



The active nightlife of diurnal birds: extraterritorial forays and nocturnal activity patterns



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ARTICLE INFO

Article history:

Received 24 May 2013

Initial acceptance 9 July 2013

Final acceptance 28 October 2013

Available online 31 December 2013

MS. number: A13-00446R

Keywords:

cuckoldry

extraterritorial foray

home range

Icterina virens

mate guarding

nocturnal activity

nocturnal movements

yellow-breasted chat

Most birds are socially monogamous, diurnally active and have small home ranges. These birds occasionally undertake extraterritorial forays, presumably to seek extrapair copulations. We used automated radiotelemetry to examine nocturnal forays and activity of a diurnal, socially monogamous passerine, the yellow-breasted chat, *Icterina virens*. Males and females forayed during both day and night, but night forays were more common. In addition to varying between day and night, there were sex- and breeding-stage-specific differences in foraging behaviour. Males forayed more than females and more frequently when their female was not fertile. Conversely, females primarily forayed when fertile. We suggest that females foray at night to avoid detection, because their mate's knowledge of potential extrapair copulations may result in harassment or decreased parental care. Both sexes were nocturnally active; however, the activity of males peaked when their mates were fertile, probably to prevent their mates from foraging and guarding them from foraging males. The nocturnal behaviour of chats suggest that extraterritorial forays may be more common than previously thought and that nocturnal behaviours may be crucial for understanding the strategies males and females use to acquire extrapair copulations.

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The movement of a territorial bird into a conspecific's territory (i.e. an extraterritorial foray) is a rarely observed event, but may have important fitness consequences. Many studies have found that both males and females engage in extraterritorial forays (hereafter 'forays') to assess mates and engage in extrapair copulations (e.g. Chiver, Stutchbury, & Morton, 2008; Double & Cockburn, 2000; Mays & Ritchison, 2004; Pedersen, Dunn, & Whittingham, 2006; Stutchbury, Pitcher, Norris, Tuttle, & Gonser, 2005; Ward, 2005). Researchers generally detect relatively few forays per individual during each breeding season (Hung, Tarof, & Stutchbury, 2009; Neudorf, Stutchbury, & Piper, 1997). For diurnal birds, forays are assumed to occur primarily during the day (Akçay et al., 2012; Neudorf et al., 1997), but have also been observed to occur 1 h before sunrise (Double & Cockburn, 2000).

Females often engage in forays when they are fertile (Chiver et al., 2008; Double & Cockburn, 2000; Neudorf et al., 1997) and are frequently secretive when engaging in forays (Johnsen, Lifjeld,

Rohde, Primmer, & Ellegren, 1998; Mays & Ritchison, 2004) and extrapair copulations (Tarof & Ratcliffe, 2000; Tryjanowski, Antczak, & Hromada, 2007). Female secrecy is likely due to the costs experienced by females if extrapair mating is detected by their social mate (Birkhead & Møller, 1992; Westneat & Stewart, 2003). These costs include harassment by their social mate; males often engage in mate guarding and harassment to dissuade females from leaving their territory (Edinger, 1988; Mays & Ritchison, 2004). Also, if a male detects a female engaging in forays, he may provide less parental care to the female's offspring (Dixon, Ross, O'Malley, & Burke, 2002). Females may also respond aggressively to other females foraying into their territory (Kempnaers et al., 1992). Because of these potential foraging costs, females would benefit by secretly engaging in forays. In contrast, males are thought to frequently engage in forays seeking extrapair copulations, except when their social mate is fertile, when it may be more beneficial to protect within-pair paternity by engaging in mate guarding (Birkhead, 1979).

One obstacle to investigating forays is the amount of effort required to obtain data on these rarely witnessed events. Using conventional radiotelemetry, observers are essentially required to track individuals constantly. Given limited resources, logistical difficulties associated with nocturnal tracking, and the assumption that diurnal birds are sleeping at night, most studies have

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understandably focused on tracking individuals during the day. In addition to focusing on daylight hours, most studies track each individual for fewer than 20 h (e.g. Chiver et al., 2008; Humbird & Neudorf, 2008; Neudorf et al., 1997; Pedersen et al., 2006). The dawn singing behaviour of many diurnal species also suggests that early morning may be important and, accordingly, some studies have investigated foraging behaviour 1 h before sunrise (e.g. Akçay et al., 2012; Double & Cockburn, 2000). However, we are aware of few studies that have investigated nocturnal movements of diurnal birds (see Mukhin, Kosarev, & Ktitorov, 2005; Roth, Sprau, Schmidt, Naguib, & Amrhein, 2009).

If diurnal birds foray at night in search of mating opportunities, many nonforaging individuals would also be expected to be active at night. Given the presence of nocturnally foraging individuals, even moving within one's territory at night may increase the possibility of extrapair copulations. There is evidence that some diurnal species are active at night, including nocturnal singing by some species during the breeding season (Amrhein, Korner, & Naguib, 2002; Amrhein, Kunc, & Naguib, 2004; Barclay, Leonard, & Friesen, 1985; Canterbury, 2007), activity due to nocturnal migratory behaviour (Mukhin et al., 2005) or to prospect for new breeding locations (Roth et al., 2009).

