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Behavioral Observation and Paternal Investment of Eastern Kingbirds at Malheur

National Wildlife Refuge

by

Christopher Michael Chutter

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biology

Thesis Committee:
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Portland State University
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ABSTRACT

The population and behavioral ecology of Eastern Kingbirds breeding in riparian habitats at Malheur National Wildlife Refuge (MNWR), Harney County, OR, has been studied since 2002. The physical structure of the vegetation along the riparian corridors at MNWR create an ideal research environment that facilitated the capture and individual marking of most adults in the population. Genetic sampling of captured adults through microsatellite DNA enabled the paternity of a majority of broods to be determined in every year since 2002. I used video recordings of parental nest behavior made between 2003 and 2010 as the basis for two related projects. First, I tested the effectiveness of video sampling nesting behavior. Second, I then tested whether male kingbirds were able to affect their level of paternal investment in accordance with their level or realized paternity.

Chapter 2 was split into three distinct questions: 1) are parental nesting behaviors repeatable, 2) is a one hour sample sufficient to capture variability in these behaviors, and 3) is the first hour of recording sufficient to capture variability in these behaviors. I found overwhelming evidence that the behaviors I measured were repeatable. This is important because lack of repeatability would call into question the use of single point samples of behavior to study animal behavior. I similarly found strong evidence that a one hour sample was sufficient to capture variability in parental behaviors. From this I was able to suggest that further sampling effort would be better

spent increasing sample size rather than observation length. Results of my test of whether the first hour of recording captured accurately variability in parental behavior was less clear. While a positive correlation usually existed between behaviors recorded in the first hour and recordings made over a 2 to 3 hour observation period, most behaviors also tended to have significantly lower values in the first hour. I tested whether this was the result of a lingering observer effect or a natural effect of time of day and concluded that an observer effect was the more likely explanation.

In recent decades behavioral ecologists have shown that a majority of songbirds that breed as socially monogamous pairs are rarely genetically monogamous. This creates a conundrum for males, and in chapter 3 I address a question of long-standing debate among behavioral ecologists studying the extra-pair mating systems of birds; does loss of paternity lead to reductions in a male's investment in his social mate's current brood. I used the standard male feeding rate as a measure of male investment as well as a far more nuanced measure derived from the first eigenvector of a principal component analysis of six paternal behaviors. These were both tested using Akaike's Information Criterion against a number of variables likely to affect parental behavior, including realized paternity. Ultimately, I found no evidence that kingbirds were able to affect paternal investment in response to lost paternity, and conclude that they likely had no means to assess realized paternity within the nest of their social mate. However, from the other parameters tested I found that males increased their investment as brood size increased and as the female spent more time attending, but not feeding, the

nestlings. Also, male investment decreased as territory density increased and flight feather length increased. Theory surrounding the variability of extra-pair paternity in birds can be used to account for these results. In a denser population males are predicted to reduce paternal effort for one of two reasons; increased likelihood of paternity loss in his own nest and an increased investment in pursuing extra-pair copulations of his own. Longer flight feathers are a sign of greater age and quality in kingbirds, so males with this trait are expected to spend more time pursuing extra-pair copulations as they are more likely to be successful in this endeavour. Thus, although paternity per se did not affect male parental behavior, the extra-pair mating system of kingbirds, and the opportunity for loss and gain of young, has likely shaped the evolution of paternal behavior of Eastern Kingbirds.

Dedicated to my partner Kristie Foster.

For her patience with, and acceptance of me;
before, during, and after completion of my thesis.

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For her endless support on a personal level I would like to thank my partner, Kristie Foster. Few girlfriends would stick by a guy living in another country for as many years as she has, fewer still would visit as often as she has. Her knowledge of the lesser known capabilities in MS Excel also proved invaluable to the analysis of my data.

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Chapter 1 : OVERVIEW AND GENERAL BACKGROUND

Study context

Prior to the explosion in genetic technologies and DNA research that broadly began in the late 1970's (see Sanger & Coulson, 1975; Sanger et al., 1977), the scientific community assumed that socially monogamous bird species were in fact monogamous (Lack, 1968). As a result, research up to then assumed that nestlings in a nest were related to both adults associated with the nest, despite anecdotal evidence of extra-pair copulations (EPCs; Allen, 1914; Beer & Tibbitts, 1950). By the 1970's, researchers began to question this assumption when studies such as that of Bray et al. (1975) showed no reduction in fertility of females paired to males that had received a vasectomy. Bray et al. (1975) tested other possibilities, including sperm retention, and concluded that female promiscuity was the best explanation for the observed trend. Subsequently, scientists sought to test for extra-pair paternity (EPP) in other species and did so through a variety of now archaic techniques including heritability estimates of morphology (Alatalo et al., 1984; Møller, 1989). Despite some objections (Lifjeld & Slagsvold, 1989), these were the best options at the time.

Times change rapidly, and just over a decade later studies of parentage using heritability estimates were not even admissible in meta-analyses (e.g., Griffith et al., 2002). By the 1980s DNA minisatellite technologies had been developed for humans and other mammals, and in 1987 the pioneering study that used them on birds (Burke &

Bruford, 1987) found evidence of EPP in the House Sparrow (*Passer domesticus*). Since this time, genetics technologies have improved and become more powerful, available, and affordable. As more and more paternity studies were conducted on socially monogamous passerines (150 by 2002; Griffith et al., 2002), research was able to show that the vast majority of the species sampled demonstrated some degree of extra-pair paternity (Westneat & Sherman, 1997; Griffith et al., 2002), although sampling was admittedly biased both geographically (Stutchbury & Morton, 2001) and taxonomically. In addition, it has shown that over 200 species of birds can exhibit conspecific nest parasitism (Lyon & Eadie, 2008), most of which would have gone undetected without genetic technologies.

With the discovery of EPP within the broods of many socially monogamous birds (~87% of the 150+ passerine species sampled; Griffith et al., 2002) researchers began to question why EPP was so common and what factors might predict the variability of its frequency, both within and among species. Evolutionary theory would suggest that for a behavior or trait to evolve within a species its benefits must out-weigh its costs. The benefits for males are obvious because with each copulation a male has the potential to increase the number of young sired. Understanding why females engage in extra-pair matings is less clear because a single copulation is theoretically sufficient to fertilize all of the eggs a female will lay in a single clutch. Extra-pair mating behavior carries a number of potential, one of which that effects both species equally is an elevated risk of acquiring sexually transmitted diseases. Other potential costs, however, fall

disproportionately on females, and these include reduced parental investment of the social mate (Birkhead & Møller, 1992; Møller & Birkhead, 1993; Alonzo & Klug, 2012), and the time lost pursuing EPCs (Petrie & Kempenaers, 1998). If there were no benefit to EPP, each of these costs would likely restrict the behavior to a very small minority.

Females do not gain quantitatively from extra-pair copulations, and therefore several hypotheses have been proposed to explain why females engage in EPCs. The alternative hypotheses rely, with one exception, more on qualitative than quantitative differences of young. These have been tested with varying levels of success. Some suggested benefits include the acquisition of more desirable genetic traits for her young (Westneat et al., 1990; Birkhead & Møller, 1992; Kempenaers et al., 1997; Sheldon et al., 1997; Johnsen et al., 2000), better mix of genes (Westneat et al., 1990; Kempenaers et al., 1999; Tregenza & Wedell, 2000; Griffith & Immler, 2009), access to more resources (including nuptial gifts; Wolf, 1975; Burke et al., 1989; Colwell & Oring, 1989), and safeguarding against mate sterility (Wetton & Parkin, 1991; Sheldon, 1994) or mate death (Petrie & Kempenaers, 1998). In socially monogamous species only one female can pair with the best male in a population, but in a population with EPP multiple females can bear his young and, in so doing, potentially raise healthier, more attractive offspring. It makes evolutionary sense for any female paired to an undesirable male to acquire male gametes elsewhere, increasing her chances of raising young that will achieve higher fecundity in life. The genetic diversity argument suggests that females seek out EPP from males with genomes more distinct from their own, effectively using it

as a means of avoiding issues associated with inbreeding or deleterious recessive alleles. In some species it has been documented that males bring nuptial gifts (generally food) in exchange for EPCs (Tryjanowski & Hromada, 2005), while in others it has been documented that females are permitted access to neighboring territories after engaging in EPCs with the male on that territory. Either of these resources could improve her and/or her offsprings' chances of survival. Finally, any monogamous female paired to a male that is either sterile or dies before fertilization, will otherwise miss any opportunity to reproduce. In this light, EPCs are an excellent way to ensure fertilization in an unpredictable world, and possibly also creates existing relationships from which she might quickly find a new mate if her present one suddenly died. Each of these reasons have received support in the primary literature and to this day there is no consensus on their relative importance (Arnqvist & Kirkpatrick, 2005; Griffith, 2007). Therefore, at present, multiple hypotheses remain viable to explain the benefit to a female from engaging in EPCs, but these benefits vary by species and situation. The genetic benefits argument has probably received the most attention, and although some would say that it is the driving force behind the variability in EPP rates in birds, recent meta-analysis suggests otherwise (Akçay & Roughgarden, 2007). Additionally, while the benefits of EPP likely account for why EPP is so widespread, they alone cannot begin to explain the variability seen in nature, as all individuals of all species would benefit from healthier and more reproductively successful offspring while avoiding such things as inbreeding and unfertilized eggs.

To account for the variability in rates of EPP in birds, a series of other hypotheses were put forth and tested. These include breeding density (Stutchbury, 1998; Yezerinac et al., 1999), breeding synchrony (Stutchbury & Morton, 1995; Stutchbury, 1998), genetic diversity (Petrie & Lipsitch, 1994; Griffith, 2000), dependence on paternal care (Birkhead & Møller, 1996; Gowaty, 1996; Mulder et al., 1994), and adult mortality (Mauck et al., 1999; Wink & Dyrce, 1999). Each of these hypotheses is briefly explained below. Breeding density is expected to influence the rate of EPP as the challenge of finding EPCs would be reduced under high density conditions (Møller & Birkhead, 1993). It would likewise increase the probability of females encountering a male with desirable traits. Breeding synchrony is suggested to create a situation where females are better able to assess the quality of potential males by creating a pulse of competition among them for such opportunities (e.g. Murphy et al., 2008). In addition, it creates a situation where her social mate could not possibly guard her while she was fertile and still pursue EPCs of his own. Genetic diversity within a population is suggested to create a situation where the benefits of infidelity are more conducive to that behavior, for if a female lived in a population where the gene pool was largely homogenous (for instance on small islands) there could be little genetic benefit to her offspring of pursuing EPP (see Griffith, 2000). Dependence on paternal care was suggested as an explanation for variability in rates of EPP because females of a species whose ecological niche requires paternal investment would be less likely to engage in EPCs and risk the reduced paternal investment frequently associated with lost paternity (Møller & Birkhead, 1993;

Schwagmeyer et al., 1999; Whittingham & Dunn, 2001; Griffith et al., 2002; Alonzo & Klug, 2012). The adult mortality explanation similarly plays off the association between lost paternity and lost paternal investment, arguing that in short-lived species, males cannot afford to abandon a nest due to uncertain paternity as there is a good chance it could be their last mating opportunity. In this light, the female is afforded a greater opportunity to exploit EPCs without a major concern for losing the male's assistance. As with the explanations for why EPP is so prevalent, each of these explanations for its variability has received considerable support by studies in the primary literature (Griffith et al., 2002).

Griffith et al.'s (2002) review of the hypotheses put forth to explain the variability of EPP in birds thoroughly covered the phenomenon and concluded that while each hypothesis likely plays a role, their influence is complicated and best approached hierarchically. Griffith et al. (2002) approached their review to show the strengths and weaknesses for each explanation in the literature at four different levels of organization: among major lineages, among closely related species, among populations of the same species, and among individuals of the same population. They showed that over 50% of the interspecific variability in rates of EPP is accounted for by the variability at higher levels of taxonomy, suggesting a deep evolutionary root to the factors influencing interspecific variability. Ultimately they suggested that there is no single explanation for the variability in rates of EPP. Instead they argued that among major lineages, life history variables like adult mortality and the form of parental care

best explained variability, while at the lower levels of organization contemporary factors like density, synchrony, and genetic variability showed stronger support. As with the reasons for why EPP is so prevalent, it seems that the reason for its variability also is complicated, multifaceted, and in need of additional research.

