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NEST REUSE BY EASTERN KINGBIRDS: ADAPTIVE BEHAVIOR OR ECOLOGICAL CONSTRAINT?

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Abstract. The reuse of old nests by open-cup nesting passerines is a seemingly rare but potentially adaptive behavior if, as a consequence, females begin to breed earlier, lay larger clutches, or fledge more young. We report an unusually high rate of nest reuse (~10% of 341 nests) for Eastern Kingbirds (*Tyrannus tyrannus*) breeding at Malheur National Wildlife Refuge, Oregon. We found no difference in availability of nesting habitat or food abundance in territories in which nests were and were not reused. We also found no support for the hypotheses that kingbirds benefited from nest reuse by breeding earlier, laying larger clutches, or fledging more young, and, contrary to expectations, females that reused nests laid significantly smaller eggs than females who built their own nests. Nest reuse was independent of age: a roughly equal number of females for which we had multiple years of data both reused nests and built new nests, but at different points in their lives. Competition for nest sites seems high at Malheur National Wildlife Refuge because many open-cup nesting species utilize similar nest sites in the limited zone of riparian vegetation. A shortage of high-quality nest sites, coupled with interspecific competition, may underlie the high frequency of nest reuse in this kingbird population.

Key words: clutch size, egg mass, interspecific competition, nest reuse, timing of breeding, Tyrannus tyrannus.

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Reutilización de Nidos Antiguos en *Tyrannus tyrannus*: ¿Una Conducta Adaptativa o una Restricción Ecológica?

Resumen. La reutilización de nidos antiguos por aves paserinas que construyen nidos en forma de taza abierta es un comportamiento inusual que podría ser adaptativo si a consecuencia de éste, las hembras empiezan a reproducirse más temprano, ponen más huevos o crían un mayor número de polluelos. Presentamos datos sobre una tasa inusualmente alta de uso de nidos previamente usados (aproximadamente un 10% de 341 nidos) por parte de individuos de la especie *Tyrannus tyrannus* que se encontraban criando en el Refugio Nacional de Vida Silvestre Malheur. No encontramos ninguna diferencia en la disponibilidad de hábitat de nidificación ni en la abundancia de alimentos entre territorios en los cuales los nidos fueron usados nuevamente y territorios en los que los nidos sólo fueron usados una vez. Además, no podemos sostener la hipótesis de que estas aves se benefician de volver a usar nidos pudiendo reproducirse más temprano, poner mayor número de huevos o criar mayor número de polluelos. Además, contrariamente a lo esperado, las hembras que volvieron a usar nidos antiguos pusieron huevos significativamente más pequeños que aquellas que construyeron nidos nuevos. El uso de nidos previamente usados fue independiente de la edad: un número aproximadamente igual de hembras para las cuales teníamos datos de varios años usaron nidos de nuevo o construyeron nidos nuevos, pero en diferentes momentos de su vida. Aparentemente, la competencia por sitios de nidificación en el Refugio Nacional de Vida silvestre Malheur es alta, dado que varias especies que emplean nidos en forma de taza abierta usan sitios de nidificación similares en una zona limitada de hábitat ribereño. La escasez de sitios de nidificación de alta calidad, junto con un alto nivel de competencia interespecífica, pueden explicar la alta tasa de reutilización de nidos en esta población de *T. tyrannus*.

Nest reuse between years among open-cup nesting passerines is generally thought to occur rarely. Deterioration of nest materials between seasons likely prevents most nests from being reused, but surviving nests might also harbor ectoparasites (Clark and Mason 1985, Brown and Brown 1986, Barclay 1988) and nest predators, especially large corvids (Sonerud and Fjeld 1987), may remember the locations of nests (Yahner and Mahan 1996, but see Yahner and Mahan 1999). Observations of nest reuse have nonetheless been reported in some species (Friesen et al. 1999, Styrsky 2005), but few studies have quantified the behavior or evaluated hypotheses to explain why individuals reuse nests.

