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Hormones and behaviour: a comparison of studies on seasonal changes in song production and testosterone plasma levels in the Willow Tit *Parus montanus* [1]

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Two previously published studies giving observations on the annual cycle of song production and seasonal variations in testosterone plasma levels in the Willow Tit *Parus montanus* were compared in an attempt to elucidate the still poorly understood connection between hormones and behaviour. In Willow Tit males, the annual cycle of song production runs parallel to seasonal variations in the plasma levels of testosterone, showing peaks in both spring and late summer. In females, increased testosterone levels could be established only in late summer, but, as in the males, the increased levels in late summer are due exclusively to juvenile birds. In view of the idea that song production in birds is closely associated with testosterone, these findings confirm the conclusions that most of the singing in spring is done by adult Willow Tit males, that the chief contributors to the song period in late summer are the juveniles of either sex, and that the singing of immature Willow Tits occurs mainly in connection with aggressive encounters. The endocrinological data agree with reports of increased song activity in young Willow Tit males and females in late summer.

1. Introduction

As pointed out by Bezzel (1988), the recording of the annual cycle of song production in birds has so far not attained the popularity of, for example, observations of the seasonal course of migration or the moult. Because of this, there are only a small number of publications which give more or less detailed information about seasonal changes of song activity in birds. The best-investigated group of birds in this respect is the *Paridae*: accurate data on the annual course of song are available for the Coal Tit *Parus ater* (Goller 1987), the Marsh Tit *Parus palustris* (Rost 1987), the Great Tit *Parus major* (Alexander 1935, Rost 1990 a), and the Willow Tit (Alexander 1932).

In 1938 Hamilton first directly demonstrated the effect of an androgene on bird vocalizations by injecting immature domestic chickens with testosterone, which caused them to crow. Since then a large number of studies have illustrated

[1] Dedicated to Dr. Hans Löhrl on the occasion of his 80th birthday.

the effects of testosterone on avian vocalizations: injections of testosterone reinstated song in male birds after castration, induced song in females and augmented it in intact males (Silver et al. 1979, Balthazart 1983, Pröve 1983, Wingfield 1983, Pohl-Appel & Sossinka 1984, Heid et al. 1985, Marler et al. 1987, 1988). Furthermore, in a number of bird species spring testosterone profiles correlate with the amount of song produced in that season (Marler et al. 1988), and winter regression of the testes is usually associated with the cessation of singing in birds (Armstrong 1973). Over and above that, a close connection of song with plasma levels of testosterone was found in the Great Tit throughout the year (Rost 1990 a).

The present paper compares the results of two previously published studies on the song activity of the Willow Tit in the course of the year (Alexander 1932) and on seasonal variations of testosterone levels in this species (Silverin et al. 1986). Examination of these behavioural and endocrinological observations can be expected to yield information about the association of testosterone and song production during the year.

2. Material and methods

As data on song activity and endocrinology were not available from the same study area, a comparison was made between material from England on the Willow Tit's song (Alexander 1932) and from Sweden on the testosterone levels (Silverin et al. 1986). Alexander (1932) studied the song activity of free-living Willow Tits in Southern and Central England for 24 years by recording whether the song was audible in a given month of the year or not. Silverin et al. (1986) determined plasma levels of testosterone in free-living Willow Tits caught in coniferous forests east of Gothenburg (southwest Sweden) throughout the year.

According to Slagsvold's (1975, 1977) findings regarding latitudinal retardation in the breeding time of birds in Scandinavia, the day on which the first egg is laid by Willow Tits in the vicinity of Gothenburg can be calculated as 2 May; this agrees with Silverin et al. (1986, 1989 a), who reported that near Gothenburg the first eggs are usually laid by Willow Tits at the end of April / early May. The corresponding date for England is 1 May (Barnes 1975 — data from 1948 through 1971 included).

In winter, Willow Tits can be heard singing in both England (Alexander 1932) and southwest Sweden (Silverin et al. 1986, 1989 a), but the proportion of singing Willow Tits remains low till the end of February, increasing sharply during March, and reaching a maximum in April (Alexander 1932, Ekman 1981, Silverin et al. 1986, 1989 a).

In view of the great degree of correspondence, it can be concluded that the annual cycles of song activity and the seasonal variations in the plasma levels of testosterone do not differ to any marked extent between England and Sweden. There thus appears to be justification for direct comparison of behavioural data originating from England and endocrinological data from Sweden.

3. Results

3.1. Male Willow Tits

The annual course of Willow Tit song (broken line in Fig. 1) shows two main periods: the first in spring (maximum in April), and the second in late summer (maximum in August; Alexander 1932). In parallel with song production, the testosterone levels change with the season, showing a maximum in April and increased values in August and September (solid line in Fig. 1; from Silverin et al. 1986). Since the August and September levels ranged from very high to basal, no statistically significant difference was found between the plasma level of testosterone in August and the levels in July or September. The August level was significantly higher, however, than that of June ($P < 0.05$, two-tailed Mann-Whitney U-test).

