Review

Testosterone control of male courtship in birds

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ABSTRACT

A sequence of behaviours which we call courtship initiates reproduction in a large number of species. In vertebrates, as a component of male sexual behaviour courtship is strongly influenced by testicular androgen. Here I will review some salient issues about the regulation of courtship by testosterone in birds. The first section will briefly summarize the first 100 years of research on this topic. The specific role of testosterone or its oestrogenic metabolites in the control of different components of courtship will be the subject of the second section. Then, I will discuss how behavioural patterns can be recruited into courtship and modified in their structure by testosterone action. In the following section, the role of sexual selection and female choice in shaping the link between testosterone and courtship will be addressed. The problematic nature of the quantitative relationships between testosterone and behaviour will be topic of the fifth section. Finally, I will discuss how courtship traits that are activated by testosterone can be apparently independent of hormone blood concentrations. These issues will be examined in an evolutionary perspective, in an attempt to understand how natural and sexual selection have shaped the links between the hormone and the behaviour.

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Courtship is a fundamental component of reproduction in animals. Courtship may have several non exclusive functions: species recognition, pair bond formation, synchronization of reproductive physiology, and advertisement of mate quality. In many species reproduction involves behavioural coordination between males and females, particularly when successful fertilization requires physical contact between the sexes. Given its importance in reproduction, it is not surprising that courtship behaviour in males and females is modulated by gonadal hormones. Birds have proven to be valuable subjects for studies on the behavioural endocrinology of courtship for many years. Species with elaborate courtship are found in many other taxa, from insects to fish to mammals, however birds communicate primarily via visual and acoustic signals in a frequency range similar to that used by humans, making them a good model system for studying the evolution, endocrinology and neurobiology of sexual signals. In this paper I will discuss a few salient issues concerning the control of courtship by testosterone and its metabolites in male birds. Readers interested in the hormonal control of courtship in female birds and in other taxa can find many excellent, recent books and reviews on these topics (Adkins-Regan, 2005; Miles et al., 2007; Moore et al., 2005; Neal and Wade, 2007; Oliveira et al., 2005; Woolley et al., 2004).

A brief history of the behavioural endocrinology of avian courtship

The study of the hormonal control of avian courtship dates back to the work of Colonel George Montagu (1802), who observed that in male songbirds the singing activity was higher in the periods in which birds had enlarged testes. Almost 50 years later, Berthold (1849)
performed the first experiment in behavioural endocrinology. It was well known by breeders and farmers that castration of young cockerels prevents the development of male sexual traits including crowing and sexual behaviour. Berthold showed that these traits could be restored in the castrated male by implanting the testes of the same bird or of other males intraperitoneally, and noted that the grafted testes did not build any tissue connection with the body of the host (Berthold, 1849). Thus, almost a century before gonadal hormones were isolated, it was shown that substances secreted by the testes – ‘androgens’ – are responsible for the activation of male sexual behaviour, including courtship.