For most species, nest construction involves a considerable investment of time and energy (Collias and Collias 1984, Hansell 2000) that could be reallocated directly to reproduction if nests were reused, resulting possibly in earlier clutch initiation (Cavitt et al. 1999) or larger clutch sizes (Weeks 1978). Although it is presumed that most open-cup nesting species are not faced with a limited availability of nest sites, nests may also be reused if suitable nest sites are not common, as occurs in cavity-nesting species. Finally, nest reuse may be more common in species in which nest success is repeatable at sites between years (Martin et al. 2000), or if the condition of an old nest is an indication of a high-quality site, in which case reusing an intact nest from a previous year may lead to greater fledging success (Friesen et al. 1999).

We studied the breeding biology of Eastern Kingbirds (*Tyrannus tyrannus*) at Malheur National Wildlife Refuge (hereafter, Malheur) in southeastern Oregon from 2002 to 2005. Conspecific nest reuse appears to be very rare in Eastern Kingbirds, with only three cases detected in 1447 nesting attempts over four years in Kansas and thirteen years in New York (MTM, unpubl. data). Heterospecific nest reuse is also possible: one Eastern Kingbird was observed reusing a Western Kingbird (*T. verticalis*) nest in Nebraska (Bergin 1997), and another was detected using a Scissor-tailed Flycatcher (*T. forficatus*) nest in Kansas (MTM, unpubl. data). At Malheur, Eastern Kingbirds nest mainly in trees that line the Donner und Blitzen River. The river forms a narrow strip of wooded (mainly willow [*Salix* spp.]) riparian vegetation surrounded by marsh (dominated by *Typha* spp. and *Scirpus* spp.), which is surrounded by juniper (*Juniperus occidentalis*) woodland and sagebrush (*Artemisia* sp.) desert. Less than 2% of nests are placed outside the riparian zone (LJR, unpubl. data). Thus, appropriate habitat is spatially very limited, but suitable nest sites (i.e., the sites where nests are placed in trees) seem abundant along the river. However, several other open-cup nesting species breed syntopically with and build nests in microhabitats similar to those used by kingbirds at Malheur, thus competition for nest sites may be high.

Here we report a relatively high frequency of nest reuse by Eastern Kingbirds, and attempt to evaluate whether this represents a constraint or an adaptive behavior. The former predicts that nest reuse is associated with the use of low-quality territories, whereas the latter predicts that nest reuse results in earlier breeding, laying larger eggs or clutches, or higher nest success.

METHODS

STUDY SITE AND FIELD METHODS

We recorded nest reuse by Eastern Kingbirds (henceforth, kingbirds) between 2002 and 2005 near the town of Frenchglen (42°49′N, 118°54′W) at Malheur, southeastern Oregon. The primary study area included all sections of the Donner und Blitzen River and all roads between the southern end of the refuge near Paige Springs and a point 2 km north of the bridge to Krumbo Reservoir (18 km between southern and northern boundaries). We also collected data from a secondary site located ~10 km north of the main study area. We visited this site infrequently and only use data from this site to report total frequency of nest reuse. Few wooded areas existed away from the river or roads, but these were also checked for kingbird nests.

After discovering the first few reused nests in 2002, all kingbird nests were examined closely to determine if the nest was originally constructed in a previous season, and, if so, based on comparisons to active nests of other species in the area, we established the species that constructed it originally. The open-cup nests of kingbirds often appear bulky and disheveled from the outside, but the inner lining is nearly circular and neatly lined with small rootlets or down from cattails (Murphy 1996). Two of the three species whose nests were reused construct nests that are radically different from those of kingbirds. The mud nests of American Robins (*Turdus migratorius*) and woven, pendent nests of Bullock's Orioles (*Icterus bullockii*) are unmistakably different. Outer and inner dimensions of Brewer's Blackbird (*Euphagus cyanocephalus*) nests, the third species whose nests were reused, are roughly 20% and 35% larger than kingbird nests, respectively, and blackbirds use far more grass to weave their nests (LJR and MTM, pers. obs.). Misclassification of interspecific nest reuse was thus highly unlikely. Old kingbird nests appear gray and include compressed, worn material that differs from the generally brown-colored and intact materials used in new nests. Reused kingbird nests often had a bicolored appearance from the bottom layer of old and upper layer of new material. Regardless of whether it was a reused (either con- or heterospecific) or new nest, fresh material was always used to line the nest.