In juvenile Willow Tit males (closed triangles in Fig. 1), testosterone increases significantly between July and August, remains higher in September, and decreases significantly between September and October ($P < 0.05$ in all cases). With the exception of August and September, the monthly plasma levels of testosterone do not differ between adult and juvenile males (Silverin et al. 1986).

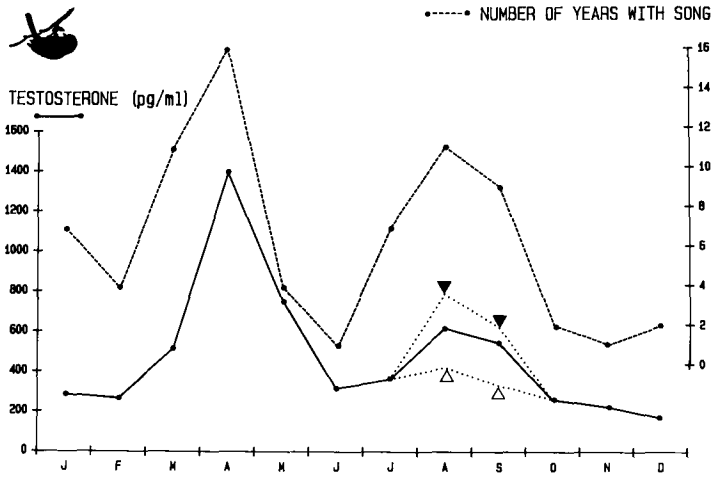

Fig. 1. Annual cycle of song activity (broken line; according to Alexander 1932) and seasonal changes of plasma levels of testosterone (solid line; mean values according to Silverin et al. 1986) in Willow Tit males. In addition, the mean testosterone levels of juvenile and adult males are given for August and September (filled triangle = juvenile males, empty triangle = adult males).

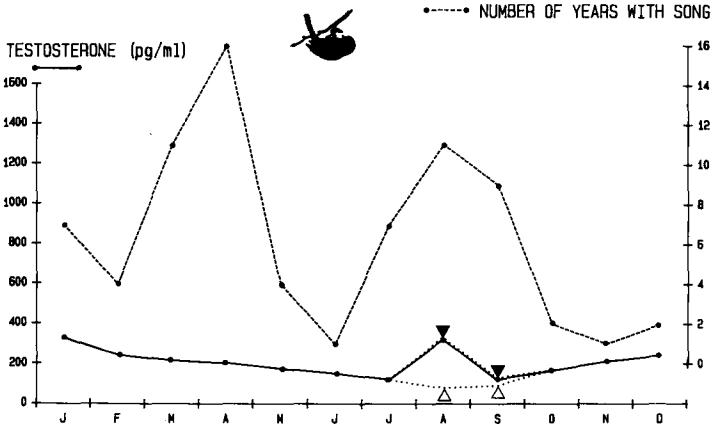

Fig. 2. Annual cycle of song activity (broken line; according to Alexander 1932) and seasonal changes of plasma levels of testosterone (solid line; mean values according to Silverin et al. 1986) in Willow Tit females. In addition the mean testosterone levels of juvenile and adult females are given for August and September (filled triangle = juvenile females, empty triangle = adult females).

Singing activity and hormone levels correlate significantly throughout the year in both adult Willow Tit males (Spearman rank correlation coefficient $r_S = 0.7443$, $n = 12$, $P < 0.005$) and juvenile males ($r_S = 0.7795$, $n = 12$, $P < 0.005$).

3.2. Female Willow Tits

Except for August, when there are indications of a testosterone peak, Willow Tit females show no significant changes in testosterone levels during the year (solid line in Fig. 2; according to Silverin et al. 1986). As in males, increased levels in late summer occur in parallel with an increase in song activity and are due to higher testosterone values in juveniles (closed triangles in Fig. 2). In juvenile females, the plasma level of testosterone in August is significantly higher than the levels in July and September ($P < 0.05$ in both cases). August is the only month in which an age-related difference in the plasma levels of testosterone can be established in female Willow Tits (Silverin et al. 1986).

4. Discussion

As in Marsh Tits (Rost 1987) and Great Tits (Alexander 1935, Rost 1990 a), the annual course of song activity in the Willow Tit is characterized by two major song periods: spring and late summer (Fig. 1 and 2). Rather little is known, however, about the contribution of different age-groups of the two sexes to the song periods.

In the Marsh Tit (sibling species of the Willow Tit) almost all the singing in spring is done by the males; female song is heard only occasionally during territory disputes with conspecific neighbours (Rost 1987). Although there is some singing by adult males, the chief contributors to the song period in late summer are clearly the juvenile birds of either sex; in juveniles the amount of song produced by males is marginally higher than that by females (Rost 1987). In the Marsh Tit song learning and song development coincide and are finished early in life; male and female juveniles are already able to utter the full song by the end of July/beginning of August (Rost 1987, 1990 b). At this time of the year, young Marsh Tits are known to form flocks (Nilsson & Smith 1988, Nilsson 1989); some juveniles even try to occupy a territory and to attract a partner (Ludescher 1973). It is probable that this early, competitive establishment has selected for juveniles able to utter the full song early in life.

