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TIMING OF MOULT IN MALE AND FEMALE SHELDUCKS *TADORNA TADORNA*: EFFECTS OF ANDROGENS AND MATES

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Düttmann H., S. Dieleman & T.G.G. Groothuis 1999. Timing of moult in male and female Shelducks *Tadorna tadorna*: effects of androgens and mates. *Ardea* 87: 33-39.



We investigated effects of testosterone treatment on timing and rate of moult of wing-feathers in male Shelducks *Tadorna tadorna*, and whether this treatment influences the timing of moult in untreated females. Three experimental treatments were conducted, each with two groups of sexual inactive male Shelducks, which were kept under natural photoperiods in The Netherlands. Each group consisted of two pairs and a single male. Males received implants with testosterone-propionate for seven weeks shortly before the natural moult onset of wing-feathers. Start of treatment was 27 June (treatment I), 5 July (treatment II), and 18 July (treatment III). Males delayed their moult until the end of hormone treatment. The degree of delay in start of moult within the same treatment was related to androgen blood levels. The untreated females of the testosterone-treated males delayed also their onset of moult. The timing of the end of moult was unaffected by the hormonal treatment. Males that moulted late did not speed up the rate of moult, or changed the pattern of moult, but some of these birds stopped moult before completion. The data indicate that under natural photoperiods the start of moult is quite flexible, requires low levels of androgens, and is under the influence of social factors, while the end of moult is fixed.

Key words: *Tadorna tadorna* - moult - androgens - mates - synchronisation - annual cycle

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INTRODUCTION

Gonadal hormones are known to influence the onset and rate of moult (see Hahn *et al.* 1992). Experimental studies demonstrate that elevated androgen levels delay the onset of moult in altricial and precocial bird species (Schleussner *et al.* 1985; Rutschke *et al.* 1989; Kobayashi 1954; Nolan *et al.* 1992). Additionally, Schleussner *et al.* (1985) observed a decrease in growth of new feathers during moult in testosterone-treated Common Starlings *Sturnus vulgaris*. Gonadal hormones do not seem to influence the end of moult. Several studies demonstrated that castration does not influence the timing of the end of moult (Payne 1972; Gwinner 1986). Moreover,

testosterone-treated late-moult Common Starlings even stopped moult at the normal time before its completion (Schleussner *et al.* 1985). The timing of the end of moult is probably under the control of daylength and a circannual program (Schleussner *et al.* 1985).

Since the timing and length of the yearly reproductive period may vary considerably and as reproduction is not compatible with moult, birds should possess a mechanism to adjust the timing of moult to the timing of reproduction. This can be fulfilled by gonadal hormones. The fixed end of moult is functional since birds have to finish moult before environmental conditions deteriorate in autumn and winter.

The importance of the reproductive behaviour

of the partner on the timing of moult has only been tested in Song Sparrows *Melospiza melodia*. Estrogen-implanted females that extended their reproductive period delayed the onset of moult in their mates for up to a month (Runfeldt & Wingfield 1985). Curiously, females mated to testosterone-implanted males did not delay the onset of their moult. This sex difference may be understood from a functional point of view since in this species the female ultimately determines timing of reproduction.

The present study focuses on the influence of sex hormones and social factors on the timing of moult in the Shelduck *Tadorna tadorna*. This species is an intriguing model for this topic since: (1) Shelducks shed all their wing- and tail-feathers simultaneously within a few days and therefore become flightless for about four weeks. As a consequence they are vulnerable for predation and inclement weather conditions during that period. The end of moult may not be as fixed as in other species since a rapid moult is already so important under normal conditions that any delay due to elevated levels of gonadal hormones can not be compensated for by an even further increase in rate of moult. (2) Wing-moult in this species is incompatible with reproductive activities. So we expect a clear influence of gonadal hormones on the timing of the start of moult. (3) The autumnal termination of moult in males is associated in time with an increase in testosterone production (Ratermann 1991). This suggests that this hormone may not only influence the start but also the end of moult. (4) The timing of moult in Shelducks may be influenced by social cues. Mate fidelity is high (Williams, cited in Patterson 1982): more than 80 % of the pairs remain together from year to year, while the arrival at the moulting grounds seems to be related to the timing of breeding and raising the young (Bauer & Glutz von Blotzheim 1979). In view of the differences with the Song Sparrow the Shelduck provides a good case with to test the hypothesis of Runfeldt & Wingfield (1985) that pair synchronisation of moult is related to the social system.

