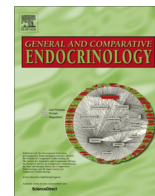




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## Effects of experimentally sustained elevated testosterone on incubation behaviour and reproductive success in female great tits (*Parus major*)



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### ABSTRACT

In many seasonally breeding birds, female and male testosterone (T) levels peak at the start of the breeding season, coinciding with pair bonding and nesting activities. Shortly after the onset of egg laying, T levels slowly decline to baseline levels in both sexes, but more rapidly so in females. During this period, T in males may still function to facilitate territorial behaviour, mate guarding and extra pair copulations, either via short lasting peaks or elevated basal levels of the hormone. In some species, however, males become insensitive to increased T after the onset of egg laying. It has been postulated that in these species bi-parental care is essential for offspring survival, as T is known to inhibit paternal care. However, only very few studies have analysed this for females. As females are heavily involved in parental care, they too might become insensitive to T after egg laying. Alternatively, because territorial defence, mate guarding and extra pair copulations are expected to be less important for females than for males, they may not have had the need to evolve a mechanism to become insensitive to T during the period of maternal care, because their natural T levels are never elevated during this part of the breeding season anyway. We tested these alternative hypotheses in female great tits (*Parus major*). Male great tits have previously been shown to be insensitive to T after egg laying with regard to nestling feeding behaviour (but not song rate). When females had started nest building, we experimentally elevated their T levels up to the nestling feeding phase, and measured incubation behaviour (only females incubate) and reproductive success. T did not significantly affect nest building or egg laying behaviour, although egg laying tended to be delayed in T females. Females with experimentally enhanced T maintained lower temperature during incubation but did not spend less time incubating. This might explain the reduced hatching success of their eggs, smaller brood size and lower number of fledglings we found in this study. As in this species T-dependent behaviour by females during the phase of parental care is not needed, the results support the hypothesis that in this species the need for selection in favour of T-insensitivity did not occur.

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### 1. Introduction

Testosterone (T) concentrations in males remain important for reproductive success in many seasonally breeding birds after territory establishment and pairing, although they decline gradually

after the onset of egg laying (Ketterson et al., 2005; Wingfield, 1990). T is known to facilitate mate guarding, extra-pair fertilisation, secondary female acquisition, and/or territorial defence during parental care. For example, experimentally elevated T has been shown to increase singing behaviour to attract additional mates (European starling (*Sturnus vulgaris*), De Ridder et al., 2000), courtship behaviour (house sparrow (*Passer domesticus*), Hegner and Wingfield, 1987; red bishop (*Euplectes orix*), Adler et al., 2011), extra-pair fertilisation rate (dark-eyed junco (*Junco*

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hyemalis), Raouf et al., 1997) and attractiveness to females (dark-eyed junco, Enstrom et al., 1997) later on in the breeding season. Yet T has also been shown to suppress incubation behaviour (spotted sandpiper (*Actitis macularia*), Oring et al., 1989; yellow-legged gull (*Larus cachinnans*), Alonso-Alvarez, 2001) and nestling provisioning (Hegner and Wingfield, 1987) in males. Thus, elevated levels of T in males appear to moderate the trade-off between mating effort and parental effort (Adkins-Regan, 2005). In certain species, however, males do not respond to T elevation after egg laying with a reduction of parental behaviour (lapland longspur (*Calcarius lapponicus*), Hunt et al., 1997; chestnut-collared longspur (*Calcarius ornatus*), Lynn et al., 2002; great tit (*Parus major*), Van Duyse et al., 2002; black-tailed gull (*Larus crassirostris*), Kazama et al., 2011). Such variation in sensitivity of male parental behaviour to T after egg laying may be explained by the essential paternal care hypothesis, which postulates that in species where bi-parental care is essential for the survival of offspring, males, becomes insensitive to T (in terms of their parental behaviours) during the period of increased paternal care (Lynn et al., 2002; Lynn, 2008) in order to avoid the detrimental effects of the hormone.