We used an automated radiotelemetry system (Kays et al., 2011; Ward, Sperry, & Weatherhead, 2013) to track male and female yellow-breasted chats, *Icteria virens*, a diurnal species, during both day and night. We examined whether nocturnal forays are a strategy that females use to avoid being detected by their mate and whether males engage in nocturnal forays because females are active at night and potentially receptive. The chat is an ideal species to investigate foraging behaviour, as chats will sing at night (Canterbury, 2007) and will settle at locations in response to nocturnal song during migration (Alessi, Benson, & Ward, 2010). Extrapair paternity has been documented in this species, and both sexes engage in forays (Mays & Ritchison, 2004). Furthermore, Mays and Hopper (2004) used conspecific models to demonstrate that female chats display aggression towards other females in their territory; this suggests that female chats attempt to deter foraging females from their mate's territory. Moreover, male chats engage in mate guarding and harass females that attempt to leave their territory (Mays & Ritchison, 2004). Males are also documented to be less efficient at guarding females in dense habitats, and females may foray to denser habitat to avoid being detected by their social mate (Mays & Ritchison, 2004). We examined the foraging behaviour of male and female chats during both day and night, including the time of day when forays occurred, the length of time and distance travelled during forays, and the breeding stages when forays were most common. Because individuals may also be active at night without leaving a territory, we also investigated nocturnal activity of males and females during each breeding stage.

METHODS

Species

Yellow-breasted chats are Neotropical migrants that breed in shrubland habitat, primarily in eastern North America. Female chats build the nest and incubate alone, whereas both the male and female care for nestlings (Schadd & Ritchison, 1998). Females may reneest after nest failure, but few (<8%) are double brooded (Thompson & Nolan, 1973). We conducted this research at Kennekuk Cove County Park in Vermilion County, Illinois, U.S.A., from May to July in the 2008–2011 breeding seasons. Kennekuk is approximately 1200 ha with scattered patches of shrubland habitat ranging from 4 to 24 ha dominated by autumn olive, *Elaeagnus umbellata*, bush honeysuckle, *Lonicera maackii*, and multiflora rose,

Rosa multiflora. We captured male and female chats using targeted mist netting with song playbacks, or by flushing females from their nests into a mist net. Upon capture, birds were aged and sexed according to Pyle (1997) and fitted with a U.S. Geological Survey numbered leg band and a unique combination of three colour bands. Birds were also fitted with a 0.8 g radiotransmitter, which was approximately 3% of the adult's body weight; the transmitters were purchased from JDJC corps (Fisher, IL, U.S.A.). Transmitters were attached at the base of the central rectrices using heat-shrink tubing (Alessi, Raim, Beveroth, Barron, & Ward, 2009), or in some cases the backpack attachment was used (Rappole & Tipton, 1991). While birds tolerated and flew well with both attachment techniques, the backpack attachment was more reliable. In some cases, especially late in the field season, moulting birds would lose their rectrices along with the transmitter. We used cotton thread to secure the backpack transmitters and found that, due to the cotton thread deteriorating, most transmitters fell off before an individual migrated. Many radiotagged birds returned in the following year, all of which returned without their transmitters.

We located chat nests from 1 May to 31 July by incidentally flushing females, observing parental behaviour or tracking radiotagged females to their nest. We recorded nest locations and checked nests every 2–3 days until nestlings fledged or the nest failed. We considered females to be fertile if they did not have a nest with a full clutch of eggs or nestlings and they had not fledged young. Females and males that could not be immediately associated with a social mate received additional attention to confirm they were in fact not mated. The fertile period was approximately 5 days before the first egg was laid until the penultimate egg was laid (Neudorf et al., 1997). A male was categorized as 'fertile' if his social mate was fertile. All research was conducted under the University of Illinois' Institutional Animal Care and Use Committee Protocol Number 10127.

Automated Telemetry

We documented nocturnal activity and forays using an automated radiotelemetry system (ARTS; Kays et al., 2011; Steiger et al., 2013; Ward et al., 2013). The ARTS consisted of four automated recording units (ARUs; JDJC Corp., Fisher, IL) located approximately 300–400 m apart (Fig. 1). A comprehensive overview of the methods used to track snakes at the same study site using the same system is available via Ward et al. (2013). In short, each ARU was connected to an array of six, three-element Yagi antennas attached to the top of a tower. The azimuths of the six antennas were spaced by 60° to give 360° coverage. Each ARU was programmed to tune at intervals of 2–3 min to the radio frequency of each transmitter. The ARUs provide signal strength data for each antenna, which can then be used to estimate the bearing of the transmitter from the ARU as well as activity. We used the ARU with the strongest average signal strength for a given chat to determine the activity of that chat. Activity was quantified by changes in the bearing and signal strength. Every time a radiotagged individual moves, the orientation of its transmitter's antenna to the ARU changes, resulting in, at least, a change in signal strength and often a change in the bearing (Sperry, Ward, & Weatherhead, 2013; Steiger et al., 2013; Ward et al., 2013). When quantifying activity, it is important to derive a threshold for when an individual is considered to be active. In this case we define activity as moving around an area. We used incubating females to derive this threshold. Incubating females often move to roll their eggs, so while the orientation of the transmitter's antenna to the ARU changes, the location of the bird does not change and thus we would not consider these small movements to be true activity. To set the threshold for activity, we used the average standard deviation of the bearings (3.0°) and twice the

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