



Testosterone secretion in a socially monogamous but sexually promiscuous migratory passerine



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ABSTRACT

The steroid hormone testosterone (T) influences a multitude of traits critical to reproduction in vertebrates. In birds, high male T supports territory establishment and mate attraction, but is thought to interfere with parental care. Interspecific comparisons indicate that migratory species with short, synchronous breeding seasons have the highest peak T, and that the seasonal profile of T exhibits a rapid decline with the onset of incubation by females. We describe the T profile of the migratory, socially monogamous, and biparental Eastern Kingbird (*Tyrannus tyrannus*) from the high desert of eastern Oregon, USA, where breeding occurs within a short 2–3 month period. Eastern Kingbirds are socially monogamous but exhibit high rates of extra-pair paternity as ~60% of broods contain extra-pair young. We therefore evaluate whether Eastern Kingbirds exhibit the “typical” T profile expected for a synchronously breeding migratory species, or whether T is maintained at a more constant level as would be predicted for a species with opportunities for mating that extend over a majority of the breeding season. Our samples were divided into six periods of the reproductive cycle from territory establishment to the feeding of fledglings. T did not change across stages of the nest cycle. Instead, T declined with sampling date and nest density, and increased with the number of fertile females in the population. Male kingbirds advertise their presence through song for most of the breeding season, and we suggest that T is maintained throughout most of the breeding season because male fitness is equally dependent on within- and extra-pair reproductive success.

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1. Introduction

The secretion of steroid hormones is an important proximate physiological mechanism governing the expression of many vertebrate reproductive characteristics (Adkins-Regan, 2007; Hau, 2007). In male birds, testosterone (T) is an especially important hormone because of its influence on male-male aggression and territoriality (Chandler et al., 1994; Canoine and Gwinner, 2002; Silverin et al., 2004), dominance status within groups (Peters et al., 2001), mate attraction displays such as song (Van Duyse et al., 2000; Foerster et al., 2002), mate guarding (Moore, 1984; Saino and Møller, 1995a), and possibly extra-pair mating behavior (Raouf et al., 1997; Garamszegi et al., 2005; Eikenaar et al., 2011a). T has also been shown to affect the development of sexual

ornaments (Peters et al., 2006; Redpath et al., 2006; but see Owens and Short, 1995; Schlinger et al., 2008).

The stimulatory effect of T on mating behaviors can also result in the inhibition of parental behaviors (e.g., Raouf et al., 1997; Schoech et al., 1998; Peters et al., 2002) because high T males direct their activity to obtaining extra copulations, leaving less time for parental care (Oring et al., 1989; Cawthorn et al., 1998; De Ridder et al., 2000; Van Roo, 2004). Therefore, in species with male parental care, including most monogamous species, T is expected to decline rapidly prior to the commencement of paternal care (Hunt et al., 1995; Logan and Wingfield, 1995; Van Roo et al., 2003; Pinxten et al., 2007). Overall, a species' mating system is an important predictor of its seasonal T profile (reviewed by Hirschenhauser et al. (2003)). For example, in polygynous species, T secretion exhibits a much slower decline throughout the nest cycle because males participate little in parental care and, instead seek additional mating opportunities (Beletsky et al., 1989). The opportunity to obtain extra-pair copulations in monogamous species (Griffith et al., 2002) should also be considered as an important source of reproductive success and as a possible contributor to

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variation in testosterone among males. However, very little is known about how T secretion is modulated to balance extra-pair mating activity with parental behavior (but see Peters et al., 2001; Horton et al., 2010; Eikenaar et al., 2011b), and more attention needs to be given to monogamous species in which extra-pair fertilizations are important contributors to male reproductive success.

Peak T and T profiles (i.e., change with the reproductive cycle) also appear to vary with geographic distribution and migratory behavior. For instance, the breeding biology of many tropical birds is characterized by relatively long breeding seasons, year-round territoriality, and low breeding synchrony (Hau et al., 2008; Robinson et al., 2010; Stouffer et al., 2013). By contrast, temperate species are faced with relatively short breeding seasons, an intense period of territory establishment, and high breeding synchrony. These differences have been offered as an explanation for the generally lower peak T of tropical species compared to temperate species (Goyman et al., 2004). Similar reasoning presumably explains why migratory birds typically have higher peak T than resident species (Garamszegi et al., 2008).

A number of sources of intra-population variation in T secretion have been identified (reviewed by Kempenaers et al. (2008)). Testosterone declines with time of day in many diurnal species (Bachman et al., 1987; Foerster et al., 2002; Hau et al., 2002) and with date in the breeding season, irrespective of day in the nest cycle (Hunt et al., 1995; Johnsen, 1998; Kempenaers et al., 2008). Male–male or male–female interactions can also influence the amount of T secreted by a male. As predicted by the ‘challenge hypothesis’ (Wingfield et al., 1990), aggressive interactions between males should result in an increase in circulating T. This prediction has been confirmed in some species (Moore, 1984; Wingfield, 1984; Wikelski et al., 1999; McGlothlin et al., 2007), but not in others (Van Duyse et al., 2004; Landys et al., 2007, 2010). Aggressive male–male interactions are expected to increase as conspecific density increases, contributing to the positive association between T and conspecific density in some species (Wingfield and Hahn, 1994; Sasvári et al., 2009; Horton et al., 2010). Because of its role in mate attraction, T secretion also increases as a male’s partner becomes fertile (Johnsen, 1998; Schwabl et al., 2005) and as the pool of fertile females within a population grows (Peters et al., 2001).