Study Site and species

This thesis is the culmination of eight years of work undertaken in the Malheur National Wildlife Refuge (MNWR), near Burns, Oregon. I contributed to the research efforts during the final two seasons. Our study was conducted on the population of Eastern Kingbirds (*Tyrannus tyrannus*, Passeriformes: Tyrannidae; hereafter kingbirds) breeding within MNWR.

MNWR encompasses 187,000 acres of what historically had been constituted primarily by marsh habitat. That habitat has changed significantly in recent times due to the canalization of the Donner und Blitzen River flowing through the MNWR. The area surrounding MNWR is predominately arid high desert (1,400m asl) sparsely vegetated with sagebrush (*Artemisia tridentata*) and rabbitbrush (*Ericameria* spp.), with juniper (*Juniperus occidentalis*) found on steeper slopes. This habitat is very seldom used by kingbirds. Much of MNWR is now dry and covered in grass and other low herbaceous growth that also is not used by kingbirds, which require shrubs or trees for nesting, and feed on large flying insects, such as dragonflies, that often are associated with water-influenced habitats. As a result, MNWR contains a kingbird population that almost

exclusively nests in willows (*Salix* spp.) within the very narrow riparian habitats associated with the Donner und Blitzen River and other smaller water courses.

The kingbird is a Nearctic-Neotropical migratory passerine that breeds throughout most of temperate North America and winters in South America (Jahn et al., 2013). Kingbirds are aerial insectivores and while in MNWR specialize on dragonflies and other large flying insects. The kingbird is a socially monogamous species that demonstrates high site and mate fidelity between years (Murphy, 1996). Despite these social bonds, kingbirds demonstrate one of the highest known rates of EPP with extra-pair young found in ~60% of nests (Rowe et al., 2001; Dolan et al., 2007). The reason for this exceptional rate of EPP is largely unknown.

MNWR was an ideal setting for this study for a number of reasons. It contains a fairly small population of kingbirds, making it of manageable size for studies involving activities such as nest searching, nest monitoring, color banding, and DNA sampling. The size of this population has resulted in most individuals having been banded and sampled for DNA. In addition, nearly all nests have been located in the course of each breeding season. Also, the population has very clearly demarcated boundaries, occurring exclusively within a long, narrow stretch of habitat along the edges of the Donner und Blitzen River. Through a combination of either floating down the river or driving/walking the road that parallels it, most nests were quickly found due to their conspicuous nature, limited strata for nesting, and aggressive territorial behavior of adults that often times we used to locate nests. The access road along one side of the river made it

possible to set up cameras early in the morning with minimal disturbance to the adults. Also, kingbirds have been shown to exhibit high breeding site fidelity (Murphy, 1996), a desirable trait for our research, and the fact that the nearest area of appropriate habitat is approximately 10 kilometers away could only heighten their site fidelity. Due to this, surviving birds were usually relocated each season. Site fidelity also meant that banding and DNA sampling nestlings went a long way towards keeping on top of population recruitment. A final benefit of MNWR is that its high desert environment leads to an even shorter breeding season than kingbirds usually experience throughout the rest of their breeding range, frequently delaying breeding until mid-June. A long, cold winter, combined with the effects of high elevation means that MNWR frequently has late snow melt and a delayed emergence of the insects upon which kingbirds feed. This leads to greater breeding synchrony, which is one factor predicted to influence rates of EPP in birds (Stutchbury & Morton, 1995; Stutchbury, 1998; Griffith et al., 2002).

We endeavoured to use this population to study the effects of lost paternity on male parental behavior. This was an ideal species with which to work in addressing that question for a number of reasons. Most importantly, its exceptionally high rate of EPP made it possible to test theories with moderate sample size; it also made this study more interesting as this high rate of EPP has not been well explained. While factors such as high breeding synchrony, low life expectancy, and no dependence upon male investment (Hayes & Robertson, 1989) are all predicted to increase rates of EPP, none of these factors are so unusual within this population as to explain the exceptional rate of

EPP observed. Also the kingbird generally builds a low, conspicuous cup nest that is easily located and lends itself to video recording. In addition, the aforementioned banding and DNA sampling that has been conducted on this population assisted other aspects of our studies. The color bands were critical to identification of the sexes of the birds in video recordings as they are only cryptically sexually dimorphic (Murphy, 2007). And, the existing genetic information for the adults of the population was critical for us to run paternity tests on the on the DNA samples collected from the nestlings.

Chapter 2 : THE EFFECTIVENESS OF VIDEO RECORDING PARENTAL BEHAVIOR

Abstract

The methods used in studies of parental behavior are largely idiosyncratic and are rarely tested to verify that they yield reliable data. In particular, the minimum number and length of observations used to describe behavior accurately is rarely, if ever, justified. Using data on parental behavior of Eastern Kingbirds (*Tyrannus tyrannus*) collected by video in southeastern Oregon, we evaluated three questions regarding sampling methods: (1) Is behavior sufficiently repeatable among days such that observations from a single session are representative of parental behavior? (2) Does a one-hour sampling window fairly represent parental behavior, or is a longer period needed to accurately describe behavior? And (3) Assuming that a one-hour period is sufficient, does the first hour immediately after disturbance to start recordings yield reliable data? We found that among-pair differences in parental behaviors were repeatable over different days and that a single hour of observation was representative of parental behavior over a longer (2 to 3 hour) period of observation. However, our data also suggested that the first hour yielded less representative data than the remaining 2 to 3 hours; nonetheless, consistent among-pair differences were still detectable. The shortcoming of data collected in the first hour appeared to be due to a lingering effect of human disturbance from setting up recording devices rather than an effect of time-of-day. We suggest that researchers test the appropriateness of their

methods, but our data nonetheless suggest that observations undertaken over relatively brief periods can yield useful and reliable data.

Key words: behavioral methods, brooding behavior, fecal sacs, feeding rate, parental behavior

Introduction

The ability to test hypotheses that further our understanding of the ecology and behavior of birds requires that we collect data using methods that accurately record natural processes and events. Unfortunately, this is not always the case. For instance, Wilcove (1985) was among the first of many (e.g. Small & Hunter, 1988; Bayne & Hobson, 1997) to use artificial nests to estimate probability of nest predation in relation to habitat and landscape features. However, comparisons of results from studies that used artificial and natural nests suggest, that the results often differ (Major & Kendal, 1996; Moore & Robinson, 2004). Our understanding of relationships between predator behavior, and habitat and landscape structure is therefore unlikely to be advanced by the use of artificial nests.

Similarly, the use of point counts to determine presence/absence or abundance of birds to describe community composition, population density, or habitat associations has a long history. Such survey data are rife with the possibility of bias associated with species-specific detection probability and observer effects. In this case, the literature abounds with attempts to account for such biases through improved field methods

(Moore et al., 2004), laboratory evaluation of observer bias (Campbell & Francis, 2011), and statistical analysis (Royle, 2004; Riddle et al., 2010). In contrast, the question of what is a sufficient sample period for a point count has, surprisingly, not often been addressed, and survey periods in different studies vary from 5 min to 25 min (see review in Bonthoux & Balent, 2012). However, for purposes of the detection of presence or absence, the available data suggest that little appears to be gained by extending observation periods beyond five minutes (Dettmers et al., 1999; Bonthoux & Balent, 2012) and that additional time is better spent surveying more points.

The study of parental behavior is another active area of avian behavioral research. Quantification of parental care is used, among other things, to test life history theory (Maigret & Murphy, 1997; Saino et al., 1997), evaluate possible conflict between the sexes (Griggio & Pilastro, 2007; Cleasby et al., 2013), or measure male responses to losses of paternity (Chuang-Dobbs et al., 2001; Garcia-Vigón et al., 2009). Methods to quantify parental care, and in particular the feeding of young, exhibit little uniformity across studies. Length of observation periods and the number of days parental behavior are documented varies greatly, from 30 minutes (Peluc et al., 2008) to one hour (Dunn & Cockburn, 1996) on one day, 20-30 minute bouts on ≥ 3 days (Lifjeld & Slagsvold, 1991; Whittingham et al., 1993; Clotfelter, 1997), 2-4 hour observation period on 1 day (Muldal et al., 1986; Wheelwright et al., 1992; Chuang-Dobbs et al., 2001; Varian-Ramos et al., 2012), 1 hour observation bouts conducted over ≥ 2 days (Whittingham, 1989; Wright & Cotton, 1994; Sheldon et al., 1997; Kempenaers et al., 1998; Woodard &

Murphy, 1999; Peterson et al., 2001; Neudorf et al., 2013), ≥ 2 hours of observation on each of several days of the nestling period (Rosa & Murphy, 1994; Kempenaers et al., 1998; Adler & Ritchison, 2011; Mitchell et al., 2012), and even single full day watches (Norris, 1990; Johnsen et al., 2005). As with point counts, the question exists as to what constitutes a sufficient observation length for the accurate description of behavior. Differences in the intensity of sampling will depend on the hypothesis being tested, but there is undoubtedly a minimum observation length below which data must be viewed skeptically. Few studies have attempted to assess whether, for instance, a single day can be reliably viewed as representative of a pair's behavior (but see Sheldon et al., 1997), or, by contrast, whether there is any benefit to sampling multiple hours when fewer would do (but see Wheelwright et al., 1992; Johnsen et al., 2005). Given costs of both time and personnel, and the trade-off that exists between number of nests and length of time they can be sampled, it behooves us to attempt to identify minimum necessary requirements for securing accurate measures of parental behavior.

The Eastern Kingbird (*Tyrannus tyrannus*; hereafter kingbird) is a socially monogamous, Nearctic-Neotropical migrant that builds open-cup nests in conspicuous and easily observed locations in trees. Kingbirds are very amenable to observation and numerous studies exist of both nest defense (Blancher & Robertson, 1982; Siderius, 1993; Redmond et al., 2009) and parental care (Morehouse & Brewer, 1968; Rosa & Murphy, 1994; Woodard & Murphy, 1999). In the present paper, we use kingbirds to address three questions related to the adequacy of sampling design: (1) Does parental

behavior exhibit sufficient repeatability to allow a sample of behavior from a single day to be used to characterize differences in behavior among pairs? (2) Is a single hour of sampling adequate to characterize parental behavior, or, is behavior so temporally variable that multiple (3-4) hours of continuous sampling are needed? And (3) Assuming that a single hour is adequate, are recordings of behavior made in the hour immediately after a visit by researchers representative of typical behavior, or does it reflect residual and lingering effects of researcher presence?

Methods

Study site and field methods

We conducted our study on a geographically isolated kingbird population at Malheur National Wildlife Refuge (MNWR; 43°N, 119°W). MNWR is located in southeastern Oregon, at the northern end of the Great Basin Desert. Vegetation of the high desert (1,400 m asl) is primarily big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Ericameria* spp.) that kingbirds rarely use for nesting. However, the riparian zone of the Donner und Blitzen River that runs through the center of MNWR is lined with willow trees (*Salix* spp.) that kingbird use for nesting. Studies of kingbirds at MNWR began in 2002 and continued through 2011, with our daily presence on site from mid-May through the end of July or early August (depending on annual phenology). Individual kingbirds have been uniquely marked with one federal and three plastic color bands since 2002, and we collected data on parental behaviour between 2003 and 2010.

Details of field methods are described elsewhere (Dolan et al., 2007; Cooper et al., 2009) and are thus only briefly summarized here. Female kingbirds build nests and incubate eggs without male assistance. About 80% of nests are found prior to egg-laying and over 90% are found by at most midway through incubation. At MNWR, kingbirds lay 2 to 5 eggs/clutch on successive days, generally without interruption. We checked nests at 2 to 3 day intervals to document laying date, clutch size, hatching date, hatching success (number of eggs to hatch) and fledging success (number of hatched eggs to yield fledged young). Although single-brooded, kingbirds replace failed nests. We therefore located replacement nests for pairs that failed to determine seasonal productivity of all pairs. Egg-laying dates for nests found after laying was complete were established by back-dating from known events (e.g. hatching) or by aging young using measurements of known age nestlings (Murphy, 1981). We captured males throughout the breeding season using mist nets and playback of dawn songs (Murphy et al., 2008), and adults of both sexes by placing mist nets near nests to capture adults as they returned with food for the young. Birds were not captured and handled prior to recording of behavior.