At the end of the 1940s’, there was convincing evidence that in birds male sexual behaviour is facilitated by androgens secreted by the testes (reviewed by Beach, 1948; Collias, 1950). By this time, a number of observations had suggested a correlation between testicular cycles and seasonal variations in courtship behaviour, and androgen-dependence of distinctive male behaviour had been demonstrated experimentally in Galliformes, Columbiformes, Charadriiformes, Ciconiiformes, Anseriformes and Passeriformes (Beach, 1948; Collias, 1950). The establishment of a relationship between androgens and male courtship represented an important advance in the understanding of the behavioural differences between the sexes. However, several observations suggested that the differences in the circulating levels of gonadal hormones were not the sole determinant of sexual dimorphic behaviour. Already in 1918, Goodale had observed that it was not possible to elicit female sexual behaviour in capons by means of ovariectomy (cited in Young et al., 1964). Attempts to induce male behaviour in females by androgen treatment provided conflicting results. For example, Hamilton (1938) could induce crowing in young male domestic fowl by injecting testosterone (T) propionate from the second day after hatching. Crowing could not be induced in female chicks, despite “no apparent reason why the female fowl should not crow provided it had the instinct to do so properly developed” (Myers, 1917 and Appel, 1929; cited in Hamilton, 1938, pg 56). In the following 2 years three researchers were able to bring adult female canaries into song by treating them with T (Baldwin et al., 1940; Leonard, 1939; Shoemaker, 1939). T-treated female canaries not only developed a song similar to that of males, but also other male courtship behaviours never observed among untreated females (Shoemaker, 1939). In general, induction of male-specific behaviour and vocalisations in females at this time was either unsuccessful or required administration of androgen for a longer time or in larger doses (Collias, 1950). Similar observations in mammals led to the formulation of the ‘Organisation-vs.-Activation’ hypothesis for the sexual differentiation of behaviour (Phoenix et al., 1959): during development, gonadal hormones organise in an enduring way the sexual differentiation of neural tissues; in adulthood, gonadal hormones act on sexually dimorphic neural centres to activate sex-specific behaviour.

**Hormonal specificity in the activation of courtship displays**

Work with domesticated species such as the ring dove (*Streptopelia risoria*), the Japanese quail (*Coturnix coturnix japonica*), and the domestic fowl (*Gallus gallus*), elucidated the mechanisms responsible for the development and adult activation of sexual dimorphic behaviour. Similar to mammals, the sexual differentiation of sexual behaviour in birds is organized by hormones secreted by the embryonic gonads. However, while in mammals it is T secreted by the testes which masculinises the brain and behaviour, in birds the situation is reversed: a bird would develop into a male phenotype unless oestrogen secreted by the embryonic gonads de-masculinises brain and behaviour (reviewed by Adkins-Regan, 1987; Balthazart and Ball, 1995). Although gonadal hormones play a primary role in the sexual differentiation of brain and behavior, there is increasing evidence that non hormonal factors contribute to this process (Arnold, 2004; Gahr, 2007). For example, genetically male quails chimera that had received a female forebrain primordium during development before sexual differentiation had started showed only rudimentary male sexual behavior (Gahr, 2003).

The activation of courtship in adults results from the action of steroid hormones in the preoptic areas and the anterior hypothalamic (HPOA). In the 1970s it was shown in several bird species including ring doves, domestic fowls, and quails, that implantation of testosterone-T crystals directly in the HPOA of castrated males elicits courtship behaviour (Adkins-Regan, 1981; Barfield, 1971; Hutchison, 1970b; Hutchison, 1971). In all species studied so far, the activation of courtship by steroid action in the HPOA seems to be the rule (reviewed by Balthazart and Ball, 2007). Even in songbirds, that have a specialized neural network for the control of song, the activation of singing (as opposed to the quality of song produced) might depend mainly on hormonal action within the HPOA (Riters and Ball, 1999; reviewed by Ball et al., 2004).