In the present study we address the following

questions: (1) Does testosterone treatment delay the onset of moult in male Shelducks? (2) If so, does this treatment also delay the end of moult or is the termination of moult in males more or less fixed? (3) If hormonal treatment delays the onset but not the end of moult, are testosterone-treated male Shelducks able to speed up the rate of moult after cessation of treatment, or do they change the pattern of moult or arrest moult before its completion? (4) Does sexual activity in testosterone-treated male Shelducks cause a delay in the start of moult in their untreated female mates?

METHODS

Birds and housing condition

The male and female ducks available included adult and subadult birds. In order to determine possible differences between these categories we first analysed the data of Kröning (1989) and Prieshof (1990) on the onset of the moult of wing-feathers in adult and subadult Shelducks of both sexes. These analyses revealed neither a sex-specific nor an age-specific difference in the onset of moult (Mann-Whitney *U*-test of a sex-specific difference: $Z = 0.88$, $df = 16$, $P = 0.37$, 9 males, 9 females; Mann-Whitney *U*-test of an age-specific difference: $Z = 0.38$, $df = 16$, $P = 0.7$, 12 adults, 6 subadults). This is in line with several field studies (Eltringham & Boyd 1963; Dirksen 1968; Goethe 1961; Nehls *et al.* 1992). Therefore we included all categories of birds. Twelve pairs and six unpaired males were housed near the Zoological Laboratory in Haren, The Netherlands (53°10'N, 6°36'E) in groups of 2 pairs and a single male. They were kept in 1.5 x 3 m² outdoor aviaries that included a 0.75 m² water basin with a continuous replenishment. Four pairs and two unpaired males were adult, the others subadult. The birds were fed ad libitum with grain and pellets as used in duck and geese farms.

Experimental design

The effect of testosterone on the start, rate, and end of moult of wing-feathers was tested by

implanting sexually inactive males with silastic tubes containing testosterone-propionate for a period of 7 weeks in summer 1993. In order to analyse whether a progressive delay in treatment induces a progressive delay in the start and end of moult and an increase in rate of moult, the six groups of 5 birds were randomly assigned to one of three treatments that differed in the start and end of hormone treatment: 27 June – 15 August (treatment I), 5 July – 23 August (treatment II), and 18 July – 5 September (treatment III; Fig. 1). All birds performed neither sexual nor social displays, nor showed any indications of wing-moult before the application of testosterone-propionate. Since sexes do not differ in the timing of moult, we used the untreated female birds for analysing whether the timing of moult in the males influences the timing of moult in their females. Our investigations started on 15 June 1993 and ended a year later before the onset of the next wing-moult. In this period we checked almost daily for the onset, rate and end of wing-feather shedding. We defined the loss of the first primary, secondary, or alula feather as the onset of moult. The end of shedding was defined as the loss of the last old wing-feather. The effect of the implants on blood plasma androgen levels was checked by radioimmunoassays on blood collected three days before and one week after implantation. The possible effect of endogenous testosterone production on the termination of moult was studied by analysing blood levels of testosterone, collected in the beginning of October, the beginning of November and the beginning of December. All statistical analyses were done by non-parametrical tests. Details are given throughout the text.

Hormonal treatment and measurements

For the hormone treatment we used silicone tubes, filled with 30 mg testosterone-propionate (3.5 cm length, sealed at both ends with silicon glue; inner diameter: 1 mm, outer diameter: 3 mm). These tubes were implanted subcutaneously in the neck region. Implantation and explantation were carried out under the local anaesthesia with lidocaine. Approximately 500 µl blood for radio-

immunoassays was taken from the wing vein and immediately centrifuged. Afterwards plasma was stored at minus 80°C. Testosterone blood levels were analysed by radioimmunoassay in the laboratories of the Department of Herd Health and Reproduction in Utrecht (The Netherlands). We used the method developed by Verjans *et al.* (1973) with modifications by Dieleman *et al.* (1983). The main cross reactivities of the antibodies used were 49.7 % for 5 alpha-dihydrotestosterone, 7.64 % for 4-androstene-3β, 17β-diol, and 3.35 % for androstenedione. The interassay coefficient was 14 %. The limit of quantification was 0.05 ng/ml.