Behavioral observations

We recorded behavior between day 5 (hatching = day 0) and 12, generally within the period when parental feeding rates are asymptotic with respect to age (Rosa and Murphy 1994). We recorded parental behavior at the nest using Sony SteadyShot CCD-TRV608 video cameras housed within a waterproof green box, mounted on tripods placed within 10 m of the nest. Film units were placed on site on the morning that the

nest was to be filmed, and recordings were made on four-hour Hi8 video cassettes.

Cameras were centered on the nest and focused to capture a roughly 30 cm radius area around the nest. The 1 to 4 hour filming sessions began anywhere between 0600 PST and 1000 PST on days without precipitation or strong winds. Videos were recorded with the timestamp and date to aid later analysis.

We digitized the video cassettes using a StarTech USB 2.0 video capture cable along with GrabBee software. To save memory and processing time, a separate file was created for each visit to the nest such that the intervening periods when both adults were absent were not digitized. We then reviewed the digitized files to gather behavioral data that included number of trips to the nest during which an adult visited and (1) did not feed young, (2) fed young, (3) ingested fecal sacs, (4) transported fecal sacs away from the nest, (5) positioned its body over the young to warm or shade them (“sheltering”), and (6) exhibited behaviors indicative of nest maintenance (“housekeeping”). We recorded the timestamps of arrival and departure for all visits, and combined feeding and nonfeeding visits into “total visits”. We also recorded the total time the pair was in attendance (“nest attendance”) using the time stamps, and summed fecal sacs ingested and fecal sacs transported away to compute total fecal sac removals. Kingbirds are single prey loaders; only a single nestling is fed at each feeding visit. All trips during which an adult dipped its bill into the mouth of a begging nestling, regardless of whether food items could be seen, was classified as a feeding visit. We then classified food items into 1 of 4 size categories: (1) small (adult bill appeared closed

or nearly closed while holding the food item); (2) medium (adult bill open while holding a visible food item that did not protrude beyond the edge of the bill); (3) large (food item easily seen with portions extending beyond both sides of the bill); (4) extremely large (reserved for large Anisopteran dragonflies). All variables are reported as hourly rates with the exception of prey size and nest attendance (%). For the latter, times were doubled for when both parents were simultaneously present.

Statistical analysis

Question 1: Is parental behavior repeatable?

We compared the behavior of 18 pairs of kingbirds that were recorded on different days of the nestling period to evaluate the repeatability of behaviors. Behaviors were averaged over the 1 to 2 (2 pairs) or 3 to 4 hour observation period (16 pairs), and were compared between days using paired *t*-tests. We also used least squares linear regression with the first day of observation as the independent variable to predict behavior on the second day of observation. Separate regressions were run for all behaviors. Results indicative of repeatable behavior would be (1) failure to detect significant differences between days using *t*-tests, and (2) significant associations when behavior from the second observation day is regressed on that from the first day, with, ideally, regression coefficients that do not differ significantly from a value of 1.0.

Question 2: Does a single hour of observation accurately describe parental behavior?

Behavioral data were available for 41 pairs of kingbirds, 18 of which were observed twice and constituted the sample for our previous question. For the latter group we used a sample from one day that was either randomly chosen, or if a difference in observation length existed (3 or 4 hours), we used the day with the longer observation period. To conduct these analyses each 3 to 4 hour observation period was subdivided into 3 or 4, respectively, 1-hr long samples. We then used a random number generator to select one 1-hr sample for each of the 41 pairs. The remaining 2 to 3 hours of observations were averaged, and that mean was then compared to the randomly chosen hour for all pairs using a paired t -test. The entire process was repeated ten times (i.e., 410 randomly chosen hours [41 pairs x 10 iterations]) to yield 90 comparisons made by paired t -tests (10 tests of 9 behaviors). To summarize our results, we computed the average of the 10 iterations for each behavior for all 41 pairs. The average for each behavior for all pairs was then averaged to generate a grand mean for the randomly chosen hour for each behavior. Similarly, we computed the grand mean from the 10 iterations for the remaining 2-3 hours, and compared the two grand means using a two-sample t -test. Lastly, for all of the 10 iterations we evaluated the degree to which behavior recorded in the randomly chosen hour predicted behavior in the remaining 2 to 3 hour period for all nine behaviors using least squares linear regression. Indications that a single hour was a satisfactory sampling period would be (1) failure to detect significant differences between behavior in the randomly chosen hour and behavior

recorded over the remainder of the observation period, and (2) significant associations between behavior in the randomly chosen hour and the other hours.

Question 3: Does behavior recorded in the first hour accurately predict behavior over the remainder of the observation period?

To address this question, we used methods that mirrored those of the between-days analysis (Question 1), except that we used the 41 pairs from the randomly chosen hour analysis, and the first hour of observation was compared to the 2 to 3 hours that followed it. As before, paired *t*-tests and least squares linear regression were used to compare behavior between the two time periods. We report statistics as means $\pm$ SE, and assumed $P \leq 0.05$ and $0.05 < P < 0.10$, respectively, to indicate significant and marginally significant results.

Results

Is parental behavior repeatable?

Nestling age on the first day of filming varied from 5 to 12 days, and averaged 8.3 (SE = 0.31 days, $n = 18$). The number of days between first and second filming averaged 2.1 (SE = 0.19 days, $n = 18$) and ranged from 1 to 4 days (1 day, $n = 4$; 2 d, $n = 10$; 3 d, $n = 3$; 4 d, $n = 1$).

Visitation rate and feeding rate were slightly, but not significantly, higher on the second observation date (Table 2-1). Likewise, differences in nest attendance, food size,

and rates of sheltering, and housekeeping, between the first and second observation days did not differ (Table 2-1). In contrast, a greater number (Table 2-1) and a higher proportion of fecal sac were ingested on the first observation date but more fecal sacs were transported on the second date. As a consequence of the opposing tendencies in fecal sac ingestion and transport, rate of total fecal sac removal did not differ between observation bouts (Table 2-1).

The latter results suggest that differences among pairs were consistent over time. In support, 8 of 9 behaviors exhibited significant positive associations between the first and second observation bout (Table 2-2), and the ninth (sheltering) was marginally significant ($r^2 = 0.161$, $P = 0.099$), and became significant ($r^2 = 0.340$, $P = 0.014$) by the omission of a single data point (Figure 2-1). However, the significance of the associations between rates of fecal sac ingestion rate and housekeeping on the first and second observation dates were in both cases dependent on one point (Fig. 2-2). Examination of regression coefficients further supported the conclusion that parental behavior was repeatable; although relationships were generally highly variable (i.e., all r^2 were < 0.5 when the single point driving the significance of fecal sac ingestion was removed), 5 of 9 regression coefficients included 1.0 within their 95% confidence interval (Table 2-2).

Does a single hour of observation accurately describe parental behavior?

Nine of the 90 paired comparisons between the randomly selected hour and the average of the remaining 2-3 hours of observations differed significantly. On the basis of

chance we would expect only 4 or 5 using $\alpha = 0.05$. However, the nine differences were not spread evenly across variables, or the 10 iterations. No differences existed for the randomly chosen hour and the remaining hours for nest attendance, fecal sac transport, or total fecal sac disposal. By contrast, food size and rate of fecal sac ingestion exhibited 2 and 3 differences, respectively. Visitation and feeding rates were highly correlated ($r = 0.974$, $P < 0.001$), and although not as strong, rates of sheltering young and housekeeping also were correlated ($r = 0.392$, $P = 0.011$). All four behaviors showed a single difference between the randomly chosen hour and the remaining 2 to 3 hours and, not surprisingly given the correlation between variables, it was from the same randomly generated data set in all cases. One of the three differences detected between the randomly chosen hour and the remaining hours for rate of fecal sac ingestion was also from this same randomly generated data set. Hence, 5 of 9 differences stem from only 1 of the 10 iterations, and among variables that were significantly correlated. Consideration of the results from only the other nine iterations (81 paired t -tests) yielded an error rate ($4/81 = 0.049$) equal to that expected using $\alpha = 0.05$. The grand mean for the randomly chosen hour and the grand mean of the remaining hours were very similar, and none of the differences were significant (Table 2-3). Taken together, these results suggest that a randomly chosen hour performed reasonably well at characterizing behavior over the longer period.

Results of the regression of average behavior for the 2 to 3 hour period against the randomly chosen hour supported this conclusion. Although average coefficients of

determination tended to be low (Table 2-4), behavior in the randomly chosen hour predicted behavior over the remainder of the observation period in 87 of 90 possible cases. Two of the nonsignificant relationships were for food size, while the third was for rate of sheltering young. Percent time in attendance, and rates of fecal sac ingestion and housekeeping showed the strongest relationships between the random hour and longer time periods, whereas food size, and rates of visitation and sheltering exhibited the weakest relationships (Table 2-4).

Does behavior recorded in the first hour accurately predict behavior over the remainder of the observation period?

Five of nine comparisons of behavior found significantly lower values in the first hour than what was found in the remaining 2 to 3 hours (Table 2-5). Nest attendance in the first hour was reduced by nearly 50%, while the rate at which parents sheltered young, and performed housekeeping was only 52% and 64%, respectively, of that detected in later hours. The rate at which nests were visited was roughly 16% lower in the first hour and, perhaps as a consequence, the rate at which fecal sacs were transported away dropped by a similar amount (20%). Differences in the rate of total fecal sac disposal only approached significance because rate of fecal sac ingestion did not differ (Table 2-5). Mean food size and feeding rate in the first and later hours did not differ, although a weak tendency existed for young to be fed less in the first hour.

Differences in behavior between the first and remaining 2 to 3 hours of observation likely had 1 of 2 causes. First, they are consistent with the hypothesis that

observer effects existed. An alternative hypothesis is that they represented temporal changes expected over the course of the morning. As a test of the time hypotheses, we used backwards elimination stepwise regression to evaluate the extent to which the five variables that differed between the first and remaining hours varied with start time, while also testing for possible effects of date of the observation bout, and age and number of young in the nest. If depressed behavior in the first hour was an effect of normal temporal changes, then start time should be retained in the final model, and regression coefficients between start time and the dependent variable should be positive. Start time was retained in 3 of 5 cases, but in all three cases the regression coefficient was negative (Table 2-6), indicating a behavioral reduction associated with start time, a result contrary to the increase that we found when comparing first hours to later hours. The declines indicated by these three coefficients are not consistent with our results and led us to reject the daily cycle hypothesis in favor of the observer effect hypothesis.

Despite the existence of differences in parental behavior between the first and remaining hours of observation (Table 2-5), the first hour successfully predicted, to varying degrees, behavior in the next 2 to 3 hours (Table 2-7). By this we mean, that although values were significantly different between observation periods, if a given nest were below average for a behavior in the first hour it would suggest that future observations would also be below average, despite the average possibly being a different value. All regression analyses yielded significant relationships, and for nest

attendance, and rates of fecal sac ingestion and housekeeping, roughly half the variation among pairs in behavior during the later hours was accounted for by behavior recorded in the first hour (Table 2-7). Mean food size exhibited the weakest relationship among time periods, while the remaining coefficients of determination indicated that the first hour was able to account for, on average, about a quarter of the among pair variation in parental behavior in later hours.

Discussion

Parental behavior is sensitive to many environmental influences and it is normal to find, even within pairs, considerable variability over the course of the nesting cycle. One can eliminate obvious sources of variation generated by nestling age, diurnal changes in behavior, or poor weather, by proper experimental design. On the other hand, the variability introduced by unknown or uncontrollable factors such as differences in food availability (Naef-Daenzer et al., 2000; Hoi-Leitner et al., 2001), long-term (Eggers et al., 2008; Zanette et al., 2011) or recent (Eggers et al., 2008; Tilgar et al., 2010) exposure of parents to predators, and for males, uncertainty of paternity (Briskie et al., 1998; Sheldon & Ellegren, 1998), introduces variability that potentially compromises our ability to unequivocally test hypotheses. The general solution is to maximize data collection in the hope that the power of large sample size swamps extraneous variation.

Maximizing statistical power while minimizing cost, whether measured in units of time or money, is always desirable, and much research in other fields has addressed this topic (Ferraro et al., 1989; Park & Kim, 2007; Guo & Luh, 2009; Guo et al., 2011). This is not the case in studies of parental behavior of birds. It is unreasonable to expect that a standard number and length of observation periods can be prescribed for all studies because the requirements of these studies will depend on the questions being asked, and on the logistics of the field work. It is, nevertheless, a question worthy of our attention, and, our attempt to delineate minimum sample periods for Eastern Kingbirds helps better define appropriate protocols for sampling avian parental behavior.