In many avian species, female testosterone (T) levels rise, as in males, at the start of their breeding season but decline shortly after the start of egg laying (Ketterson et al., 2005). Although less well studied than in males, there is some evidence that the seasonal peak in T levels might be beneficial for females too. For example, early peak T levels are linked to female aggression (red-winged blackbird (*Agelaius phoeniceus*), Searcy, 1988; European starling, Sandell, 2007; blue tits (*Cyanistes caeruleus*), de Jong, 2013; tree swallow (*Tachycineta bicolor*), Rosvall, 2013a,b). This can help securing male care by outcompeting rivaling females (great tit, Slagvold, 1993, dunnock (*Prunella modularis*), Langmore et al., 2002; Sandell, 2007). Also, more aggressive females had higher reproductive success (dark-eyed junco, Cain and Ketterson, 2012). Females of many species also remain sensitive to elevated T levels later in the breeding season. However, in contrast to males, this prolonged sensitivity to T in females has mainly been associated with costs that could reduce reproductive success. For example, experimentally prolonged elevated T levels have been shown to delay the onset of egg laying (Searcy, 1988; dark-eyed junco, Clotfelter et al., 2004; zebra finch (*Taeniopygia guttata*), Rutkowska et al., 2005), decrease incubation temperature (Rosvall, 2013a,b), reduce brooding of nestlings (dark-eyed junco, O'Neal et al., 2008), and decrease the number of hatchlings and fledglings (spotless starling (*Sturnus unicolor*), Veiga and Polo, 2008; spotless starling, Lopez-Rull and Gil, 2009; Rosvall, 2013a, b; dark-eyed junco, Gerlach and Ketterson, 2013) in various passerine birds. In other passerine species, however, prolonged experimentally elevated T levels does not affect the onset of egg laying (de Jong, 2013) or incubation behaviour (European starling, Sandell et al., unpublished manuscript cited in Ketterson et al., 2005). Moreover, a few studies suggest that remaining sensitive to elevated T levels after egg laying might be advantageous for females. For example, prolonged elevated T levels are linked to female aggression (Searcy, 1988; Sandell, 2007; Rosvall, 2013a,b) which can secure male care by enabling females to outcompete rivals (European starling, Sandell, 2007; Langmore et al., 2002). A similar suggestion was made by Rosvall, 2013a, demonstrating sensitivity to T during the period of parental care in tree swallow.

Thus, in several bird species, female parental care appears to remain sensitive to elevated T levels after egg laying. This has been explained by the “essential mating effort hypothesis”, (Rosvall, 2013a,b). This hypothesis postulates that females in these species did not evolve insensitivity to T, since sensitivity to T is required for mediating other behaviours that are important for reproductive success, such as securing mates and nest sites, also during the period of parental care. Therefore, the benefits remaining sensitive to

T by T dependent mating effort may outweigh the potential costs of suppression of parental care.

However, the majority of studies of sensitivity to T in females after egg laying have applied T implantations to test behavioural sensitivity. This may have induced much higher T levels than the endogenously produced low levels during that time period. It is therefore conceivable that females react to these artificially elevated levels, showing sensitivity to the hormone, because selection for becoming insensitive to the hormone was never necessary. In such species the costs of maintaining T production and remaining sensitive to it (reduction of parental care) would outweigh the benefits. This may be the case in many species in which females during the phase of parental care do not participate in nest defence or mate competition. On the other hand, aggression, sexual behaviour and parental care are influenced by partly the same brain areas, all containing androgen receptors (Rosvall, 2013b). Therefore it is also possible that females only become insensitive to T in their parental behaviour, but not in aggressive and sexual behaviour. This is suggested by data on male great tits where experimentally elevated T levels increased the expression of song while not affecting parental care (Van Duyse et al., 2000).

In this study we examine the effects of sustained experimentally elevated T levels on incubation behaviour and reproductive success in female great tits (*P. major*). The great tit is a socially monogamous species with bi-parental care, which is essential for the survival of the offspring (Bjorklund and Westman, 1986a). Among females there is competition for males that own a territory (Gosler, 1993), which might explain female–female aggression at the beginning of the breeding season (Slagvold, 1993). Only females build nest and incubate eggs, but both parents provide food to their nestlings. The great tit is one of the few species in which elevated T levels in males do not suppress paternal care measured as food provisioning rate, although it does increase song rate (Van Duyse et al., 2000).

It is currently unclear whether female great tits remain sensitive to elevated T levels later in their breeding season after egg-laying, when natural T levels have declined. By comparing reproductive behaviour and reproductive success between females treated at the start of nest building with long lasting T-implants or with empty implants (controls), we tested to what extent great tit females remain sensitive to T. Since the effectiveness and pattern of incubation might be influenced by T and affect hatching success, we also measured nest temperature during incubation. The only other similar study that looked at experimentally elevated T levels and incubation behaviour in females was conducted on tree swallows, a species in which females need to defend mates and their nest cavities against intruders also during the phase of parental care (Rosvall, 2013a). In great tits there is competition for nest cavities during the winter/pre-breeding period (Gosler, 1993) but later in the season, when birds are incubating, female–female aggression in the neighbourhood of the nest box has rarely been observed (more than 20 h of personal observations BdJ). Also polygyny rarely occurs in this socially monogamous species (Bjorklund and Westman, 1986b). This suggests that T levels during the parental care period are not beneficial. During this period natural T levels are indeed low (Rost, 1990). Therefore, we hypothesised that selection against remaining sensitive to T has never been needed and that females will still respond behaviourally to artificially increased levels of this hormone. Under natural conditions female great tit probably never experienced detrimental behaviours induced by elevated T levels later in the breeding season. Therefore, it is unlikely that selection has acted on reducing sensitivity to T during this period. By experimentally elevating T level for a long period we expect to expose these behaviours that might otherwise have been negatively affected by selection.

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