Courtship, however, is not a unitary behaviour but rather the co-ordination or assemblage of several distinct behavioural patterns that might have separate hormonal control. The ring dove remains one of the best-studied species in this respect. The courtship of the male ring dove includes three principal patterns: the bowing display, the chasing display, and the nest-soliciting display. The first two displays, chasing and bowing, have been called ‘aggressive’ displays because they are also used in male-male aggressive interactions, whereas nest-soliciting is exclusively a courtship display (Davies, 1970; Lovari and Hutchison, 1975; Martinez-Vargas and Erickson, 1973; Miller and Miller, 1958). A series of classical studies demonstrated that the aggressive displays (chasing and bowing) are androgen treatment, whereas the nest-soliciting is oestrogen-dependent (Adkins-Regan, 1981; Cheng and Lehrman, 1975; Hutchison, 1970b; Hutchison, 1971). For example, intra-hypothalamic implantation of T induces the full courtship that includes both aggressive and nest-oriented displays, whereas implantation of 17β-oestradiol (E2) crystals elicits nest-soliciting specifically (Barfield, 1971; Hutchison, 1970b; Hutchison, 1971). Courting male doves have elevated levels of T but very low levels of E2 (Korenbrot et al., 1974), and it was therefore suggested that nest-soliciting is elicited by oestrogen formed within the brain by aromatization of circulating androgen (Hutchison, 1976). Later work provided further support to this hypothesis (Hutchison and Steimer, 1984; Steimer and Hutchison, 1980, 1981). But why are different courtship displays controlled by different hormones? One explanation could lie in the separate contextual origins of the displays. It is not unusual that courtship sequences are composed of behavioural patterns that also occur in other contexts, and aggressive displays in particular are typical components of courtship (Berglund et al., 1996; Tinbergen, 1965). For example, in several species of bowerbirds courtship includes displays that have been co-opted from aggressive contexts (Borgia and Coleman, 2000). In the ring dove, chasing is a typical aggressive display shown by both sexes during aggressive interactions (Lovari and Hutchison, 1975; Miller and Miller, 1958), and bowing is a male-specific display performed by males during territorial interactions (Davies, 1970). Nest-soliciting, on the contrary, is performed by both males and females during nest-building and incubation (Miller and Miller, 1958). Most likely, the three displays have been assembled to form the courtship but each has maintained its own hormonal control mechanisms. This separation could have been maintained because of developmental constraints related to the sexual differentiation of the courtship behaviour. For example, bowing is a male-specific behaviour, whereas nest-soliciting is common to males and females. Thus, it appears that androgen-dependent bowing undergoes developmental sexual differentiation whereas oestrogen-dependent nest-soliciting does not.

The hypothesis of a combination of behavioural patterns with different origins, in fact, may apply also to the coordination of the vocal and postural components of the display (Fusani et al., 1997b).
The vocalizations of the bowing display and of the nest-soliciting are very similar and the small structural differences between bow-calls and nest-calls are probably due to the different postures in which they are emitted (Fusani et al., 1997b). The best evidence for the fact that postural movements and vocal patterns assembled in a display can have separate origins comes from studies on crowing of quail–chicken midbrain chimeras, which crows like roosters but with the typical head-shaking of quails (Balaban, 1997).

An alternative (but not exclusive) hypothesis is that the separate hormonal control might function to regulate the behavioural transitions that occur during the progression of courtship. Initially males perform all three displays, but the performance of nest-soliciting increases progressively to peak 2–3 days after the first courtship interactions, and the aggressive displays become infrequent (Lovari and Hutchison, 1975). The increase in nest-soliciting follows the sharp rise in the rate of aromatization within the brain, which starts increasing as soon as 4 h after the beginning of the courtship (Dudley et al., 1984). We tested if aromatization of circulating androgen could be responsible of the changes in the composition of courtship by treating intact males that were already courting with an aromatase inhibitor, Fadrozole (Fusani et al., 2001a). In males treated with a relatively low dose of Fadrozole, targeted to reduce significantly aromatase activity without blocking it completely, nest-soliciting decreased during the 6 days of treatment (Fusani et al., 2001a). Thus, it is likely that the regulation of brain aromatization of gonadal T is the mechanism that allows rapid changes in courtship behaviour in male doves. Importantly, these behavioural changes directly influence female reproductive development: High rates of aggressive displays result in a longer interval between pairing and egg laying (Hutchison and Lovari, 1976).