Is parental behavior repeatable?

Field studies of parental behavior sample variables over time periods that usually represent a small fraction of the total time spent caring for young. In kingbirds, for instance, a four-hour film amounts to 1.7% of the typical nestling period ($14 \text{ active hours day}^{-1} \times 17 \text{ days} = 238 \text{ hours}$). For purposes of comparing parental behavior between pairs to evaluate, for instance, the influence of loss of paternity on feeding effort (e.g. Chuang-Dobbs et al., 2001), is one such 4 hour period likely to yield useful data? The assumption is generally, yes, but if we are to rely on short sampling periods to measure behavior, it is essential to demonstrate that behavior is repeatable (see Bell et al., 2009).

Our comparisons of behaviors between time periods ranging from 1 to 4 days for 18 kingbird pairs indicated that pairs maintained comparable levels of care for 7 of 9 behaviors, the two exceptions being associated with fecal sac removal. Total rate of

fecal sac removal for any given pair did not differ between sample periods, but ingestion and transport of fecal sacs were more frequent, respectively, in the first and second filming period. Given that these are reciprocal behaviors, it actually amounts to a single difference. The declining proportion of fecal sacs that were ingested as nestlings aged is not uncommon in altricial birds (Blair & Tucker, 1941; Glück, 1988; Dell'omo et al., 1998; McKay et al., 2009). Parents regularly ingest fecal sacs, possibly to recapture nutrients or energy that would otherwise be lost presumably because of the inefficient digestive systems of the young (the parental nutrition hypothesis; Glück, 1988; McGowan, 1995; Dell'omo et al., 1998). Older nestlings are believed to more fully extract energy and nutrients and therefore fecal sacs appear to be of declining value as a dietary supplement to parents as nestlings age (McKay et al., 2009). The existence of inverse relationships between the proportion of fecal sacs ingested and nestling age in our first ($r^2 = 0.259$, $\beta = -0.092 \pm 0.039$, $P = 0.031$) and second ($r^2 = 0.230$, $\beta = -0.093 \pm 0.043$, $P = 0.044$) observation periods is consistent with predictions of the parental nutrition hypothesis, and indicate that the lower fecal sac ingestion in the second time period was age-related and to be expected. We therefore conclude that pairwise comparisons of all other behaviors confirmed the consistency of among pair differences in behaviors across time.

Nevertheless, we feel it prudent to temper our conclusions because most of the variation in parental behavior in the second period was unaccounted for by behavior in the first sampling period. Between 40% and 46% of the variation in nest attendance, and

fecal sac transport and total disposal of fecal sacs on the second date was accounted for by behavior on the first date, but this dropped to 31% for feeding rate (Table 2-2). The latter value is considerably lower than the 51.8% reported by Sheldon et al. (1997) for feeding rates on different days for 39 Collared Flycatcher (*Ficedula albicollis*) broods, the only report of similar data that we could find. As we have shown for mean food size and housekeeping (Table 2-2), single observations can have disproportionately strong effects, especially when sample sizes are small. When we omitted the feeding rate that diverged most from the value predicted based on the least squares regression of feeding rate on the two dates, the explained variation increased by 52.1% ($r^2 = 47.0\%$, $P = 0.002$; Fig. 2-2). Differences in food size possibly account for the lower r^2 in the full sample as feeding rate and mean food size were inversely related on the second date ($r^2 = 0.395$, $P < 0.005$), and together, feeding rate on the first date and food size on the second date explained nearly the same level of variation in feeding rate on the second date (45.9%, $P = 0.010$) as when we omitted the most divergent point. A similar pattern exists for time spent in nest attendance. The explained variation increased by 50.9% ($r^2 = 0.649$, $P = 0.007$) for nest attendance when a single point was omitted (Fig. 2-2). Removing points without strong justification is always questionable and our exercise is simply meant to show that single points greatly reduced what were apparently otherwise strong associations. Regardless of whether more weight is given to the full or restricted data sets, however, the conclusion remains the same; pairs exhibited consistent differences in behaviors across time.

Does a single hour of observation accurately describe parental behavior?

Field observations of parental behavior are occasionally carried out in fractions of an hour (Lifjeld & Slagsvold, 1991; Whittingham et al., 1993; Clotfelter, 1997; Peluc et al., 2008), but our review of the literature suggests that 1 to 2 hours on one (Dunn & Cockburn, 1996) or more days (Whittingham, 1989; Wright & Cotton, 1994; Freeman-Gallant, 1996; Sheldon et al., 1997; Kempenaers et al., 1998; Woodard & Murphy, 1999; Peterson et al., 2001; Neudorf et al., 2013) is more common. We suspect that 1 to 2 hours is chosen out of convenience and convention because only rarely are attempts made to evaluate whether the length of observation used by researchers yields data representative of longer time periods. Among the few examples, Wheelwright et al. (1992) used several independent (but all small) tests of male Savannah Sparrow (*Passerculus sandwichensis*) feeding rate to show that data collected in two hour blocks was similar to that recorded over longer time periods. Similarly, Johnson et al. (2005) found that feeding rates of Blue Tits (*Cyanistes caeruleus*) recorded over 1 to 2 hour periods were similar to feeding rates obtained using day-long records collected by transponders. On the basis of our comparison of behavior in a randomly chosen hour to the behavior expressed in a 2 to 3 hour long period on the same morning, we find support for the validity of using short (one-hour) observation bouts to assess behavior in Eastern Kingbirds.

However, we acknowledge that less than 50%, on average, of the among pair variation in behavior over the longer time period was accounted for by behavior in the

randomly chosen hour, indicating a lack of precision that would likely improve with a longer observation bout. Neither Wheelwright et al. (1992) nor Johnsen et al. (2005) performed regression analyses similar to ours, and this is unfortunate because comparison of mean rates calculated across a number of individuals can yield similar values even if individuals exhibit low repeatability. In our sample, average behavior on the second day was always within 92% to 101% of that expressed on the first day, but as noted above, we never accounted for more than about 50% of the variation across days. Future tests of the reliability of using a particular sampling period to characterize behavior should use regression analyses, or at minimum, within individual paired comparisons of means rather than simple comparison of population means.

On the basis of our tests and review of the literature, it appears that one hour observation periods yield adequate data to capture the natural variability in parental behavior. Researchers should evaluate whether a moderate increase to two hours would improve precision to a degree sufficient to offset probable reductions in sampling breadth across a population. To increase precision, the best tact may be to collect data in 1 to 2 hour bouts on at least two days as a compromise between intensity of sampling pairs and the entire population.

Does behavior recorded in the first hour accurately predict behavior over the remainder of the observation period?

Our final question addressed the issue of whether data collected at the start of an observation bout are representative of average behavior, or do they carry the

signature of observer disturbance. Some researchers explicitly assume that observer effects do not exist (e.g. Kempenaers et al., 1998) or acknowledge that observer effects are sometimes evident and exclude what they believe to be biased observations (Sheldon et al., 1997; Chuang-Dobbs et al., 2001). Others wait until the first feeding visit is made before collecting data (Clotfelter, 1997; Woodard & Murphy, 1999; Dickinson, 2003), while some go so far as to discard a uniform amount of time at the start of all observation bouts (Rosa & Murphy, 1994) in the belief that residual effects of human disturbance inevitably exist. Most studies, however, make no mention of how they deal with data at the start of an observation bout and presumably tacitly assume that human disturbance is minimal.

Our results suggest this is not a safe assumption for all behaviors. In Eastern Kingbirds, declines in total visits to the nest (85% of later hours) and fecal sac transport away from the nest (80% of later hours) in the first hour were moderate, but total nest attendance by the pair, and the number of times young were sheltered and housekeeping occurred was between 51% and 64% of that seen in later hours, respectively. The rate at which young were fed, the variable of likely greatest interest for most researchers, showed a small but nonsignificant reduction compared to later hours. Our evaluation of an alternative to the observer effect hypothesis eliminated time of day as a possible explanation. If less time and lower rates in the first hour were a result of time of day when the observations were made, then the behaviors in question should have shown an increase over the course of the morning. We found the opposite,

which suggests that parents responded negatively to the disturbance created when the video camera was placed in the territory just prior to filming.

However, despite the disturbance, we found that observations in the first hour were still able to predict, with essentially the same ability as the randomly chosen hour (compare r^2 values in Tables 4 and 7), behavior during the remainder of the observation period. This suggests that, although kingbird parental behavior was to some extent disrupted by the observer's visit, most birds responded in a similar way. As a result, reductions in time spent at the nest or several other behaviors was substantially lower in the immediate hour following video camera set up, but the decline occurred in an equivalent manner in most birds.

Summary

The approaches used to collect data in studies of avian parental behavior vary greatly and only rarely have attempts been made to assess minimum necessary time periods over which reliable data can be collected. Our comparisons of parental care behavior by Eastern Kingbirds using 1 to 4 hours of observations recorded on each of two days suggests that parental care was repeatable. Moreover, one hour of observation appeared to provide a reasonable estimate of among pair variation in behavior. Researcher effects clearly existed in the first hour of data collection, but did not egregiously bias the data to the point that they could not be used to represent among pair variation in behavior. Although our data suggest that a one hour sample of parental behavior collected on a single day could be justified statistically, we

nonetheless recommend that caution guide decisions regarding minimum sample periods and that, if possible, data be collected over at least two hours and two days to minimize sampling error and improve precision.

Tables

Table 2-1. A comparison by paired *t*-test of parental behaviors between observation periods separated by, on average, two days, for Eastern Kingbirds breeding at Malheur National Wildlife Refuge, OR. Behaviors that differed significantly between days are shown in bold.

Behavior	N	Day 1 $\bar{x}$ (SE)	Day 2 $\bar{x}$ (SE)	<i>t</i> (<i>P</i>)
Nest attendance time	18	24.88 (3.49)	20.98 (3.16)	1.408 (0.177)
Visit rate	18	11.63 (0.84)	12.92 (0.90)	-1.513 (0.149)
Feeding rate	18	10.50 (0.91)	11.91 (0.99)	-1.569 (0.135)
Food size	17	1.98 (0.17)	1.96 (0.14)	0.221 (0.828)
FS^a ingestion rate	18	1.07 (0.29)	0.64 (0.26)	2.618 (0.018)
FS^a transport rate	18	1.77 (0.21)	2.41 (0.30)	-2.773 (0.013)
FS ^a disposal rate	18	2.84 (0.31)	3.04 (0.33)	-0.761 (0.457)
Rate of sheltering young	18	2.12 (0.39)	2.14 (0.42)	-0.025 (0.981)
Rate of housekeeping	18	1.40 (0.31)	1.75 (0.42)	-1.151 (0.266)

^a FS = fecal sac

Table 2-2. Regression statistics describing the relationship between behaviors measured on the first (independent variable) and second (dependent variable) observation dates, for Eastern Kingbirds breeding at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Additional statistics include the 95% confidence interval for the coefficient, and the coefficient of determination.

Variable	Regression equation	95% CI of β	r^2 (P)
Nest attendance time	$Y = 6.204 + 0.594(X)$	0.232 to 0.956	0.430 (0.003)
Visit rate	$Y = 6.460 + 0.556(X)$	0.070 to 1.041	0.269 (0.027)
Feeding rate	$Y = 5.580 + 0.603(X)$	0.123 to 1.083	0.307 (0.017)
Food size	$Y = 0.467 + 0.755(X)$	0.514 to 0.996	0.748 (<0.001)
FS ^a ingestion rate ^b	$Y = -0.147 + 0.729(X)$	0.457 to 1.001	0.669 (<0.001)
FS transport rate ^a	$Y = 0.787 + 0.917(X)$	0.330 to 1.504	0.407 (0.004)
FS disposal rate ^a	$Y = 1.089 + 0.688(X)$	0.265 to 1.110	0.427 (0.003)
Rate of sheltering young ^c	$Y = 1.218 + 0.432(X)$	-0.091 to 0.955	0.161 (0.099)
Rate of housekeeping ^b	$Y = 0.491 + 0.902(X)$	0.385 to 1.418	0.461 (0.002)

^a FS = fecal sac

^b Significance due to one point (with point removed FS ingestion: $r^2 = 0.009$ and $P = 0.722$; Housekeeping: $r^2 = 0.151$ and $P = 0.124$)

^c Lack of significance due to one point (with point removed $r^2 = 0.340$ and $P = 0.014$)

Table 2-3. Comparisons of the mean of the random hour of behavior to the grand mean of each behavior obtained through 10 iterations of randomly choosing one of the 3 or 4 hours to compare to the remaining 2 to 3 hours of observations for 41 pairs of Eastern Kingbirds observed at Malheur National Wildlife Refuge, OR, from 2003 through 2010.