RESULTS

In all blood samples of male Shelducks taken before the start and after the end of the hormonal treatment, testosterone concentrations were below the detection level. One week after implantation androgen levels significantly increased in all males on 4.36 ng/ml on average (Wilcoxon-test: $Z = 3.59$, $n = 18$, $P = 0.001$). We could not detect differences in testosterone levels during the implantation phase between the three experimental groups (Kruskal-Wallis test: $F = 2.38$, $df = 2$, $P = 0.13$).

All birds, including the testosterone-treated males, started to moult the wing-feathers in the normal way and did not skip part of the moulting sequence. The untreated female Shelducks started to loose wing-feathers between the middle of July and the beginning of September with a peak of five birds in the beginning of August. Testosterone-implanted males shed these feathers significantly later than their mates (Mann-Whitney U -test: $Z = 3.23$, $df = 28$, $P = 0.001$). None of the males started to moult before removal of the hormone implants. Therefore, the onset of the moult of wing-feathers in males was clearly related to the end of the hormonal treatment (Fig. 1B). The difference in the start of moult between the three experimental groups was statistically significant (Kruskal-Wallis test: $F = 6.17$, $df = 2$, $P = 0.012$).

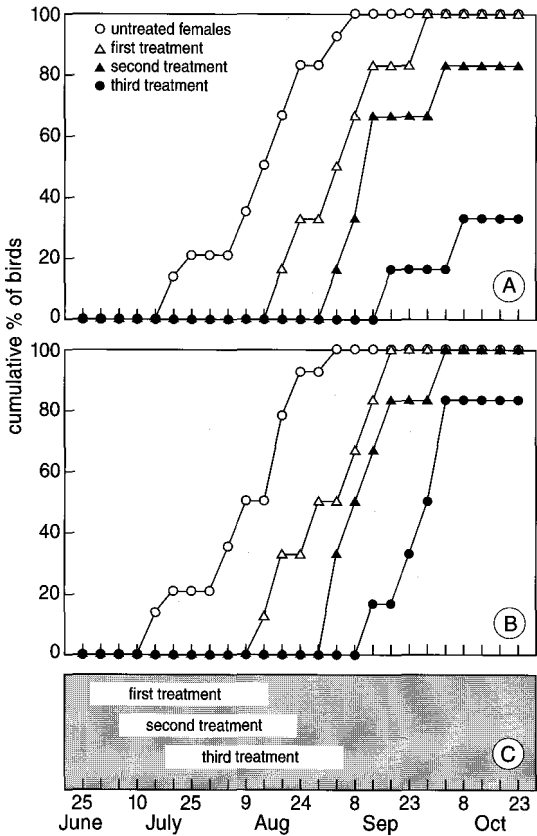


Fig. 1. Cumulative percentage of Shelducks that started (B) and finished (A) to moult the wing-feathers as a function of date of testosterone implantation (C). Three groups were implanted with testosterone-propionate for seven weeks. A group of untreated females was used as an additional control. Horizontal bars in C refer to the different time periods of implantation in the hormone-treated groups.

From the 6 males which we explanted latest (treatment III) only five individuals started to moult wing-feathers since one bird did not moult at all (Fig. 1B). The latest date an explanted male was found to shed his first wing-feathers was the 4th of October.

Treatment I was the only condition in which we could collect blood of all birds. Timing of the onset of moult in these males was significantly and positively related to their testosterone blood titers during the implantation phase (Fig. 2;

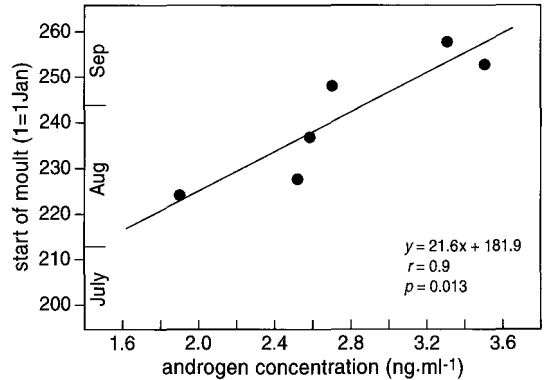


Fig. 2. Correlation between the plasma testosterone levels in 6 testosterone-implanted male Shelducks (group I) and the onset of moult of wing-feathers in these birds after explantation. The onset of moult is numbered from 1 January onward (31 July = day 212).