Changes in display structure related to courtship context

In the large majority of seasonally breeding birds of temperate European and North American regions, the testes are regressed in autumn and start growing in size in winter, with the lengthening of the photoperiod after the winter solstice (Dawson et al., 2001). Gonadal recrudescence and the consequent rise in circulating T levels activate the full set of reproductive behaviours including territorial aggression and courtship (Wingfield and Farner, 1993). Thus, the appearance of courtship is one indicator that the birds have gone from a non-breeding to a breeding condition, and this transition is marked by the increase in circulating T. Courtship, as a component of sexual behaviour, follows an on-off mechanism: it appears at the beginning of the breeding season and disappears at its end. Thus, there is a qualitative difference between sexual behaviours including courtship and other behaviours associated with reproduction and increased plasma T levels: Whilst the former are not shown in other periods of the year or life history stages, the latter might be present all the time but are enhanced by T during the breeding season. For example, in most species in which males defend a territory during the breeding season territorial aggression is regulated by T (Wingfield and Farner, 1993; Wingfield et al., 1990). However, some species defend a territory also outside the breeding season, and in these cases territorial aggression can be independent of T (Canoine and Gwinner, 2002; Schwabl et al., 2005; Schwabl and Kriner, 1991; Soma et al., 1999).

In the previous section, we pointed out that courtship displays often include behaviour common to other social contexts, and we made the example with aggressive displays. In some cases, hormones not only recruit behavioural patterns into courtship, they also modify the structure of these behaviours. In the grey partridge (Perdix perdix) males and females spend the winter in groups and monogamous pairs form in the late winter. A key factor in pair formation is the long-distance call of the male (Beani and Dessi-Fulgheri, 1995), which has been called ‘rusty-gate’ call for it resembles the noise made by a rusty gate when opened (McCabe and Hawkins, 1946). The rusty-gate call functions as a gathering call during the winter but becomes a territorial, courtship and mate contact call in the breeding season (McCabe and Hawkins, 1946). The call, however, changes seasonally in its structure, becoming longer in duration in winter as compared to spring (Fusani et al., 1993; Rotella and Ratti, 1988). Because this transition parallels the vernal rise in circulating androgen (Lupo et al., 1990), we hypothesized that the lengthening of the call was driven by the seasonal increase in circulating T. Indeed, when male partridges are given T implants in the early winter, their calls become longer in duration and resemble spring calls (Fusani et al., 1994). Interestingly, T has another effect on the behaviour of the male: it increases the amount of time the animal spends in vigilance behaviour, i.e. screening the surrounding to detect the presence of predators (Fusani et al., 1997a). This effect might appear, at a first glance, unrelated to the effect on call duration. However, there is a link between the two traits, the call and the vigilance, and this link relates to criteria used by females to choose males. In fact, females prefer to mate with males who spend more time in vigilance, probably because this indicates that they will effectively protect them and their offspring (Dahlgren, 1990). This brings us to an important point: to understand more clearly the proximate mechanisms of hormonal control of courtship, we need to examine them in an evolutionary framework, that is, in light of the interplay between male courtship traits and female choice.

The role of sexual selection in shaping the link between testosterone and courtship