Behavior	Random hour $\bar{x}$ (SE)	Remaining hours $\bar{x}$ (SE)	t (P)
Nest attendance time	38.83 (4.74)	37.39 (3.79)	0.716 (0.566)
Visit rate	13.39 (0.85)	12.29 (0.63)	1.186 (0.348)
Feeding rate	12.20 (0.87)	11.92 (0.66)	0.996 (0.399)
Food size	1.82 (0.08)	1.83 (0.06)	1.149 (0.376)
FS ^a ingestion rate	0.84 (0.18)	0.78 (0.16)	1.125 (0.369)
FS ^a transport rate	2.13 (0.22)	2.11 (0.17)	0.414 (0.681)
FS ^a disposal rate	2.97 (0.27)	2.92 (0.21)	1.030 (0.374)
Rate of sheltering young	2.30 (0.37)	2.20 (0.54)	0.947 (0.463)
Rate of housekeeping	1.54 (0.29)	1.56 (0.27)	0.704 (0.582)

^a FS = fecal sac

Table 2-4. Average statistics from the 10 least squares linear regression in which a single randomly chosen hour was used to predict Eastern Kingbird parental behavior for a 2 or 3 hour observation period. Average statistics reported for the regression coefficient (β), and Y-intercept (Intercept), and coefficient of determination (r^2).

Behavior	β (SE)	Intercept (SE)	r^2 (SE)
Nest attendance time	0.541 (0.012)	16.40 (0.88)	0.457 (0.019)
Visit rate	0.326 (0.013)	8.58 (0.29)	0.196 (0.018)
Feeding rate	0.379 (0.009)	7.29 (0.21)	0.252 (0.013)
Food size	0.273 (0.025)	1.34 (0.04)	0.149 (0.022)
FS ^a ingestion rate	0.623 (0.036)	0.26 (0.03)	0.488 (0.019)
FS ^a transport rate	0.358 (0.021)	1.38 (0.04)	0.236 (0.028)
FS ^a disposal rate	0.412 (0.018)	1.70 (0.07)	0.292 (0.035)
Rate of sheltering young	0.340 (0.032)	1.44 (0.06)	0.206 (0.031)
Rate of housekeeping	0.615 (0.020)	0.62 (0.04)	0.455 (0.027)

^a FS = fecal sac

Table 2-5. Comparison of parental behaviors recorded in the first hour of observations to that recorded in the subsequent 2 or 3 hours for 41 pairs of Eastern Kingbirds that bred at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Tests whose results showed significant *P* values are shown in bold.

Behavior	First hour $\bar{x}$ (SE)	Remaining hours $\bar{x}$ of others (SE)	<i>t</i> (<i>P</i>)
Nest attendance time	23.17 (3.47)	43.41 (4.10)	6.657 (0.000)
Visit rate	11.44 (0.98)	13.56 (0.59)	2.381 (0.022)
Feeding rate	10.98 (0.99)	12.33 (0.62)	1.570 (0.124)
Food size	1.87 (0.10)	1.79 (0.06)	0.843 (0.404)
FS ^a ingestion rate	0.76 (0.21)	0.81 (0.15)	0.378 (0.708)
FS^a transport rate	1.80 (0.21)	2.26 (0.17)	2.234 (0.031)
FS ^a disposal rate	2.56 (0.30)	3.07 (0.20)	1.985 (0.054)
Rate of sheltering young	1.34 (0.27)	2.59 (0.33)	3.983 (0.000)
Rate of housekeeping	1.10 (0.28)	1.71 (0.28)	2.960 (0.005)

^a FS = fecal sac

Table 2-6. Results of the backwards elimination stepwise regression of five behaviors that differed between the first hour of observation and the remaining 2 to 3 hours for 41 pairs of Eastern Kingbirds that bred at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Behavior in the first hour was examined in relation to start time (S), number of nestlings (N), age (A), and date (D).

Behavior	Variables retained	Model R^2 (P)	Coefficient of start time (SE)
Nest attendance time	A	0.005 (0.663)	n/a
Visit rate	S, D	0.132 (0.068)	-3.300 (1.692)
FS ^a transport rate	N, D	0.260 (0.003)	n/a
Rate of sheltering young	S	0.122 (0.025)	-0.968 (0.415)
Rate of housekeeping	S	0.264 (0.001)	-1.505 (0.403)

^a FS = fecal sac

Table 2-7. Results of the regression analysis describing the ability of parental behaviors recorded during the first hour of an observation to predict parental behavior in the remaining 2 to 3 hours for 41 pairs of Eastern Kingbirds that bred at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Regression coefficients (β), Y-intercept (Intercept), and coefficient of determination (r^2) are reported.

Behavior	β (SE)	Intercept (SE)	r^2 (P)
Nest attendance time	0.815 (0.137)	24.52 (4.377)	0.475 (0.000)
Visit rate	0.270 (0.087)	10.48 (1.130)	0.198 (0.004)
Feeding rate	0.317 (0.086)	8.86 (1.090)	0.257 (0.001)
Food size	0.231 (0.075)	1.38 (0.149)	0.204 (0.004)
FS ^a ingestion rate	0.519 (0.083)	0.42 (0.126)	0.501 (0.000)
FS ^a transport rate	0.367 (0.115)	1.60 (0.258)	0.208 (0.003)
FS ^a disposal rate	0.356 (0.090)	2.16 (0.288)	0.285 (0.000)
Rate of sheltering young	0.569 (0.174)	1.82 (0.375)	0.216 (0.002)
Rate of housekeeping	0.700 (0.108)	0.95 (0.226)	0.521 (0.000)

^a FS = fecal sac

Figures

Figure 2-1. Relationship between the rate of sheltering for first and second observation bouts of Eastern Kingbird that bred at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Regression line calculated on the basis of the solid points. Correlation was only significant with the open point excluded.

Figure 2-2. Hourly rate of fecal sac ingestion (A) and housekeeping (B) on observation day 1 versus day 2 for Eastern Kingbirds breeding at Malheur National Wildlife Refuge, OR, between 2003 and 2010. With the most isolated datapoint in each analysis removed, the relationships were no longer significant.

Figure 2-3. Relationship between (A) feeding rate, and (B) total time spent at the nest ("nest attendance") for first and second observation bouts of Eastern Kingbird that bred at Malheur National Wildlife Refuge, OR, between 2003 and 2010. Regression line calculated on the basis of the solid points. Correlations were still significant with open points included.

Chapter 3: Does realized paternity affect male parental investment in eastern Kingbirds?

Abstract

We tested the hypothesis that male eastern kingbirds reduce their level of parental investment with increasing levels of lost paternity. We did this by means of comparing male feeding rate to realized paternity within his nest, as well as by comparing the results of an Akaike's Information Criterion (AIC) analysis of multiple male parental behaviors to realized paternity. We found no evidence in either analysis that kingbirds adjust paternal investment and suspect that males are unable to assess realized paternity within their nest. We did, however, find inverse relationships between paternal effort and both male attractiveness (as measured by length of flight feathers) and territory density. Further research is needed to assess the basis for these relationships. We also found that males within our study delivered as much food as females, a result at odds with previous research and suggest the difference is owing possibly to observer effect in previous studies.

Keywords: paternal investment, realized paternity, parental behavior, extrapair paternity

Introduction

Life history theory (Stearns, 1976) is built on the premise that trade-offs exist among reproductive traits. Among these, parental care has been shown to negatively affect parental condition (Maigret & Murphy, 1997; Golet et al., 1998), survival (Golet et al., 1998; Murphy, 2000; Descamps et al., 2009), and future fecundity (Gustafsson & Sutherland, 1988; Murphy, 2000; for review see Alonso-Alvarez & Velando, 2012; Balshine, 2012). As such, parental investment is viewed as a costly behavior for which a substantial benefit must exist, that being the ability to pass parental genes on to offspring (Balshine, 2012). Parental investment through extended care of young is a requisite for altricial bird species that must, with the exception of brood parasites, devote much time and energy to the care, feeding and defense of helpless young. The extensive care required to bring young to independence is doubtless a major factor explaining why ~80% of bird species exhibit biparental care (Cockburn, 2006).

While biparental care and social monogamy are the norm for birds (Lack, 1968; Silver et al., 1985; Cockburn, 2006), genetic analyses have in recent decades shown that sexual relations often occur among individuals outside the pair bond and that extra-pair paternity (EPP) is a common phenomenon (Westneat & Sherman, 1997; Griffith et al., 2002). This creates two dilemmas for males of species in which EPP occurs frequently. First, parental investment typically comes at the expense of reproductive investment (Chandler et al., 1994; Raouf et al., 1997) and therefore males must often “choose” to invest in current offspring with their social mate or seek mating opportunities with

extra-pair (EP) females (Magrath & Komdeur, 2003). Second, and independently of his response to the first dilemma, males must again “decide” at what level to invest in his social mate’s current brood. Depreciable forms of parental care (i.e., that which cannot be shared; Westneat & Sherman, 1993) such as food deliveries should not be provided indiscriminately when unrelated young may reside in the nest and parental care is costly (see above). Investment in young that a male did not sire is maladaptive, especially if it may compromise his survival and future fecundity, and interspecific comparative data suggest that paternal care varies inversely with frequency of EPP (Møller & Birkhead, 1993; Møller & Cuervo, 2000).

It follows, all else being equal, that male energetic investment into parental care should be contingent upon the proportion of young that he sired (Trivers, 1972). However, all else is rarely equal and this possibly explains why only a minority of studies have supported this prediction (Chuang-Dobbs et al., 2001; Suter et al., 2009; Perlut et al., 2012). Paternity and paternal care are unrelated in most studies (Rytönen et al., 2007; LaBarbera et al., 2012; reviewed by Whittingham & Dunn, 2001), and the simplest explanation may be that males simply cannot assess their share of paternity. If this is the case, then the best option for males of short-lived species may be to deliver care in the expectation that he has sired at least a portion of a brood (Whittingham et al., 1992; Mauck et al., 1999). In addition, paternal care may persist when loss of paternity is high if female preference for parental males, demonstrated by caring for young regardless of

paternity, improves a male's prospects of siring young with his social mate in the future (Freeman-Gallant, 1996; Freeman-Gallant, 1997; Rowe & Weatherhead, 2007).

Other factors also shape paternal care. Sexual conflict over parental care is often substantial (Westneat & Stewart, 2003; Lessells, 2006), and a male's contribution to the feeding of young may be contingent on his other options (Magrath & Komdeur, 2003; Westneat & Stewart, 2003), which may depend on his "quality" or "attractiveness" compared to other males in the population (Burley, 1986; Burley et al., 1996). For instance, low quality males may opt for high paternal investment in the face of potential loss of paternity if prospects of success outside their current pair bond are negligible (Kokko, 1998). Similarly, females may accept a reduced feeding effort from high quality males if that male provides good genes or a high quality territory from which to forage (Burley et al., 1996; Johnsen et al., 2005; Mitchell et al., 2007). And regardless of either sex's quality, a dearth of fertile females may be the determinant of paternal effort; without available females there is no conflict between mating and parental effort (Magrath & Komdeur, 2003).

Eastern kingbirds (*Tyrannus tyrannus*; hereafter kingbirds) are tyrant flycatchers that breed across much of temperate North America and overwinter in South America (Jahn et al., 2013). They are socially monogamous, biparental, and pair bonds often persist for multiple years (Murphy, 1996; Woodard & Murphy, 1999). Despite the high fidelity to social mates, kingbirds exhibit one of the highest frequencies of EPP known among socially monogamous passerines as 60% of broods have EP young (Rowe et al.,

2001; Dolan et al., 2007; MTM unpubl. data). As a consequence, a significant opportunity for sexual selection exists through EP mating behavior (Dolan et al., 2007). Although biparental, Woodard and Murphy (1999) showed that females in a New York population provided a greater share of the feeding effort. Parental care is costly in kingbirds (Maigret & Murphy, 1997; Murphy, 2000), and Woodard and Murphy (1999) suggested that the disparity in male and female feeding effort was an evolved response to consistently high losses of paternity. An unanswered question is whether loss of paternity would produce variable levels of paternal care among males within a population.