As part of a companion study of habitat selection by kingbirds at Malheur, we quantified the availability of nesting habitat and food abundance within kingbird territories in 2003, 2004, and 2005 (LJR, unpubl. data). We used the proportion of a 1 ha square centered on each kingbird nest that was covered with willow trees as our measure of nesting habitat availability. This was easily quantified by measuring the proportion of the river and road lined with willows (almost no willows grew away from the river or roads). Although this is not a direct measure of nest sites, we assumed it provided a good index of the number of nest sites available in a territory. Insect abundance was assessed through the use of an index derived from 3 min visual counts of flying insects conducted between 10:00 and 14:00 at sampling locations distributed across the study site (four replicates per habitat type) throughout the breeding seasons of 2003–2005. Weather at the time of counts was also recorded using a Kestrel 3000® Pocket Weather Station (Nielsen-Kellerman, Boothwyn, Pennsylvania) and the variables temperature, humidity, dew point, and windspeed were used to control for the effects of weather on insect counts prior to computing a mean insect abundance for each habitat type (willow, meadow, marsh, and sagebrush). Although only an estimate of insect abundance, this method has been shown to strongly correlate with insect biomass (Blancher and Robertson 1987). The abundance of insects within each nesting territory was then derived by multiplying average insect abundance of each habitat type by the proportion of the 1 ha nesting area comprised of each habitat.

Kingbirds arrive in the study area by mid-May and nesting begins by early to mid-June. Starting in May, we intensively surveyed the study area to locate all kingbird nests. Once located, nests were checked every 2–4 days to determine the date on which the first egg was laid (= date of clutch initiation), clutch size, hatching success, and the number of young that fledged. Upon clutch completion we measured maximum length (L) and breadth (B) of all eggs from as many clutches as possible, and calculated egg mass using a formula specific to kingbirds (Murphy 1983a): egg mass = $0.54*(L*B^2)$. Nests were considered successful if they fledged at least one offspring, and since almost all nests (~95%) were located prior to clutch initiation, we did not correct nest success for exposure days (i.e., Mayfield 1961, 1975).

PREDICTIONS AND STATISTICAL ANALYSES

We predicted that individuals on territories with either limited availability of nesting habitat or low food abundance would be the individuals most likely to reuse nests, because either suitable nesting sites would be limiting or the restricted food supply (and extra foraging time) would reduce time or energy that could be used for nest building. Nest site and insect abundance indices were derived for each year separately, but we combined data for all years to compare nesting habitat availability and insect abundance between females who did or did not reuse nests (*t*-test). Because kingbirds that renest after nest failure rarely switch territories, we omitted replacement nests from the above analyses to avoid pseudoreplication of data.

Breeding begins relatively late at this high-elevation site (~1400 m), and kingbirds require at least 5–7 days to build a nest. Nest reuse presumably saves time and energy, and we predicted that, compared to females who constructed new nests, females who reused nests would initiate clutches earlier, or lay more or larger eggs. To increase sample size we pooled data from all four years and standardized laying date among years by subtracting the clutch initiation date of the first clutch of the year from all other clutch initiation dates for that year. We compared mean clutch size and egg mass of females who did and did not reuse nests using *t*-tests. Given that reused nests have endured the winter, old nests may indicate sheltered sites where a nest has a high probability of surviving the duration of the nesting cycle. We tested this hypothesis by comparing the probability of success for new and reused nests using a 2×2 contingency table analysis.

Due to small sample sizes for the species whose nests were reused by kingbirds, data were pooled across species for our analyses. Multiple years of data were available for some kingbird females so, to avoid pseudoreplication, we randomly used only one year for each of these females. All statistical tests were two-tailed with significance set at $\alpha = 0.05$, and results are presented as means ± SD and sample size (n). Analyses were conducted using Statistix 8 (Analytical Software, Tallahassee, Florida).

