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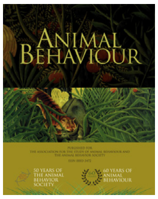

Experimental examination of nest reuse by an open-cup-nesting passerine: time/energy savings or nest site shortage?

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Reuse of open cup nests is rare among passerine birds despite possible savings of time and/or energy that might yield reproductive advantages. Anecdotal observations of the open-cup-nesting eastern kingbird, *Tyrannus tyrannus*, at Malheur National Wildlife Refuge (MNWR), OR, U.S.A., showed that 10% of females reuse old nests of mainly American robins, *Turdus migratorius*. We therefore deployed artificial nests in 2010 and 2011 at MNWR to provide female kingbirds with the opportunity to reuse nests to test predictions of the time/energy saving hypothesis. We also used a flood that submerged nest sites in 2011 as a natural experiment to test the nest site shortage hypothesis' prediction that nest reuse by kingbirds should increase when the availability of nest sites is reduced. Female kingbirds used artificial nests heavily in both years, and, contrary to the time/energy saving hypothesis, they did so more in the year of earlier breeding. We also rejected three other predictions of the time/energy saving hypothesis, namely that, within seasons, females nesting in artificial nests (1) breed earlier, (2) produce larger clutches and eggs and (3) fledge more young. The only prediction of the time/energy saving hypothesis that we failed to reject was that time to lay replacement clutches following nest failure tended to be earlier in females that used artificial nests. Nest reuse was significantly more frequent in the flood year. Given this result, and our rejection of most predictions of the time/energy saving hypothesis, we conclude that frequent nest reuse by kingbirds at MNWR is likely the result of a shortage of quality nest sites.

Nests are critical for the reproduction of birds, and much effort and skill are required to build them (Hansell 2000). Finding and delivering specific materials for nest construction requires numerous flights, which take time and are energetically costly, and potentially attract predators to the nest location (Withers 1977; Lens et al. 1994; Moreno et al. 2008). Costs to nest building may include delayed onset of breeding (Cavitt et al. 1999; Hauber 2002; Safran 2006), reduced clutch size (Weeks 1978; Eberhardt 1994 cited in Walters et al. 2002; but see Conrad & Robertson 1993), lower seasonal production of young (Hauber 2002; Safran 2006), and possibly even reduced adult annual survival (Gill & Stutchbury 2005).

Reuse of nests to avoid or reduce costs of nest construction would thus seem prudent, especially if a nest that survives between seasons provides information on the structural integrity of a nest site, and, if nests that previously fledged young are also likely to fledge young in the future (e.g. Ellison 2008; but see Cavitt et al. 1999; Styrsky 2005). Indeed, nest reuse is common among raptors, some woodpeckers and colonial-nesting birds (Wimberger 1984; Siegel-Causey & Hunt 1986; Brown & Bomberger Brown 1996; Safran 2006). Secondary-cavity-nesting birds also regularly reuse nests presumably because, in part, usable nest sites are limited (Brawn & Balda 1988; Dobkin et al. 1995; but see Waters & Noon 1990; reviewed by Newton 1998). By contrast, although nest reuse occurs in open-cup-nesting passerines (e.g. Mountjoy & Robertson 1988; Curson et al. 1996; Bergin 1997; Cavitt et al. 1999; Friesen et al. 1999; Richmond et al. 2007), it is uncommon, presumably because suitable nest sites are abundant, nests survive infrequently between years and/or the possible costs of nest reuse are high. Such costs may include an increased probability of nest failure because (1) reused nests are weathered and weak and (2) can accumulate ectoparasites between years, which depresses offspring growth and survival (Brown & Bomberger Brown 1986; Rendell & Verbeek 1996), and/or (3) nest locations are remembered by predators such as corvids (Sonerud & Fjeld 1987). Given the rarity of nest reuse among open-cup-nesting passerines, the potential costs would usually seem to trump the potential savings of time and energy that might otherwise permit earlier breeding or the production of more or larger eggs.

The eastern kingbird, *Tyrannus tyrannus* (hereafter kingbird), is a socially monogamous, Nearctic–Neotropic migrant that breeds over much of North America (Murphy 1996a). They build open-cup

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nests in trees (MacKenzie & Sealy 1981; Murphy 1983), exhibit high site fidelity (Murphy 1996b) and frequently renest on the same branch in the same tree used in previous years (Blancher & Robertson 1985; Murphy 1996a, 2004). Prior to Redmond et al. (2007), kingbirds were not reported to reuse nests of conspecifics or heterospecifics either within or across seasons (Montana, U.S.A.: Davis 1955; Manitoba, Canada: MacKenzie & Sealy 1981; Ontario, Canada: Blancher & Robertson 1985; Kansas, U.S.A.: Murphy 1986; New York, U.S.A.: M. T. Murphy, personal observation), except for Bergin's (1997) single observation in western Nebraska, U.S.A. Nest reuse in the kingbird population breeding at Malheur National Wildlife Refuge (MNWR) in southeastern Oregon accounts for about 10% of nest starts, and it is most common for kingbirds to refurbish old nests of American robins, *Turdus migratorius* (48.6% of reused nests; Redmond et al. 2007).