We studied individual and seasonal variation in T in Eastern Kingbirds (*Tyrannus tyrannus*) breeding in eastern Oregon, USA. Eastern Kingbirds (hereafter kingbirds) are territorial, Nearctic–Neotropical migratory passerines that breed over much of North America as socially monogamous pairs. Although biparental, females build nests and incubate eggs without male assistance. However, males do feed nestlings, though in at least some populations, females contribute more to nestling provisioning than males (Woodard and Murphy, 1999). While males do not feed the female during incubation, they take the lead in nest defense (Woodard and Murphy, 1999; Redmond et al., 2009a) and are therefore a critical component of nest success (e.g., Hayes and Robertson, 1989).

Extra-pair copulations are common in kingbirds (Rowe et al., 2001) and within- and extra-pair mating success contribute equally to male reproductive success (Dolan et al., 2007). Variation in extra-pair mating success is sufficiently strong to create a significant opportunity for sexual selection (Dolan et al., 2007). Thus, this population of kingbirds provides an opportunity to examine variation in T in a migratory, socially monogamous species breeding in a highly seasonal environment where paternal care and extra-pair mating activity are likely to create conflicts between mating and paternal effort. Given the combination of migratory behavior, short breeding season, and the important role that males play in successfully raising offspring, we might predict a high peak T early in the season followed by rapid decline during incubation

(Wingfield et al., 1990). However, because extra-pair fertilizations are an important component of male kingbird reproductive success (Dolan et al., 2007), we predicted that T would not exhibit a sharp drop during incubation as seen in most monogamous species and would instead change little across stages of the nest cycle. Assuming males are sensitive to their individual social environments, we anticipated that males would respond to their competitive environment and opportunities for additional fertilizations through extra-pair relations. Consequently, we predicted that T would vary positively with nesting density and with the availability of fertile females at both local and population level scales.

2. Methods

2.1. Study area

We conducted this study from 2005 to 2009 at Malheur National Wildlife Refuge (MNWR), located near Frenchglen, Harney County, Oregon (42.817° N, 118.900° W). The study site has been described in detail elsewhere (Redmond et al., 2009b; Redmond and Murphy, 2012). Briefly, the refuge consists of a large wetland complex surrounded by dry shrub-steppe habitat. Kingbirds nest almost exclusively in willows along the watercourses that run through the refuge (Redmond et al., 2009b). Between 35 and 50 pairs of kingbirds nested within the study site each year and birds of both sexes have been color-banded at Malheur since 2002 as part of demographic and parentage studies of this population.

Kingbirds arrive at Malheur over a six-week period beginning in mid-May, but the majority arrive between the last week of May and mid-June (Cooper et al., 2009a). Nesting typically begins by mid-June and nearly all reproductive activity is finished by early to mid-August. Beginning in mid-May, we exhaustively surveyed the study site daily to determine the identity of kingbird pairs by resighting color-banded birds. If individuals were not banded then we would attempt to capture them at some point during the season. High frequency of banded birds in the population (85–95%) coupled with observations at each nest ensured our confidence that we assigned the correct individuals to nests. Once located, nests were checked every two to three days to track the progress of females through the laying cycle so that we could determine when they were fertile. Similar to previous work on other species, we assumed that females were fertile from five days before the first egg was laid to the day the penultimate egg was laid (Birkhead et al., 1989; Birkhead and Möller, 1992; Gil et al., 1999). In addition to documenting date of clutch initiation, we determined clutch size, hatching success (number of eggs to hatch), and nest success (number of young to fledge). Kingbirds raise only a single brood per year, but failed nests (a range of 55–80% fail annually) are usually replaced up through the first to second week of July, and therefore we located all replacement nests for pairs that failed. Nest locations were recorded using a Garmin GPS 72 (± 3 –4 m) and nest distances were measured with ArcMap v. 9 (ESRI, Redlands, CA, USA).

2.2. Capture and blood sampling

Kingbirds were captured using mist nets in one of two ways. First, mist nets were positioned to surround nests to capture both parents as they returned to feed nestlings during daylight hours, a passive capture technique which occurred from late June and onward. Second, throughout the breeding season we used mist nets in conjunction with a playback recording of the ritualized dawn song male kingbirds sing prior to sunrise (0230 to 0600 PST, Sexton et al., 2007) to capture males by simulating a conspecific territorial intrusion. Time to capture was recorded as the length

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