It was Daniel Lehrman, a founder of behavioural endocrinology, who first studied how males and females influence the endocrine state of each other through the behavioural interactions of courtship (Cheng and Lehrman, 1975; Erickson and Lehrman, 1964; Silver et al., 1973). Lehrman and his collaborators illustrated how the courtship behaviour of the male affects the development of the female reproductive system, in a perspective of behavioural and physiological coordination between the sexes. In fact, at that time courtship was mainly seen as a behavioural tool to recognize a conspecific mate and synchronize breeding. Later progress in evolutionary theories (e.g. see Andersson, 1994; Trivers, 1985) highlighted the existence of a conflict between the sexes because of differences in the extent of parental investment: For males, reproductive success depends mainly on the number of females, thus males will try to mate with as many females as possible. Females, on the contrary, will try to select the best males to make a good investment for their energetically expensive eggs. Females may choose their mates on the basis of many different factors, which range from territory size, to morphological traits, to behaviour. Female choice is one of the processes of sexual selection, that particular type of selection described by Darwin as the force behind the evolution of ‘odd’ seemingly maladaptive morphological and behavioural traits — i.e. elaborate ornaments and courtship (Darwin, 1871). Such traits may reduce the survival of the bearer and thus they seem to have evolved ‘against’ natural selection. However, the survival costs of ornaments and courtship are balanced by the increased reproductive success of males that are preferred by females. Current theories on the evolution of elaborate courtship traits have addressed the link between testosterone and sexually selected male traits. To be a reliable indicator of the quality of the male, the trait needs to be an honest signal: only males of good quality can afford the costs of elaborate courtship. It has been hypothesized that sexual selection is based on traits which are testosterone-dependent, because high testosterone levels are ‘costly’ in term of energy, metabolism, immunocompetence, and more (Folstad and Karter, 1992; Wingfield et al., 2001; Zuk et al., 1995). However, calculating the actual costs of T is not an easy task and it is still unclear if and how costly high plasma T levels are (Adkins-Regan, 2005).
Birdsong is a classical example of a behavioural ornament. It would be hard to explain the evolution of this behaviour without putting sexual selection in play. It has been shown in many species that singing activity is closely related to gonadal androgen (reviewed by Ball, 1999). It is more difficult, however, to link a specific aspect of the song structure – i.e. extension of the syllable repertoire, spectral features, complexity – with hormonal action (Gil and Gahr, 2002). The literature on the influence of hormones on song development and expression is vast and reviewing it is beyond the scope of this paper. I focus here on one specific aspect: the action of oestrogenic metabolites of T. In the 1970s, Naftolin and collaborators showed that the action of T within the brain can be mediated by its aromatization into E2 (Naftolin et al., 1975). Songbirds have very high concentrations of aromatase in the forebrain (Schlinger and Arnold, 1991, 1992) (Metzdorf et al., 1999; Saldanha et al., 1998). The ‘master’ nucleus of the neural song system, the HVC, contains oestrogen receptors (Gahr et al., 1987, 1993; Nordeen et al., 1987) (Bernard et al., 1999) and is surrounded by the forebrain region with the highest density of aromatase, the caudo-medial nidopallium (NCM) (Metzdorf et al., 1999; Saldanha et al., 1998; Shen et al., 1995; Vockel et al., 1990). The expression of aromatase in NCM changes between seasons in parallel with T levels (Fusani et al., 2000; Soma et al., 1999; but see Silverin et al., 2000) and is increased after T treatment (Fusani et al., 2001b). Several authors had described effects of oestrogen on the structure of the song (DeVoogd et al., 1986; Marler et al., 1986; Marler et al., 1987; Weichelt et al., 1989; Weichelt et al., 1988) and in two species oestrogen are specifically involved in the regulation of courtship song, i.e. song clearly directed at females (Harding et al., 1988; Walters et al., 1991). We studied the specific role of oestrogen in defining the structure of song using a peculiar model: the induction of song development in female canaries by T treatment.

Female canaries usually produce little or no song, but when they are treated with T they develop a robust, male-like song within 3 weeks (Leonard, 1939). This behavioural development is accompanied by the masculinisation of the song system (DeVoogd et al., 1985; Heid et al., 1985; Nottebohm, 1980). We compared the songs of females that were implanted with Talone or with T and the aromatase inhibitor Fadrozole to reduce the formation of oestrogen. Females canaries implanted with T and Fadrozole developed male-like songs that did not differ from those of T implanted males in their overall structure (Fusani et al., 2003). However, songs of females treated with T and Fadrozole had a lower proportion of tours – i.e. repetition of the same syllable – with high syllable repetition rates (Fusani et al., 2003). The interesting aspect of these results is that sexually receptive female canaries show higher sexual responses to songs with high syllable repetition rates, no matter if the songs are recorded from males (Vallet and Kreutzer, 1995) or T-treated females (Vallet et al., 1996). Thus, one of the sexually attractive parameters of canary song, the syllable repetition rate, seems to depend on oestrogenic metabolites of T. Similar effects of Fadrozole on the syllable repetition rate were described recently for male canaries (Rybak and Gahr, 2004), suggesting that our results in females (Fusani et al., 2003) represents a more general phenomenon.