Spearman-rank-correlation: $r_s = 0.90$, $n = 6$, $P = 0.013$). This finding is supported by the fact that the male of group III that did not moult at all had the highest testosterone titer of all testosterone-treated males of which we analysed blood samples (6.3 ng/ml). An analysis to see whether the males started to moult sooner after cessation of the hormone treatment later in the season revealed no difference in the time between explantation and start of wing-moult in the males of the different groups (Kruskal-Wallis test: $F = 0.01$, $df = 2$, $P = 0.98$). Thus, we have no evidence for a quicker start in the onset of moult with a later start/end of the hormonal treatment.

Three male Shelducks of group III and one male of group II did not finish moult. They stopped during the shedding of coverts and alula. Since one male in group III did not moult at all, only two of the six males of group III and five of the six males of group II finished the moult of wing-feathers (Fig. 1A). The difference in number of birds finishing the shedding of wing-feathers is borderline significant between groups I and III (Fisher exact test: $n = 12$, $P = 0.06$) and highly significant between group I+II versus group III (Fisher exact test: $n = 18$, $P = 0.02$). Those males which shed their wing-feathers latest (end of Sep-

tember/beginning of October) were able to fly again at the end of October.

Since only two males of group III finished their wing-feather moult, we restricted our analysis on the timing of hormone treatment and rate of moult to groups I and II, and the females. As the rate of moult we defined the number of days in which a Shelduck shed all its wing-feathers. A Kruskal-Wallis test revealed that a later testosterone treatment did not enhance the rate of shedding ($F = 1.32$, $df = 2$, $P = 0.29$). In addition, we analysed the relationship between onset and rate of shedding more directly by correlating these two variables for these birds as well as the two treatment III males that finished moult. Again, we found no significant correlation between the variables. Late-moulting birds shed their wing-feathers no faster than early moulting individuals (Spearman-rank-correlation: $r_s = -0.33$, $n = 25$, $P > 0.05$). Although females moulted earlier than males, there was a positive correlation between the onset of moult in the 11 drakes and that of their females (Spearman-rank-correlation: $r_s = 0.65$, $n = 11$, $P < 0.05$).

DISCUSSION

In line with studies in other avian species (Kobayashi 1954; Schleussner *et al.* 1985; Rutschke *et al.* 1989; Nolan *et al.* 1992), androgen treatment delayed the onset of prebasic moult in male Shelducks. This conclusion is based not only on the comparison of females with testosterone-treated males, but more importantly also on the comparison between groups of male Shelducks implanted during three different time periods. That the delay in moult is really due to testosterone, and not to the implantation procedure, is further supported by the finding that the delay in the onset of moult in the testosterone-treated drakes was positively correlated with the blood plasma concentration of the hormone. The effect of androgens on the delay in moult is likely to be due to its antagonistic relation with the production of thyroid hormones known to stimulate moult (Hahn *et al.* 1992).

Birds that started to moult later in the season did not adjust for this by starting further in the moulting programme like it has been observed in the Common Starling (Schleussner 1990). We found evidence that testosterone-treated displaying males delayed the start of moult in their untreated female mates. Such a social effect has been demonstrated also in the Song Sparrow: estradiol-treated females were found to delay moult onset in their mates (Runfeldt & Wingfield 1985). These males had higher levels of testosterone than unpaired males, probably due to social stimulation by their females, and these elevated levels probably caused the delay in prebasic moult. A similar scenario might apply to the moult delay in the female Shelducks. Testosterone-treated males frequently performed social displays and we noticed that females responded specifically to their testosterone-treated mates with frequent performance of behavioural displays that are probably under the control of gonadal hormones as well.