The frequent reuse of heterospecific and conspecific nests is thus unusual compared to other open-cup-nesting passerines (see Styrsky 2005; Ellison 2008). Kingbirds begin to nest later at MNWR than at all other sites where they have been studied (see studies cited above), probably because of the delayed phenology associated with MNWR's high elevation (1256 m). In kingbirds, delayed breeding is associated with smaller clutch size (Murphy 1986), reduced probability of replacing failed initial nesting attempts (Cooper et al. 2011), and, at least among male offspring, reduced probability of recruitment (Dolan et al. 2009). The delayed breeding season at MNWR thus possibly favours nest reuse as a means to save time and/or energy so that females can initiate egg laying sooner, produce more young and/or fledge young with a higher probability of recruitment.

On the other hand, nesting habitat for kingbirds at MNWR is restricted almost exclusively to the riparian zone of the Donner und Blitzen River running through the centre of the refuge, which is composed primarily of relatively young willow trees (*Salix* spp). Elsewhere, kingbirds usually place nests along the distal half of horizontal branches, which provides high-quality structural support (MacKenzie & Sealy 1981; Murphy 1983) and air space for parental defence of nests (Murphy et al. 1997; Redmond et al. 2009a). The branching structure and mainly vertical orientation of relatively young willow trees (*Salix* spp.), which make up more than 95% of the tree species along the river at MNWR (Redmond et al. 2009b), may provide few high-quality nest sites and thus could favour reuse of more structurally sound mud nests of robins that survived the winter, and which are likely to also survive milder summer conditions. In other words, kingbirds may be making the best of a bad situation.

We used artificial nests as surrogates of old nests to test the hypotheses that frequent nest reuse by kingbirds is either a time and/or energy saving mechanism, or a response to a shortage of quality nest sites. The time/energy saving hypothesis predicts that nest reuse (i.e. use of an artificial nest) (1) should be more common in years when breeding is delayed, and as a corollary, (2) become more frequent as the end of the breeding season approaches. Within years, the time/energy saving hypothesis also predicts that females using artificial nests should (3) breed earlier and invest more in clutches (more and possibly larger eggs) and (4) more rapidly replace failed first nesting attempts than females that build their own replacement nests. By contrast, expectations of the nest site shortage hypothesis are that reproductive variability will be independent of the use of artificial or natural nests, and that the use of artificial nests should increase when nest site availability is reduced. To test the latter prediction, we used the response of kingbirds to a natural flooding event that temporarily reduced the availability of nest sites during the nest-building phase of the reproductive cycle in one of the 2 years of our study.

METHODS

Study Species

Spring arrival of kingbirds at MNWR begins in mid-May in most years, and nest construction generally begins by late May or early June. Female kingbirds are primarily responsible for nest site selection and build the nest without male assistance in an average ± SE of 7.3 ± 0.35 days ($N = 24$; range 5–10 days). Materials used to construct the outer wall of the often bulky and conspicuous nests are small twigs, coarse roots, strips of bark and stems of herbaceous plants, while the distinct inner lining is composed of finer rootlets and soft materials such as cattail, *Typha* spp., down, fine grass stems, and occasionally feathers. Kingbirds exhibit biparental care, but males do not incubate, and make fewer trips to feed nestlings than females (Woodard & Murphy 1999). On the other hand, males are primarily responsible for nest vigilance and nest defence (Redmond et al. 2009a). Post-fledging parental care lasts 3–5 weeks (Morehouse & Brewer 1968), and as a consequence, kingbirds rear only a single brood/year. On average, two-thirds of nests fail, due almost entirely to nest predation by corvids. Failed first nesting attempts are almost always replaced by construction of a new nest within 150 m of the initial nests.

Study Site

MNWR is located in southeastern Oregon (42°49′N, 118°54′W) at the northern end of the Great Basin Desert. Demographic and behavioural research has been conducted on kingbirds at MNWR since 2002. From a demographic perspective, the riparian and wetland habitats of the refuge represent an ecological island for kingbirds surrounded by uninhabitable high desert (Redmond & Murphy 2012). MNWR runs north–south for roughly 50 km and its east–west width varies between 1 and 10 km. We conducted our experiments in 2010 and 2011 at two locations: the main study site was situated in the southern third of the refuge, and a smaller study site was situated about 5 km north of the northern boundary of the main study area (Buena Vista; see map in Redmond & Murphy 2012). Access to riparian nesting habitat at both sites was provided by the refuge's main gravel road that paralleled the Donner und Blitzen River (Center Patrol Road) from a distance of ≤5 m throughout most of its length. Additional roads paralleled East Canal and Bridge Creek on the main study area at a distance of ≤3 m.

General Field Methods

A complete census of kingbird nesting habitat at MNWR has been conducted during mid- to late May (depending on weather) each year since 2002, roughly 4 weeks before peak egg laying. In the present study, we checked all suitable habitat to locate nests by searching trees where pairs were repeatedly found. We located 80–85% of nests before or during egg laying; nearly all other nests were found during incubation. Nests in which the contents could not be examined directly were viewed using a mirror attached to an extensible 5 m pole. Nests were checked at intervals of 2–3 days, but more frequently near laying and hatching. We documented the dates on which first eggs were laid (= breeding date), clutch size, number of eggs to hatch (= brood size) and young to fledge, and determined incubation period (hatch date of last egg − laying date of last egg). Breeding dates for nests found after egg laying were established by backdating from known events (e.g. hatching), by ageing young using measures of size (Murphy 1981), and assuming a 15-day incubation period (see below). The maximum length