These studies points to a trade-off between androgen- and oestrogen-controlled traits: androgen is responsible for the development and stabilization of the sexually dimorphic song structure, whereas oestrogen favours the organization of sexually selected aspects of the song (Fusani et al., 2003). In such a scenario, enhancing the sexual attractiveness of the trait would be at the cost of androgen-dependent components that may be important for male–male interactions (Adkins-Regan, 2005; Fusani et al., 2003) (Fig. 1).

### The puzzling relationship between plasma T concentrations and courtship behaviour

Modern theories on the evolution of sexually selected traits assume that the selective value of the trait is related proportionally to circulating T levels (Folstad and Karter, 1992). Although this has been shown for some morphological traits (Briganti et al., 1999; Peters et al., 2000), there is little support for the view that courtship displays are correlated with testosterone in a proportional fashion (Adkins-Regan, 2005; Hews and Moore, 1997). Several studies that reported a dose-dependent relationship between courtship behaviour and testosterone examined courtship in males who had been castrated and then treated with exogenous hormone. For example, in castrated Japanese quails the frequency of behaviour shown by males given testosterone implants of variable lengths is proportional to the size of the implant (and thus probably to the amount of circulating testosterone) but the maximum frequencies does not differ from those recorded in intact males (Balthazart et al., 1990). These effects do not require a proportional correlation between the hormone and the behaviour. The activation of courtship could require a threshold concentration of androgen to be reached, and the apparent dose-dependent response would result from the existence of individual thresholds: a larger dose would activate courtship in a larger proportion of birds (“Multiple Threshold Hypothesis”, Hews and Moore, 1997). Female choice for T-dependent behavioural traits, however, implies that among males in reproductive conditions – i.e. above the activation threshold – there are individual differences in the plasma concentration of T that are proportionally related to the expression of the traits under selection. So far, there is little evidence that behavioural traits follow this type of relationship when courtship is fully expressed (this issue is reviewed in detail by Adkins-Regan, 2005; Ball and Balthazart, 2007). In part, this is due to the fact that few studies have specifically tested this hypothesis (Hews and Moore, 1997). In ring doves, T treatment of intact males already in full reproductive condition and actively courting produces no change either in the amount of courtship or in the relative proportion of courtship displays (Fusani and Hutchison, 2003). In some cases the lack of a proportional correlation between behavioural traits and circulating T could result from the choice of the behavioural variables or the level of analysis. Studies on the behavioural aspects of the courtship have focused on the latency of courtship (frequency and duration of display) and less on its structure. However, in male ring doves a detailed behavioural analysis of both vocal and postural components of the bowing display found no effect of increased circulating T (Fusani and Hutchison, 2003), suggesting that courtship traits in this species do not reflect T concentrations.

### Can courtship be androgen-dependent and -independent at the same time?

Whatever the relationships between T and courtship, we usually say that a behaviour is hormone dependent if its expression is robustly...
associated with the presence of a substantial amount of the hormone. In the first section of this article, I reviewed the experimental work which showed how in birds the sexual differentiation of male sexual behaviour including courtship is regulated by testicular T, and the same hormone is responsible for the appearance of the behaviour in adult males. However, there are several examples of species in which castration does not abolish courtship, at least not immediately (Hutchison et al., 1996; Moore and Kranz, 1983). This does not prove that the behaviour is androgen-independent, because steroidogenesis can occur at many extragonadal sites including the brain (London et al., 2006; Simpson, 2003).