In Great and Willow Tits it is not known how the sexes contribute to the song period in spring. In all probability, however, the situation is similar to that found in the Marsh Tit, in which males do almost all the singing (Rost 1987). More is known about the behaviour of the two species in late summer.

After they have left their family and the summer flock, young Great Tits join a winter flock in September / October (Röhss & Silverin 1983). Since birds of the year are always subordinate to adults (for identical findings in Marsh and Willow Tits see Foster & Godfrey 1950, Morley 1953, Anvén 1961, Ekman & Askenmo 1984; but cf. also Hogstad 1987), juvenile Great Tits, trying to establish themselves in a basic flock and to minimize flock size, are almost exclusively involved in aggressive interactions (Hinde 1952, Röhss & Silverin 1983). In breaks between combats and after skirmishes are over, singing is a common phenomenon among juveniles (Hinde 1952).

As in the Marsh Tit (Rost 1987, 1990 b), juvenile Willow Tits of either sex finish song development at the age of about two months (August; Thönen 1962), and singing is intensified in both juvenile males and females in late summer (Heckershoff 1979). At the same time (August / September) the young either occupy vacant territories (Ludescher 1973) or try to establish themselves in a group of conspecifics, usually consisting of an adult mated pair and two to four non-kin juveniles (Ekman 1979, Hogstad 1987). However, not all young Willow Tits succeed in joining such a group, and some move between territories as floaters before they disappear from the area (Silverin et al. 1989 b).

Compared to the Great Tit (Alexander 1935, Rost 1990 a), the Marsh Tit (Rost 1987) and Willow Tit (Fig. 1. and 2.) have a shorter song period in spring. This can be put down to the fact that unlike the Great Tit, which is known to breed twice a year in many cases (Berndt 1938, Harrison 1975), Marsh and Willow Tits rear young only once a year (Barnes 1975, Harrison 1975, Perrins 1979). Furthermore, in the Great Tit the second annual song peak in late summer does not occur until September (Rost 1990 a), whereas the Marsh and Willow Tit show maximum song output as early as July and August, respectively (Fig. 1. and 2.; Rost 1987). The reason for this might be that juvenile Marsh and Willow Tits join the basic flocks or try to occupy vacant territories earlier in the year than young Great Tits.

As in Great Tit males (Rost 1990 a), the plasma levels of testosterone in male Willow Tits show two annual peaks, in spring and late summer (Fig. 1). In the males of both species, the increased testosterone levels in late summer are exclusively due to juvenile males (Fig. 1; Röhss & Silverin 1983). When testosterone was measured in Willow Tit females, increased levels were found only in late summer, but, as in the males, these higher levels were due exclusively to juvenile birds (Fig. 2). In view of the idea that the production of song in birds is closely associated with testosterone (Marler et al. 1988), the endocrinological findings in the Willow Tit accord with and supplement the observations of the vocal behaviour of this species during the year. The annual course of song in Willow Tit males and females of different ages can be described as follows. Because of increased testosterone levels in males and basal levels in females in spring, it can be concluded that, as in Marsh Tits, almost all the singing at this time of the year is done by Willow Tit males. In the second period, on the

other hand, the increased levels of testosterone observed in juvenile birds of either sex and the basal testosterone levels in adult males and females together with the increase in song production in juvenile birds (Heckershoff 1979) indicate that the chief contribution to the late summer song is made by young males and females, as it is also the case in the Marsh Tit (Rost 1987).

However, only about 30% of the migrating and territorial juvenile Willow Tits of either sex showed high plasma levels of testosterone; the rest had basal levels like the adult birds (Silverin et al. 1986, 1989 b). In addition, the number of testosterone-implanted young that succeeded in becoming a member of a winter group did not differ from the number of successful control birds (Silverin et al. 1989 b). For these reasons Silverin et al. believe that autumn territoriality and migration in the Willow Tit are testosterone-independent, and that the high testosterone values detected in one third of the young are the result of recent social interactions. Aggressive displays and chasing are common among immature Willow, Marsh and Great Tits in late summer and are generally accompanied by song (Foster & Godfrey 1950, Hinde 1952, Morley 1953, pers. observ.). As testosterone is known to induce aggressiveness and singing, and to influence the frequency of song in birds (Silver et al. 1979), it seems reasonable to assume that most of the singing in juvenile Willow Tits in late summer occurs in connection with aggressive encounters.

Although the joint examination of endocrinological and behavioural data made in the present paper provided clues about a close connection between testosterone and song production in the Willow Tit during the year, additional investigations of the song activity of Willow Tit males and females of different age-groups can be recommended. Finally, it would also be desirable to investigate the effects of testosterone-inhibiting substances on the production of song.

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