs is abandoned after about 21 days and no female has been observed to incubate for more than 23 days (Silverin & Goldsmith 1984). Why does not the female abandon the nest after e.g. 17 or 25 days instead? If the eggs are not hatched after a certain

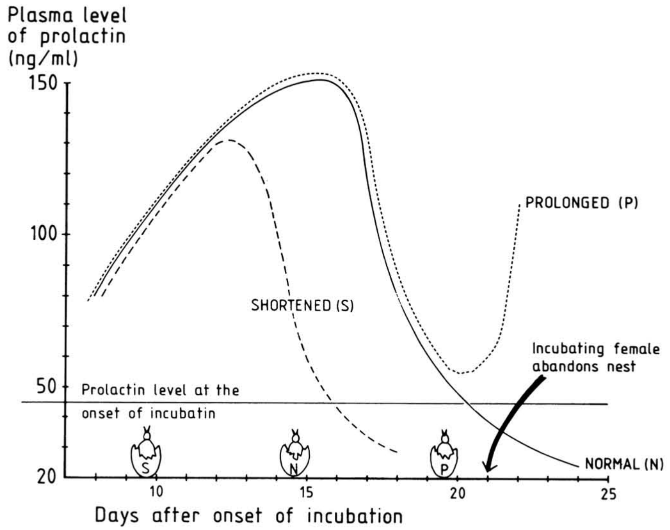

Fig. 3. Schematic illustration of plasma prolactin concentrations in three groups of incubating female Pied flycatchers. By exchanging early and late clutches two experimental groups were produced: one group of females with a shortened incubation period (10 days) and one group with a prolonged incubation period (19 days). The results indicate that it might be a decrease in the prolactin secretion that makes a female abandon the nest after approximately 21 days, if the eggs have not hatched by this time.

number of days it is likely that they are sterile or that the embryos are dead, and thus maladaptive for the female to continue incubation. But what makes her stop incubating?

There are several controversial questions regarding prolactin and its role in the initiation and/or maintenance of the incubation behaviour. However, the incubation period is invariably associated with high plasma levels of prolactin, although the detailed temporal pattern of its secretion differs between species.

In the Pied Flycatcher there is a steady increase of the prolactin concentration throughout the incubation period and the level declines markedly between two and four days after the eggs have hatched (Fig. 3) (Silverin & Goldsmith 1983, 1984). One of the experiments I have carried out on prolactin and incubation in the Pied Flycatcher was aimed at finding out it the duration of high prolactin secretion is set by an endogenous timing mechanism or if the decline is caused by a change in the external stimuli. In this study prolonged and shortened incubation periods were produced by exchanging early and late clutches. Serial blood sampling from females with the artifically shortened incubation period clearly showed that the duration of high prolactin levels are not fixed by an endogenous rhythm, but presumable maintained by external stimuli from the eggs and young. On the other hand, the results from the experiment with prolonged incubation showed that the high prolactin levels can not be maintained by visual or tactile stimuli from the eggs for more than 16–18 days, i.e. as long as in normally incubating females. At about 20 days after the onset of incubation plasma levels have declined to the same level as during the first day of incubation, despite the fact that the female is still sitting on the eggs. These results make it tempting to conclude that the eventual desertion of the nest is a result of the decline in prolactin secretion.

References

Alatalo, R. V. & Lundberg, A. 1984: Polygyny in the Pied flycatcher. — Ann. Zool. Fennici 21:217–228.

Askenmo, C. 1977: Some aspects of the reproduction strategy of the Pied flycatcher Ficedula hypoleuca (Pallas). —Ph. D. Thesis, University of Gothenburg, Sweden.

von Haartman, L. 1951: Successive polygamy. — Behaviour 3:256–274.

—"— 1967: Clutch size in the Pied Flycatcher. — Proc. 14th Int. Ornithol. Congr. Oxford 1966:155–164. Oxford.

Hyytiä, K. & Vikberg, P. 1973: Autumn migration and moult of the Spotted Flycatcher Muscicapa striata and the Pied Flycatcher Ficedula hypoleuca at the Signilskär bird station. — Ornis Fennica 50:134–143.

Källander, H. 1975: Breeding data for the Pied Flycatcher Ficedula hypoleuca in southernmost Sweden. — Ornis Fennica 52:97–102.

Ojanen, M. & Orell, M. 1982: Onset of moult among breeding Pied Flycatchers (Ficedula hypoleuca) in northern Finland. — Vogelwarte 31:445–451.

Silverin, B. 1975: Reproductive organs and breeding behaviour of the male Pied Flycatcher Ficedula hypoleuca (Pallas). — Ornis Scand. 6:15-26.

—"— 1980a: Effects of long-acting testosterone treatment on free-living Pied Flycatchers Ficedula hypoleuca during the breeding period. — Anim. Behav. 28:906-912.

—"— 1980b: Seasonal development of reproductive organs in the female Pied Flycatcher Ficedula hypoleuca and experimental studies on duration of her re-nesting ability. — J. Zool., Lond. 190:241-257.

—"— 1981: Reproductive effort, as expressed in body and organ weights, in the Pied Flycatcher. — Ornis Scand. 12:133-139.

—"— 1983a: Population endocrinology and gonadal activities of the male Pied flycatcher (Ficedula hypoleuca). — In: Mikami, S. (ed.), Avian endocrinology: Environmental and ecological perspectives: 289-305. Springerverlag. Japan Sci. Soc. Press, Tokyo.

—"— 1983b: Population endocrinology of the female Pied flycatcher, Ficedula hypoleuca. — In: Balthazart, J., Pröve, E. & Gilles, R. (eds.), Hormones and behaviour in higher vertebrates: 388-397. Springer-Verlag Berlin/Heidelberg.

Silverin, B. & Wingfield, J. C. 1982: Patterns of breeding behaviour and plasma levels of hormones in a free-living behaviour and plasma levels of hormones in a free-living population of Pied Flycathers, Ficedula hypoleuca. — J. Zool., Lond. 198:117-129.

Silverin, b. & Goldsmith, A. R. 1983: Reproductive endocrinology of free living Pied Flycatchers (Ficedula hypoleuca): prolactin and FSH secretion in relation to incubation and clutch size. — J. Zool., Lond. 200:119-130.

—"— 1984: The effects of modifying incubation on prolactin secretion in freeliving Pied Flycatchers. — Gen. Comp. Endocrinol. 55:239-244.

Wingfield, J. C. 1980: Fine temporal adjustments of reproductive functions. — In: Epple, A. & Stetson, M.S. (eds.), Avian endocrinology: 376-389. Academic press, New York and London.

Wingfield, J. C. & Farner D. S. 1979: Some endocrine correlates of renesting after loss of clutch or brood in the White-crowned Sparrow, Zonotrichia leucophrys gambelii. — Gen. Comp. Endocrinol. 38:322-331.

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