Some cases, however, are puzzling and illustrate the complexity of hormonal regulation of behaviour. The golden-collared manakin (Manacus vitellinus) is a Neotropical sub-oscine passerine. The males of this species – and of manakins in general – have some of the most elaborate courtship behaviour in the animal world, including acrobatic displays, mechanical sound production – ‘wingsnaps’, and group displays (Chapman, 1935; Fusani et al., 2007b; Lill, 1974; Prum, 1990). We have investigated if and how androgen influences the courtship behaviour of male manakins. A number of observations and experiments indicate that manakin courtship is in fact activated by androgen. Treatment of males with the antiandrogen Flutamide during the displaying season reduces courtship activity (Fusani et al., 2007a). Females and juvenile males, which usually do not produce wingsnaps, can be induced to perform them by T treatment (Day et al., 2006). Similarly, treatment of adult males with T outside the breeding season, when displaying activity and plasma T levels are low, induces an increase in wingsnapping (Day et al., 2006). Other experiments have provided contrasting results. The courtship season of manakins is long lasting up to 7 months. However, plasma T levels are relatively high only at the beginning of the displaying season and decrease significantly afterwards although courtship activity is unchanged (Fusani et al., 2007a). Moreover, treatment with T of adult males who are actively courting cause no change in courtship activity (Day et al., 2007). Altogether these data suggest that T activates courtship in male manakins, but courtship is then maintained by basal levels of circulating T and is unaffected by manipulation of plasma T levels. Nevertheless, courtship remains still sensitive to androgen as illustrated by treatments with Flutamide (Fusani et al., 2007a).

Clearly, other factors are involved in the control of courtship in manakins (Fig. 2). Perhaps after its activation at the beginning of the displaying season the expression of courtship requires only small concentrations of T, because the androgen sensitivity is increased in neural centres controlling courtship. For example, in another tropical passerine, the spotted antbird, the expression of androgen and oestrogen receptors in key brain areas is increased in the non-breeding season, probably to maintain territorial behaviour when circulating androgen levels are low (Canoine et al., 2007). Alternatively, androgen and/or oestrogen might be synthesized within the manakin brain de novo from circulating precursors (e.g. see London et al., 2006). Social stimuli can maintain hormone-activated behaviour, like in the case of maternal behaviour that is maintained by the presence of pups after the initial hormonal stimulation (Rosenblatt et al., 1979). Social stimulation could play an important role in maintaining courtship in male manakins, which have a lek mating system in which several males display simultaneously in individual courts placed few meters from each other. Finally, we need to study in more detail the courtship behaviour to see whether androgen and oestrogen can modulate specific aspects of the displays. Recently, we have shown that there are individual differences in the structure of the jump-snap display, the main component of the courtship (Fusani et al., 2007b). For example, the speed and the duration of the jumps and the time required by males to restore posture after each jump differ consistently between individuals, and these features could be those under sexual selection and more directly influenced by T.

Conclusions

The hormonal regulation of male courtship is one component of a complex set of mechanisms that requires a multi-level approach to be better understood. It will be particularly important in the future to examine in the same species both the proximate and ultimate causes of courtship. Our knowledge of the action of hormones in the brain areas controlling courtship has greatly increased in the last decade, and we have discovered the importance of steroid receptors and steroid metabolic enzymes in regulating local hormone action. Additional molecules such as steroid-binding proteins and steroid receptor co-regulators may influence hormone action and modulate courtship (reviewed by Ball and Balthazart, 2007). Furthermore, an evolutionary perspective will help to identify the aspects of courtship that are more relevant for female choice and eventually for the reproductive success of the male and to reveal links between the behavioural effects of hormones and other physiological parameters. Bridging neuroendocrinology and behavioural ecology is a challenging but very promising approach.

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References


Fig. 2. In male golden-collared manakins, courtship is activated by T at the beginning of the breeding season. Plasma levels of T decline then substantially but courtship activity does not. Thus, other factors such as increased brain androgen sensitivity, brain androgen formation, or social cues may contribute to maintain intense courtship activity after the decrease in plasma T levels.