In the present paper I test whether paternal care in kingbirds is contingent on paternity. Loss of paternity in kingbirds is not spread evenly among males, and a consistently high proportion of kingbird males either lose (0.20 to 0.33) or secure all paternity (~ 0.25) every year (Dolan et al., 2007). I thus predicted that variation in paternity should produce substantial differences in paternal care. This presupposes that males can detect their share of paternity in a brood, which is perhaps questionable (Kempnaers & Sheldon, 1996), and therefore males may resort to surrogate information to assess the probability of loss of paternity. Because high breeding density equates too many potential EP suitors and high potential for loss of paternity (Westneat & Sherman, 1997; Møller & Ninni, 1999), I also predicted that males might provide less care when breeding in high density environments. Paternal care is potentially shaped by a male's quality in relation to other males, or in response to the availability of fertile EP

females, and therefore I further predicted that paternal care would decline with increasing male quality (defined below) and increased availability of fertile females in the population.

Methods

Study site and field methods

My study was conducted on a kingbird population nesting in willow trees (*Salix* spp.) in the riparian zone of the Donner und Blitzen River at Malheur National Wildlife Refuge (MNWR; 43°N, 119°W). Most of the surrounding area is high desert (1,400 m asl) sparsely vegetated with big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Ericameria* spp.), with juniper (*Juniperus occidentalis*) found along mountain slopes. Kingbirds rarely nest away from riparian habitat, where they are found at high densities. Kingbird studies at MNWR began in 2002 and continued through 2011. Study seasons ran from mid-May through to the end of July or early August. Since 2002 kingbirds have been marked with unique combinations of one federal and three plastic colored leg bands. Data on parental behaviour were collected in five years in the period between 2003 and 2010.

I provide only a brief overview of field methods given that fuller descriptions exist (Dolan et al., 2007; Cooper et al., 2009). Daily surveys of nesting habitat yielded essentially complete censuses of the kingbird population in our study areas. Nests are built in trees, are generally conspicuous, and their locations were mapped and/or

marked with a Garmin GPS 76 from 2003 onward at an accuracy of $\pm 3-4$ m. About 80% of nests were found prior to egg-laying and over 90% were found before midway through incubation. Laying dates of nests found after clutch completion were backdated from hatching dates or by comparisons of the size of young to offspring of known age (Murphy, 1981). All nests were checked once every 2 to 3 days to document laying date, clutch size, hatching date, hatching success (number of eggs to hatch), and ultimately nest failure or success. Although single-brooded, kingbirds usually renest after failures; pairs were therefore followed after nest failures to determine whether renesting occurred to quantify seasonal reproductive success.

Males were captured for blood sampling and banding most often in the predawn period using mist nets and playback of “dawn songs” (Sexton et al., 2007; Murphy et al., 2008). Both sexes were captured later in the day by placing mist nets near their nests. Blood was sampled using a 22-gauge sterile, disposable needle to puncture a brachial vein, and heparinized capillary tubes were used to draw ~ 50 μL of blood from adults and 5-6 day old nestlings. Blood samples were transferred to Eppendorf tubes containing 1.5 mL of Longmire’s buffer (Longmire et al., 1988), and refrigerated until processing. Bled nestlings were returned to the nest, and banded and bled adults were released within their territory after standard measurements were taken, including body mass (± 0.1 g; 50-100 g Pesola scale), unflattened wing chord (± 0.5 mm; wing ruler), and bill (± 0.05 mm; dial callipers), tarsus (± 0.05 mm; dial callipers), and tail lengths (± 0.5 mm; wing ruler).

Behavioral observations

Parental behavior was recorded at nests using Sony SteadyShot CCD-TRV608 video cameras mounted on tripods and placed within 10 m of the nest. Cameras were placed on-site just before recording commenced, and recordings were made on 4-hour Hi8 video cassettes. Camera focus was adjusted to capture an area of ~30 cm radius around the nest. Recordings ranged from 1 to 4 hours, began any time between 0600 PST and 1000 PST, and were made with the timestamp in the bottom right corner to aid later analysis.

Video cassettes were digitized using a StarTech USB 2.0 video capture cable along with the GrabBee software provided by the manufacturer. This step enabled us to save all visits to digital media for more convenient and efficient processing and reference. To save hard-drive space and processing time, only periods when an adult was at the nest were transferred to digital media; all intervening periods of inactivity were ignored. Each nest visit was then reviewed to gather behavioral data. The timestamps of arrival and departure for each visit were recorded. I also recorded whether the adult (1) fed young, (2) ingested fecal sacs, (3) transported fecal sacs away from the nest, (4) positioned its body over the young to warm or shade them ("shelter"), (5) exhibited behaviors indicative of nest maintenance ("housekeeping"), and (6) "harassed" the other adult in an apparent attempt to drive them from the nest to induce foraging. The latter was recorded any time one adult acted in a seemingly agonistic manner towards its mate when both were at the nest, in what appeared to be

an attempt to force it to leave and forage. This was almost always accompanied by a vocal outburst from both birds.

The timestamps of arrival and departure were used to calculate the duration of each visit, and the sum of these visit durations were compared to the total recording length to determine percentage of time the nest was attended (“attendance”). Each visit was treated separately, so that any time both adults were simultaneously present I effectively had 200% attendance (this was usually a rare and fleeting event and no nest approached 100% attendance). I assumed that a nestling was fed any time a newly arrived adult dipped its bill into the mouth of a begging nestling. Feeding and nonfeeding visits, and fecal sacs ingestions and fecal sacs transports away from the nest (i.e., fecal sac in bird’s bill as it flew from the nest) were combined into total visits and total fecal sac disposals, respectively. All behavioral variables were calculated as hourly rates except for nest attendance (%).

Determination of parental sex

Kingbirds are sexually monochromatic, and although size and morphology differ (Murphy, 2007), differences are difficult to detect with the naked eye. Regardless, I could unambiguously determine sex of the parent at the vast majority of visits to the nest because at least one member of a pair was color banded in all cases. Leg bands were not always visible and in these cases I used a combination of more subtle visual and behavioral cues to sex the adults. These included known differences in call, posture (the male’s being more vertical), approach angle (individuals reliably approached and

left the nest from the same direction; see Lessells et al., 2006), idiosyncrasies such as missing feathers and injuries, and strongly sex biased behaviors such as female sheltering (Woodard & Murphy, 1999). It was also often possible to reliably sex adults on the basis of sequence of visits. For instance, when the visit of an adult that I could not sex overlapped with a visit from its known-sex mate, which occurred often when adults fed at high rates, I could confidently assign sex. For every visit, confidence in the identification of adult sex was assigned a value between 0 and 100%, and only nests with high average confidence (>75%) were used.

Assignment of paternity

Detailed methods for the determination of nestling parentage are described in detail elsewhere (Dolan et al. 2007). Briefly, I compared nestling and adult genotypes at seven microsatellite loci that amplified a total of 80 alleles. I confirmed maternity assignment by direct comparison of mother and offspring genotypes. All loci were in Hardy–Weinberg equilibrium, and every nestling genotype matched the putative mother at every locus, indicating that mutation events and nonamplifying alleles were rare or absent. I determined paternity using Cervus 2.0 (Marshall et al., 1998) by direct exclusionary analysis using the nestling’s non-maternal genotype. The total exclusionary power of the primers was 0.998 (Dolan et al., 2007); social mates were therefore deemed to be genetic fathers if they shared all seven non-maternal alleles with the offspring.

Statistical analysis

I used the 49 nests that I was left with after eliminating nests with low confidence of sex assignment to adults to characterize general male and female behavior. To evaluate paternal behavior in relation to paternity, my sample was reduced to 45 nests because paternity was not determined at four nests. Several males and females were recorded more than once (never in the same year), but in only one case were they of the same pair in different years.

Male quality, nesting density, and number of fertile females

I used morphometric data (body mass, wing chord, and lengths of the tarsus, tail and bill) to assess male quality. My assumption was that high quality individuals were of large overall size, and because relative flight feather length and timing of male song in a previous study were inversely correlated (i.e., long-tailed males were the earliest singers; (Murphy et al., 2008), and reproductive success was highest among early singers (Dolan et al., 2007), I assumed that high quality individuals had relatively long flight feathers. Morphometric data for all males captured in the population between 2002 and 2011 ($n = 189$) were subjected to a principal component analysis (PCA) similar to that described by Murphy et al. (2008). Data in the latter report included a subset of the current data, and the complete analysis used here (MTM unpubl. data) closely mirrored the earlier results. All variables loaded positively on principal component (PC) 1 (eigenvalue = 1.703, 34.1% of variance; see Table 3-1) and indicated that PC1 represented a measure of “body size”. Tail length and wing chord loaded positively on

PC2 while tarsus length loaded negatively (Table 3-1). Hence, as in Murphy et al. (2008), PC2 is interpreted as representing an index of relative flight feather length (especially tail length); high scores described birds that had long flight feathers for their overall size (reflected by tarsus length; Rising & Somers, 1989).

To assess breeding density, I measured distances from each nest for which observations were made to the two nearest kingbird neighbors. Nearest neighbor distances (NND) were measured between UTM's for each nest. The inverse of the average of the two NNDs yielded a quotient with high values represented low NND. The $\log_{10}$ transformed value of the inverse of average NND was distributed normally, and I refer to this value ($\log_{10}[\text{NDD}^{-1}]$) as "nesting density."

Although kingbirds are highly seasonal breeders, fertile females were available throughout the breeding season because of frequent nest failure (>60% in all years) and consequent renesting. Renesting typically requires ≥ 1 week, and I assumed for all females that the fertile period ran from four days before the laying of the first egg until the laying of the penultimate egg. EP mates in kingbirds are often not neighbors and are regularly separated by several and even up to 15 km (Dolan et al., 2007). I thus tallied the number of fertile females from the entire population on the day of filming.

Analysis of behavior

I used the 49 nests to describe male and female parental roles (paired *t*-tests). I also conducted separate PCAs of male and female parental behavior to characterize major gradients of behavior to further explore possible differences between the sexes.

For both sexes, I eliminated total visit rate and total fecal sac disposal rate because they were highly correlated with feeding rate (males: $r = 0.993$, $P < 0.001$; females: $r = 0.901$, $P < 0.001$) and fecal sac transport rate (males: $r = 0.797$, $P < 0.001$; females: $r = 0.694$, $P < 0.001$), respectively. For males, I also excluded sheltering rate because they essentially never exhibited this behavior.

Male feeding rate and PC1 of paternal behavior (see below) were used as my two measures of paternal effort. Among-male variation in both feeding rate and PC1 were examined for the subset of males with parentage data ($n = 45$) using best subsets regression to test the a priori hypotheses that paternal effort would decline as (1) a male's share of paternity in the nest declined, (2) breeding density increased, (3) number of fertile females at the time of the recording increased, and (4) male quality increased (i.e., as body size [PC1] and/or relative flight feather length [PC2] increased). Differences in feeding effort among males might also be a consequence of the number and age of young in the nest at the time of filming and therefore I included both brood size and average nestling age as predictor variables. I also felt it prudent to include time of day and day within the season to account for possible diurnal or seasonal changes in behavior. Finally, I included a female behavior, sheltering rate, in the analysis of paternal effort because females stop feeding young when they shelter them, and if feeding rate is to be maintained, males must increase their effort.

The best subsets regression analysis was conducted in an information theoretic framework. I used adjusted Akaike's Information Criterion for small sample size (AICc) to

evaluate model fit, with the assumption that all models within two AICc units of the top model ($\Delta\text{AICc} = 0$) were candidate models of potential explanatory value. Following Burnham and Anderson (2002), I calculated model weights (w_i) and evaluated the importance of parameters by calculating relative importance and by examining whether parameter estimates differed from zero (i.e., 85% confidence interval did not include zero; Arnold, 2010). Lower ranking models that were within two AIC units of the top model, but differed from a higher ranking model by the addition of one additional parameter were rejected as uninformative models (Burnham & Anderson, 2002; Arnold, 2010). To assist in model evaluation, I also report the adjusted coefficient of determination (R^2) for all models. All variables were standardized prior to analysis by subtracting the mean from each observation and then dividing by the standard deviation so that parameter estimates could be compared directly.