RESULTS

NEST REUSE

We recorded nest reuse in 35 of 341 breeding attempts (10%). Annual variation ranged from 8% to 14% and did not vary among years ($\chi^2_3 = 0.2$, $P = 0.99$). The condition of reused nests varied from a substantial foundation that provided a solid building surface, to complete nests that had only to be lined on the inner surface. Surprisingly, American Robin nests were reused more often (49% of reused nests) than conspecific nests (31%; Table 1). Brewer's Blackbird and Bullock's Oriole nests, although not used as commonly, were both used in two of three years (Table 1). Eleven of the 35 females that reused nests bred in the study site in multiple years, and all of them both reused and built new nests. Equal numbers of these females reused ($n = 6$) or built new nests ($n = 5$) in their first year at the study site, and then all switched to the opposite behavior in subsequent years.

INFLUENCE OF TERRITORY QUALITY

The hypothesis that nest reuse was more likely in territories with limited nesting habitat or where food was less abundant was not supported. The proportion of area covered by willows in territories with reused nests did not differ from territories in which females built new nests (Table 2). Similarly, the index of insect abundance in territories of reused nests was similar to that of territories with new nests (Table 2).

BENEFITS OF NEST REUSE

We found no support for the hypothesis that kingbirds benefited from nest reuse by breeding earlier. The laying date for kingbirds that reused nests was identical to that of females who built new nests (Table 2). A corollary of this hypothesis was that nest reuse would be more frequent among replacement than initial nests. To

TABLE 1. Observations of nest reuse by Eastern Kingbirds at Malheur National Wildlife Refuge, Oregon, from 2002 to 2005. Species whose nests were constructed in a previous year and used by kingbirds are listed in the left-hand column, followed by the number of kingbird nests observed for each species.

Species	Year 2002	2003	2004	2005	Total
Eastern Kingbird (*Tyrannus tyrannus*)	2	2	2	5	11
American Robin (*Turdus migratorius*)	10	3	2	2	17
Brewer's Blackbird (*Euphagus cyanocephalus*)	0	2	3	0	5
Bullock's Oriole (*Icterus bullockii*)	1	1	0	0	2
Total reused (% of all nests)	13 (14%)	8 (8%)	7 (9%)	7 (10%)	35 (10%)
Total number of kingbird nesting attempts	93	100	78	70	341

conduct this analysis we examined only nests from the primary study area where we followed nest fates very closely. This sample showed no difference in the proportion of reused nests in first (14%) and replacement nesting attempts (19%; $\chi^2_1 = 0.5$, $P = 0.46$). Nest reuse might also be expected to be more common in years in which breeding is delayed, but despite the fact that the average laying date was significantly earlier in 2003 than the other three years (MTM, unpubl. data), the proportion of females that reused nests did not differ among years ($\chi^2_3 = 0.2$, $P = 0.99$). Clutch size of females who did or did not reuse nests did not differ (Table 2) and, contrary to expectations, egg mass of females who reused nests was lower than that of females who built new nests (Table 2). Finally, the presence of an old nest did not appear to offer reliable information on probability of future success. Regardless of whether a female reused or built a new nest, over 65% of nests failed (Table 2), and the number of young fledged from successful reused and new nests did not differ (Table 2).

DISCUSSION

Nest reuse had only rarely been observed in Eastern Kingbirds prior to our study (Bergin 1997; MTM, pers. obs.), but our data indicate that roughly 10% of female kingbirds reused nests at Malheur in all years. The annual consistency strongly suggests that it is a normal behavior pattern at Malheur.

We failed to find support for any of the hypotheses that we proposed to explain the high frequency of nest reuse. Neither nesting habitat nor food supply differed between territories with reused and new nests, suggesting that nest reuse was not a means of compensating for poor territory quality. Kingbirds also appeared to gain no benefits from nest reuse. Among first nests of the season, laying dates of females who reused or built new nests were the same. Unlike Weeks (1978), who showed that nest reuse by Eastern Phoebes (*Sayornis phoebe*) was associated with larger clutch size, kingbird nest reuse was not, and, contrary to predictions, females who reused nests laid smaller eggs than females who built their own nests. Nest reuse also appeared to be independent of female age or experience, given that several individuals ($n = 11$) with multiple years of data switched behaviors between breeding seasons, but not in a predictable manner.