Interestingly, Runfeldt & Wingfield (1985) found social modulation of moult onset only to occur in male and not in female Song Sparrows. The authors explained this with the different roles of the sexes in (the timing of) reproductive activities. The egg-producing sex incurs higher costs in (delayed) reproduction and therefore ultimately determines the timing of breeding. The Shelduck differs from the Song Sparrow in that both sexes show high mate fidelity and migrate synchronously to the moulting ground where they moult wing-feathers at the same time. This may have led to a situation in which female Shelducks are open to influences from their partner in the timing of moult. Runfeldt & Wingfield's (1985) explanation on sex difference in social modulation of moult onset in the Song Sparrow might however explain why our females, despite some influence of their mates, did not wait to moult until their mates started, but rather started to moult earlier. The majority of females began to moult before the implants of the males were removed, as if they could predict when the implants were going to be removed from their mates. This is of course not possible, but females might be able to predict the onset of

moult of wing-feathers in their mates by using the regression of testosterone-dependent male sexual traits. We found that the influence of exogenous testosterone on male-typical bill features and display behaviour was maximal 2 weeks after implantation (Düttmann *et al.* in prep.). Thereafter, regression of the patterns took place, probably due to a lower release of hormone by the implant, since the hormone contents of the implants at removal was substantially reduced.

In the present study none of the testosterone-treated males started wing-moult after the natural moulting period was over. Others stopped during the shedding of coverts and alula feathers. Since Shelducks shed these feathers within just a few days the end of moult is sharply fixed. According to N. Kempf (pers. comm.) it is very important for the birds to finish moult before environmental conditions deteriorate. Hundreds of late-moulting individuals have been killed by autumnal storms on their moulting ground in the Elbe Estuary. The mechanism underlying the relatively fixed end of moult is likely to be a function of an endogenous moult programme in combination with decreasing daylength (Schleussner *et al.* 1985).

We found no evidence for an increase in the rate of moult in late-moulting male Shelducks after cessation of the androgen treatment. Acceleration in late-moulting birds has been found in a couple of species in the field (Wingfield & Farner 1979) as well as in the laboratory (Dolnik & Gravidov 1980; Meijer 1988). One explanation for our results might be that the moult of wing-feathers in the Shelduck is already so rapid (most birds shed all primaries and secondaries within 4 - 5 days), that any delay cannot be compensated for by having more wing-feathers in simultaneous moult. Thus, given the fixed end of moult Shelducks are only able to cope with a later start of moult by arresting moult before its completion.

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SAMENVATTING

In deze studie zijn de effecten van testosteron op het tijdstip en de snelheid van het ruiproces van de slagpenen in mannelijke Bergeenden *Tadorna tadorna* onderzocht. Tevens werd bekeken of het tijdstip van de rui bij mannetjes het tijdstip van ruïen bij niet-behandelde vrouwtjes heeft beïnvloed. De dieren werden onder natuurlijke lichtcondities in buitenvolières in Nederland gehouden. De mannetjes werden vlak voor het begin van de rui van de slagpenen geïmplanteerd met een implantaat dat testosteronpropionaat bevatte. Na 7 weken werd het implantaat weer verwijderd. De hormoonbehandeling werd uitgevoerd met sexueel niet-actieve dieren, welke in groepen werden gehouden van twee paren en een ongepaard mannetje. Er waren drie verschillende startdata voor de hormoonbehandeling, die ieder werd uitgevoerd met twee groepen vogels: 27 juni, 5 juli en 18 juli. Vastgesteld werd dat de mannelijke vogels de start van de rui uit tot na het eind van de hormoonbehandeling uitstelden. Daarbij bleek binnen een groep van vogels die op dezelfde tijd met het hormoon was behandeld, de mate van uitstel van de rui positief gerelateerd te zijn aan bloedwaarden van androgenen. Het tijdstip van de (uitgestelde) start van de rui van de mannetjes was positief gerelateerd aan de start van hun vrouwtjes. Het tijdstip waarop de mannetjes hun rui beëindigden werd niet beïnvloed door de hormoonbehandeling. Mannetjes die laat begonnen te ruïen, gingen niet sneller ruïen, veranderden ook niet hun rui patroon, maar stopten de rui voordat die compleet was. De gegevens laten zien dat onder een natuurlijke dag-nacht periodiciteit het tijdstip van de start van de rui flexibel is, lage androgeenwaarden vereist, en onder invloed van sociale factoren staat, terwijl het eind van de rui niet flexibel is.

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