Observation bouts were generally 3 to 4 hours in length (67% of filmed events), but a few were less than two hours (7%). Prior analyses supported the use of a one hour observation bouts to characterize a pair's behavior, but my data also suggested that two or more hours would likely yield more accurate measurements. To account for the potential weakness of short observations periods I weighted analyses by observation length by distinguishing between short (< 2 hour; 7% of bouts) and long (2-4 hour; 93% of bouts) observation bouts (scored as 1 and 2, respectively).

Results

Sexual differences in parental behavior

Division of labor was apparent in that 6 of 9 behaviors differed between the sexes (Table 3-2). Females (1) made more total flights to the nest, (2) spent more time at the nest, (3) sheltered the young more, (4) tended to the nest more (i.e., housekeeping), and (5) ingested more fecal sacs than males. Males harassed their mate more, in what appeared to be attempts to induce her to leave the immediate nest environment. By contrast, I did not detect sexual differences in rates of (1) food delivery, (2) transport of fecal sacs away from the nest, or (3) total fecal sac disposals. Eigenvalues for the first three factors from the PCA of parental behavior (eigenvectors all ≥ 1.0) accounted for ~75% of total variance in parental behavior of both sexes (Table 3-3). Factor loadings for males indicated that PC1 was primarily related to feeding effort because of the high loadings for male feeding rate and male harassment of females (presumably an attempt to compel her to leave the nest area and forage). Males that fed nestlings at high rates also transported many fecal sacs from the nest and spent more time at the nest. Males with high scores on PC2 spent more time at the nest, ingested fecal sacs while there, and as a consequence, transported few fecal sacs away from the nest. PC3 described the rare instances in which males tended to the nest. Unlike males, the major gradient of variation in female behavior was associated with behaviors related to nest attendance. Females with high scores on PC1 spent more time at the nest sheltering young and maintaining the nest (Table 3-3). Female PC2, like male

PC1, described feeding effort. Female PC3 was interpreted similarly to male PC2 because it described differences in the disposal of fecal sacs as either ingested or transported (Table 3-3).

Paternity

EP young were present in 26 of 45 nests (57.8%) in our sample, and 54 of 132 young (40.9%) were sired by EP males. Paternity did not differ among years (Kruskal-Wallis test; $H = 1.04$, $P = 0.400$). By contrast, after accounting for a tendency for paternity within a nest to decline seasonally ($\beta = -0.263$, $P = 0.115$), the proportion of young sired by a male in his nest decreased with increasing nest density ($\beta = -0.318$, $P = 0.045$; 2-variable model $R^2 = 0.115$). As described previously (Rowe et al. 2001, Dolan et al. 2007), a substantial proportion of males lost all paternity in their nest (20%; 9 of 45), while all paternity was secured by roughly twice as many males (42.2%; 19 of 45).

Variation in paternal effort

After eliminating uninformative models (Arnold, 2010), my analyses of male feeding rate yielded three competitive models (Table 3-4). Brood size and female sheltering rate appeared in all three, while PC2 of male morphology (i.e., relative flight feather length) and nesting density each appeared in two. Uninformative models included, in addition to some of the factors just mentioned, start time of observation bout, number of fertile females, and paternity. Model averaged parameter estimates for the latter three factors were not different from zero (data not shown), confirming the

designation of the models in which they appeared as uninformative. Model averaged parameter estimates for the four variables in the top three models all excluded zero from the confidence interval (Table 3-5), indicating that male feeding rate increased with brood size and female sheltering rate, but that young were also fed less by males with relatively long flight feathers (Table 3-5; Fig. 3-1) and when males bred in a high nest density environment (Table 3-5). Between 30% and 35% of the variation in male feeding rate was accounted for by the various combinations of the four variables (Table 3-4). Direct comparison of the proportion of food deliveries by males that sired none, some, or all of the young in their nest (i.e., paternity class) showed that a male's feeding effort was independent of paternity (analysis of variance: $F = 0.21$, $df = 2, 42$, $P = 0.813$). Brood size was independent of paternity class ($F = 0.24$, $df = 2, 42$, $P = 0.786$), and direct comparison of both standard mean and least squares mean feeding rates (i.e., effects of variables in Table 3-5 removed) indicated that male feeding rate was independent of paternity class (Fig. 3-2).

Analysis of paternal effort, as measured by PC1 of the PCA of male behavior, yielded two models with virtually identical AICc values. Strictly speaking, the combination of brood size, female sheltering rate, relative flight feather length, and number of fertile females had the lowest AICc (61.86), but number of fertile females added nothing to the model because without it the AICc was virtually identical to the resulting three-variable model of brood size, female sheltering rate, and relative flight feather length (61.87). Moreover, the combination of brood size, female sheltering rate

and number of fertile females was not competitive ($\Delta AICc = 2.88$). Thus, paternal effort (as expressed by PC1) exhibited a significant decline with increasing relative flight feather length ($\beta = -0.518 \pm 0.202$ SE; Fig. 3-3), but did not vary with number of fertile females ($\beta = 0.381 \pm 0.204$ SE).

Discussion

Sexual differences in parental behavior

Sexual division of parental behavior in birds is common (Zaias & Breitwisch, 1989; Emlen & Wrege, 2004), especially as the needs of young change over the course of the nestling period (Rytkönen et al., 1996). Despite parental division of labor, feeding rates of the sexes in socially monogamous passerine birds are, on average, equivalent (reviewed by Woodard & Murphy, 1999), and even male biased in some species (e.g. Gow & Stutchbury, 2013). Variability in the relative contribution of males among species is nonetheless high (Woodard & Murphy, 1999), and comparative analyses suggest that some of the interspecific differences may relate to differences in the incidence of EPP (Møller & Birkhead, 1993; Møller & Cuervo, 2000).

Eastern Kingbirds exhibited considerable sexual division of parental behavior, but feeding rates of males and females did not differ. Variance in male feeding rate exceeded that of females (F -test, $P = 0.01$), which is consistent with the finding that feeding rate was the main contributor to the primary axis (PC1) from the PCA describing variation in male parental behavior. Variation in maternal behavior was expressed

mainly as time spent tending the nest and sheltering young (PC1), with feeding rate emerging as secondary variation (PC2; Table 3-3). Compared to males, females thus provided a more consistent supply of food to the young.

My findings on relative feeding rate of the sexes differs from that of Woodard and Murphy (1999) who found that females fed young at higher rates. In both populations, the incidence of EPP (proportion of broods with EP young) is ~60% (Rowe et al., 2001; Dolan et al., 2007; MTM unpubl. data). A regular and substantial loss of paternity of this magnitude is predicted to lead to reduced male parental effort (Trivers, 1972; Westneat & Sherman, 1993), and Woodard and Murphy (1999) argued that frequent loss of paternity and documented survival costs associated with parental care (Murphy, 2000) favored lower average male feeding effort. The equal nestling feeding rates of the sexes at MNWR was thus unexpected, and may reflect either real biological differences between populations, or methodological differences in data collection. I recorded behavior using video cameras over (usually) a 3-4 hr period, whereas Woodard and Murphy (1999) recorded behavior in 1 hr periods using human observers who may have heightened male vigilance and led to lower male feeding effort given that males are the main providers of nest vigilance and defense (Woodard & Murphy, 1999; Redmond et al., 2009). However, the fact that feeding rate in the first hour of a 3-4 hr observation period in the Malheur population did not differ from that recorded in the remaining hours (Chapter 2) weakens the argument that difference in male feeding rate between New York and Kansas reflects methodological differences (Chapter 2). It is

possible that other factors, such as larger clutch (and brood) size in western populations of Eastern Kingbirds (MTM unpubl. data), may have increased needs for male participation in feeding broods. Distinguishing between the two possibilities will require collection of additional data to compare human-observed and filmed behavior in a within-pair paired comparisons framework.

Variation in paternal effort

Woodard and Murphy (1999) invoked nonfacultative adjustments (i.e., evolutionary; Westneat & Sherman, 1993; Kokko, 1999) in male effort in response to consistent and predictable losses of paternity to explain lower feeding effort by male than female kingbirds in New York. Comparative studies suggest this to be the general case among passerines (Møller & Birkhead, 1993; Møller & Cuervo, 2000). Whether individual males possess the ability to respond facultatively to losses of paternity (i.e. in the timeframe of a nesting attempt) to reduce feeding effort when certainty of paternity is low is questionable. Some experimental studies that increased uncertainty of paternity in other passerines produced reductions in male feeding effort (Hatchwell & Davies, 1992; Sheldon & Ellegren, 1998; but see Whittingham et al., 1993; Kempenaers et al., 1998). Similar findings exist for some observational studies (Chuang-Dobbs et al., 2001; Suter et al., 2009; Perlut et al., 2012), but males in most observational studies provide care independently of paternity (Rytkönen et al., 2007; LaBarbera et al., 2012; reviewed by Whittingham & Dunn, 2001). The latter is the expected outcome when clear signals of paternity are missing (Whittingham et al., 1992; Kokko, 1999), especially

when individuals tend to be short-lived and loss of paternity in the future is as likely as the present (Whittingham et al., 1992; Mauck et al., 1999).

The equal feeding rate of males and female kingbirds at MNWR cast doubt on but do not preclude the possibility that males differentially distributed care dependent on paternity, especially given the high variance in male feeding effort, the high contribution of feeding rate to the primary axis of variation in paternal behavior described by the PCA, and extreme differences in observed paternity. Nonetheless, my analyses suggest that no relationship exists between paternity and either male feeding rate or the more comprehensive measure of paternal care (PC1 from the PCA of male behavior). Thus, like most other species of relatively short-lived passerines, male kingbirds do not apportion feeding effort in relation to paternity, possibly because they lack the ability to assess paternity. The possibility that they can assess paternity, and that males direct prey deliveries to genetic young within broods of mixed paternity almost certainly does not occur (see also Sheldon & Ellegren, 1998) because feeding rates of males that lost all or no paternity were statistically indistinguishable (Fig. 3-2).

However, paternity may still influence kingbird paternal behavior. Nesting density may influence frequency of EPP if EP copulations increase when females have multiple potential partners in close proximity (for reviews see Westneat & Sherman, 1997; Møller & Ninni, 1999). The inverse relationship between male kingbird feeding rate and nesting density in the MNWR kingbird population is consistent with theoretical expectations of a decline in effort with increased uncertainty of paternity (Trivers, 1972;

Westneat & Sherman, 1993; Kokko, 1999). And, indeed, my data suggest that paternity was more likely to be lost when nesting density was high. Alternative explanations exist, however, for the trend towards reduced paternal care at high nest density. These include the possibility that areas of high nest density are habitats of abundant food resources that reduce demands on the need for male participation in feeding young, or that high nesting density increases agonistic interactions among males or attracts nest predators, either of which may compromise male feeding effort as territory and nest defense are performed mainly by males (Woodard & Murphy, 1999; Redmond et al., 2009).

Regardless of paternity, our results suggest that the divergent interests of males and females may have also contributed to variation in male feeding effort. Sexual conflict should be especially strong among species in which the opportunity for sexual selection is high (Trivers, 1972; Westneat & Stewart, 2003), and previous work on this population showed that the opportunity for sexual selection approaches that of polygynous species (Dolan et al., 2007) because within- and extra-pair success covary such that many males are either big “winners” or “losers”. Early singing males sired the most young (both within and outside pair bonds; Dolan et al. 2007) and early singing males were characterized by large body size and relatively long flight (primarily tail) feathers (Murphy et al., 2008). My finding that paternal care declined with increasing relative male flight feather (especially tail) length suggests that males that were likely to sire the most young were less parental. Copulations in kingbirds are never seen during

daylight hours and are almost certainly restricted to the predawn period of darkness when dawn song occurs (Sexton et al., 2007). Thus, unlike Dark-eyed Juncos (*Junco hyemalis*), where males trade-off mating effort for feeding effort (Chandler et al., 1994; Raouf et al., 1997), mating and parental effort in kingbirds are temporally separated within any 24 hour period. Lower feeding effort in high quality male kingbirds with a high probability of acquiring copulations thus does not appear to be the result of behavioral trade-offs. Rather, high quality males appear to simply work less than lower quality males. Tail length increases with age in kingbirds (MTM unpubl. data), and it may be that reduced effort of longer tailed males reflects age-associated dominance or inherent high male quality. Older and/or higher quality males may also possess higher quality territories that allow females to carry a larger share of the feeding effort. Future work should seek to elucidate whether male and territory quality covary, and whether male behavior is consistent across female partners or is contingent on his partner's overall quality.