Ultimately, the final arbiter of whether or not a behavior is adaptive is its impact on reproductive success. The probability that a kingbird nest would fail was very similar when reused and new nests were compared, and productivity of successful reused and new nests was the same. Friesen et al. (1999) observed a higher probability of success for Wood Thrush (*Hylocichla mustelina*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) parents that reused nests, but sample size ($n = 4$ and 1 for the thrush and grosbeak, respectively) precluded statistical analysis. Erckmann et al. (1990) concluded that although female Red-winged Blackbirds (*Agelaius phoeniceus*) could possibly infer success of a nest in the previous year based on its appearance, the blackbirds showed no tendency to

TABLE 2. A comparison of territory and reproductive characteristics between female Eastern Kingbirds who built new nests and those that reused nests constructed in a previous year at Malheur National Wildlife Refuge, Oregon, from 2002 to 2005. Data reported are for first nests of the season.

Trait	New nests; mean ± SD (*n*)	Reused nests; mean ± SD (*n*)	Test statistic (*P*)[a]
Willow cover (%)	11 ± 10 (95)	11 ± 9 (14)	0.6 (0.54)
Insect abundance	7.0 ± 2.3 (95)	6.8 ± 2.5 (14)	0.2 (0.84)
Laying date (days)	13.4 ± 7.5 (111)	13.2 ± 9.5 (17)	0.1 (0.91)
Clutch size (eggs)	3.6 ± 0.7 (109)	3.6 ± 0.7 (17)	0.2 (0.87)
Egg mass (g)	4.3 ± 0.4 (52)	4.1 ± 0.3 (13)	2.2 (0.03)
Nest success (% successful)	32 (43 of 134)	33 (7 of 21)	<0.1 (0.91)
Fledging success[b]	2.8 ± 1.1 (42)	3.1 ± 0.7 (7)	0.8 (0.43)

[a] All comparisons based on a *t*-test except for nest success which was compared with a χ^2 test.
[b] Fledging success based only on nests that fledged at least one nestling.

nest near previously successful nests. Kingbirds in Malheur select habitat based, at least in part, on past reproductive success of conspecifics (LJR, unpubl. data), but the ability to detect cues from old nests that could be used to infer past history of a specific nest site seems low, especially since most of the reused nests (~69%) were built by heterospecifics.

We suggest that a nonadaptive explanation is the most likely rationale for the extreme difference in the frequency of nest reuse between Malheur and other kingbird populations. Nest reuse seems likely to be related to the species of trees available, and to the abundance of suitable nest sites. Kingbirds in Kansas nested regularly in mulberries (*Morus* spp.) and Osage oranges (*Maclura pomifera*; Murphy 1983b), while apples (*Malus* sp.) and hawthorns (*Crataegus* sp.) were heavily used in Ontario (Blancher and Robertson 1985) and New York (Murphy et al. 1997). All four species have broad canopies with numerous horizontal branches that provide many potential nest sites. At Malheur, kingbirds constructed their nests primarily in willows, most of which were thin, oriented vertically, and lacking the horizontal branches that provide stable nest sites. Thus, at Malheur, kingbirds face a shortage of the type of nest sites regularly used elsewhere, and acceptable nest sites may be further limited as a result of competition with other species. American Robins, Brewer's Blackbirds, Bullock's Orioles, Mourning Doves (*Zenaida macroura*), and Black-headed Grosbeaks (*Pheucticus melanocephalus*) all appear to have nesting requirements that overlap those of kingbirds, and all nest at high densities along the Donner und Blitzen River at Malheur. Kingbirds are fairly late spring arrivals and begin to nest after the other species (LJR, pers. obs.). Nest reuse has only rarely been observed in robins (Sallabanks and James 1999, Martin 2002) and robins in particular may usurp many of the best nest sites, forcing some kingbirds to reuse old nests that remain in place at quality sites.

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