Despite extreme variation in paternity, the inescapable conclusion appears to be that male kingbirds cannot directly assess paternity, or if they can, it does not influence paternal behavior. Nonetheless, equivalent levels of paternal feeding effort were not provided by all males, and some provided less care under conditions of high nesting density and when they were of high apparent quality. Understanding why the latter patterns exist will not be solved easily because multiple alternative explanations exist for each (see above). Nonetheless, my findings highlight the need to take a broad

ecological perspective if we are to better understand why EP mating systems exist, and why they vary so greatly even among closely related species (Griffith et al., 2002; Westneat & Stewart, 2003). My results also indicate that the major threat to female participation in EP mating behavior, the withholding of paternal care (Arnqvist & Kirkpatrick, 2005), probably does not exist. The absence of this potential cost to females frees them to pursue EPCs, but leaves open the question of what advantages the females accrue by so doing.

Tables

Table 2-1. Loadings of the five male morphometric measurements on the top three principal components for birds caught at Malheur National Wildlife Refuge, OR, between 2003 and 2010.

Variable	Vectors		
	1	2	3
Body mass	0.487	-0.044	-0.605
Wing chord	0.518	0.336	-0.124
Tarsus length	0.467	-0.587	-0.06
Bill length	0.415	-0.247	0.747
Tail length	0.323	0.692	0.237
Eigenvalues	1.703	1.219	0.944
% of variance explained	34.1	24.3	18.9

Table 2-8. Comparison of parental behavior of male and female Eastern Kingbirds (n = 49 pairs) from Malheur National Wildlife Refuge, OR, between 2003 and 2010.

Behavior	Males Mean (SE)	Females Mean (SE)	<i>t</i> (<i>P</i>)
Nest attendance (%)	4.95 (0.745)	38.35 (3.456)	9.60 (0.000)
Visit rate	5.18 (0.423)	6.21 (0.285)	3.33 (0.002)
Feeding rate	4.94 (0.424)	5.35 (0.307)	1.20 (0.236)
FS ^a ingestion rate	0.29 (0.073)	0.54 (0.107)	2.30 (0.026)
FS transport rate	0.92 (0.093)	0.96 (0.115)	0.32 (0.747)
Total FS disposal rate	1.20 (0.121)	1.50 (0.147)	1.67 (0.102)
Housekeeping rate	0.07 (0.020)	1.69 (0.232)	7.22 (0.000)
Shelter rate	0.03 (0.017)	2.33 (0.251)	9.17 (0.000)
Harass rate	1.84 (0.272)	0.64 (0.130)	4.95 (0.000)

^a FS = Fecal sac

Table 2-9. Factor loadings for parental behaviors on principal component (PC) 1, 2 and 3 for male and female Eastern Kingbirds from Malheur National Wildlife Refuge, OR, between 2003 and 2010. Shelter rate was not included in the male analysis because of its extreme rarity.

Variable	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
Nest attendance	0.350	0.460	0.426	0.557	-0.114	-0.252
Feeding rate	0.564	-0.242	-0.101	-0.256	0.608	0.120
FS ^a ingestion rate	0.191	0.716	0.080	0.178	0.296	0.778
FS ^a transport rate	0.462	-0.361	0.059	-0.315	0.386	-0.374
Housekeeping rate	0.132	0.289	-0.893	0.420	0.346	-0.066
Harass rate	0.540	-0.060	-0.032	0.095	0.478	-0.392
Shelter rate	---	---	---	0.555	0.176	-0.135
Eigenvalues	2.418	1.218	1.013	2.404	1.693	0.999
% of variance explained	40.3	20.3	16.9	34.3	24.2	14.3

^a FS = Fecal sac

Table 2-10. Reduced model set used to examine variation in male Eastern Kingbird feeding rates from Malheur National Wildlife Refuge (n = 45 nests). Analyses weighted by duration of behavioral observation period. Predictor variables included in the analyses were date of observation, time at start of observation, nestling age, brood size (BrSize), male body size, relative male tail length (MalePC2), density of pairs (Density), number of fertile females in population on date of observation, rate of female nest sheltering (FemCover), and the proportion of young in the nest sired by the male. Only models within 2 AIC_c of the top model were included in the final model set. Number of parameters (k), residual sums of squares (RSS), AIC_c , model weight (w_i), and the amount of variation accounted for by each model (R^2) are reported. AIC_c of null model (intercept only) = 132.76.

Model	k	RSS	AIC_c	ΔAIC_c	w_i	R^2
BrSize + FemCover + MalePC2 + Density	6	508.447	123.322	0.000	0.372	0.350
BrSize + FemCover + MalePC2	5	542.954	123.605	0.283	0.323	0.306
BrSize + FemCover + Density	5	544.395	123.724	0.402	0.304	0.304

Table 2-11. Importance weight of variables, model averaged parameter estimates, and confidence intervals (85%) for variables included in the model set used to examine feeding rate of male Eastern Kingbirds breeding at Malheur National Wildlife Refuge, OR, between 2003 and 2010.

Variable	Importance weight	Parameter estimate (SE)	Confidence interval	
			lower	upper
Brood size	1.000	1.116 (0.406)	0.522	1.710
Female sheltering rate	1.000	0.947 (0.419)	0.333	1.560
Relative flight feather length	0.696	-0.561 (0.339)	-1.058	-0.064
Nesting density	0.677	-0.554 (0.346)	-1.061	-0.048

Figures

Figure 2-1. Relationship between the proportion of trips to feed young made by the male and relative male flight feather length as measured by PC2 of the principal component analysis of male morphology. Males with high positive scores on the abscissa had long remiges and rectrices in relation to tarsus length.

Figure 2-2. Mean feeding rate ($\pm$ SE) for males that lost all paternity ($n = 9$), some paternity ($n = 17$), or no paternity ($n = 19$). Rates are reported without correction for influences of other variables (Means $\pm$ SE) and as least squares means that account for variation in feeding rate attributable to brood size, the time females spent sheltering the young, nesting density, and male quality (relative length of flight feathers; see text). Data collected between 2003 and 2010 from a kingbird population breeding at Malheur National Wildlife Refuge, OR.

Figure 2-3. Relationship between male parental effort (as measured by scores on the first axis of the principal components analysis of male parental behavior), and relative flight feather length (i.e., male quality, as estimated by scores on the second axis of the principal component analysis of male morphology) for Eastern Kingbirds breeding at Malheur National Wildlife Refuge, OR, between 2003 and 2010.

CHAPTER 4: SYNTHESIS

Using eight years of behavioral recordings (2003-2010) of Eastern Kingbirds at their nests in Malheur National Wildlife Refuge, I was able to undertake two studies. The first study (chapter 2) tested whether video recordings were suitable in accurately describing and documenting parental behavior. The second study (chapter 3) tested the hypothesis that males in the MNWR population reduce parental investment when paternity was lost.

I tested whether parental behaviors were repeatable by comparing nine behaviors at 18 nests across two temporally separated recordings. My results supported what should be expected assuming behaviors were repeatable. Seven of nine behaviors were not found to have different means, while the other two (fecal sac ingestion and fecal sac carry) were different in the manner predicted by the parental nutrition hypothesis. The parental nutrition hypothesis predicts that adults should consume fewer of their nestlings' fecal sacs as nestlings age because said fecal sacs should have less nutritional value to the adults (Glück, 1988; McGowan, 1995; Dell'omo et al., 1998). More importantly, I also found significant correlation between recordings for eight of nine behaviors, and found that the one nonconforming behavior could be remedied by the omission of one possible outlier. These results are very important, as nearly all studies within the field of animal behavior require behavioral sampling; these results are also consistent with the meta-analysis of Bell et al. (2009).

I next tested whether a one hour recording was sufficient to capture the variability of parental behaviors and then whether the first hour of a recording was sufficient. I found strong evidence that a one hour segment was sufficient (no means differed and all behaviors showed correlation between samples), but support for the first hour was weaker. This dichotomy was explored and I concluded that the differences found between the first hour and all subsequent hours likely were the result of an observer effect. Analysis showed that five out of nine behavioral values were significantly lower in the first hour of a recording, and that this trend was independent of time of day. I therefore concluded that human presence in the territory prior to the observation period was the best explanation for the results, and that future studies should keep this effect in mind while designing methodologies. However, the variable of probable greatest interest to most would be parental feeding rate and my results indicated that feeding rate in the first hour did not differ from subsequent hours. This is important because it suggests that the many studies of parental feeding behavior that rely on a single hour of observations yield credible results.

Testing whether male kingbird parental behavior was affected by lost paternity resulted in the conclusion that it was not, and the belief that they, like many other species (Whittingham et al., 1992; Kokko, 1999), are unable to detect lost paternity. Theory predicts that for a short lived species, if a male cannot be sure that he has lost all paternity, then he is better off investing in the young, as each breeding attempt may be his last (Whittingham et al., 1992; Mauck et al., 1999). As discussed in chapter one, the

variability in rates of EPP within the bird world is still poorly explained. If we are to gain a better understanding of the variability in such a complicated behavior it will be necessary to have as many data points as possible. To my knowledge, this study represents the first New World flycatcher, and the first member of the genus *Tyrannus*, to be subjected to this type of study, thus helping to fill a void in scientific knowledge on the topic.

While testing for an effect of realized paternity on paternal behavior I also tested an effect of a number of other variables on male feeding effort. Not surprisingly, I found that males exhibited greater parental effort when there were more nestlings to be fed. Similarly males also exhibited greater paternal effort at nests where the female spent a greater amount of time shading the young. This makes sense because when the female is shading the nest she is unable to forage and so the male must deliver more food to keep the nestlings provisioned. A number of other parameters that I tested were intended to test some factors suggested to influence rates of EPP both within and among species (see chapter 1). Of these I found that males with longer flight feathers and males in areas of greater kingbird density showed reduced parental effort. This is consistent with two of the factors predicted to influence rates of EPP. Long flight feathers are a sign of age and quality in kingbirds, two factors that should make them more attractive to females within their population. Attractive males are hypothesized to display reduced paternal investment in brood survival for two reasons: 1) more attractive males are expected to invest more in the pursuit of EPCs as they have a better

chance of being successful in that endeavor; and 2) the mates of attractive males might put in increased effort to provision their high quality young, affording the male the opportunity to reduce his effort. Males in areas of increased conspecific density are also predicted to reduce paternal investment for two reasons: 1) increased density is expected to create a situation where the male has to direct more of his attention towards defending his territorial boundaries, 2) males may use density as an estimate of the probability of lost paternity, and so males in dense areas would reduce effort assuming that they had lost paternity.

Another finding was that within this population there was no significant difference between the rate at which males and females fed nestlings. This is in marked contrast to a previous study carried out on a population of kingbirds in New York that found females delivered the majority of food to the nestlings (Woodard & Murphy, 1999). Although this could be the result of ecological or temporal differences between the two populations, I suspect this difference is in fact the result of sampling methods. For my study, cameras were quickly setup and left within the territory, and despite some evidence that parental behavior was slightly altered within the first hour of a recording (see chapter 2), I feel the effect on parental behavior was minimal. Woodard and Murphy (1999), however, performed their sampling by situating themselves in the birds' territories for one hour observation periods. I feel it is likely that their presence caused the males to spend more time acting defensively and less time provisioning young. This is another consideration that should be allowed to influence future research

methodologies, as any observer effect could compromise the integrity of a study. For instance, Woodard and Murphy (1999) suggested that the sex biased dichotomy in feeding rate could be explained by the exceptionally high rate of EPP in the species. Either males reduced effort in response to lost paternity, or females sought out more EPCs as they could afford to lose the investment of their social mate. This illustrates the importance of sound methodology, as I found no evidence for this trend and instead suggest that what they found was male feeding rate was more affected by human presence (Redmond et al., 2009).

Overall, my methods in testing for an effect of realized paternity on paternal investment is stronger than the typically used simple comparison of male feeding rate to paternity, and I feel similar methods should be the standard in future studies. Feeding of young is not the only manner in which a male might invest in nestlings, and realized paternity is far from the only factor that might affect his level of investment. By increasing the number of paternal behaviors from one to six and by testing a number of other factors that might affect investment I feel we have greatly increased the power of our tests, and accordingly strengthened our conclusion that no relationship exists between paternal investment and realized paternity in kingbirds.

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