Paternal behaviour in a socially monogamous but sexually promiscuous passerine bird

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Abstract
We documented parental behaviour and paternity of eastern kingbirds (\textit{Tyrannus tyrannus}) to test the predictions that paternal care would decline with increasing loss of paternity, increasing nesting density (a proxy for probability of paternity loss), male quality, and number of fertile females available in the population. Extra-pair young were found in 58\% of 45 nests for which behaviour was recorded and a higher proportion of young were extra-pair as nesting density increased. Male feeding rate declined with increasing nesting density and male quality, but neither feeding rate nor a composite measure of paternal behaviour varied with number of fertile females or paternity. Although alternative explanations exist, one interpretation of the reduced paternal care at high nesting density was that it was a response to perceived threats of paternity loss. The ultimate basis for the lower paternal effort of higher quality males is unclear but we discuss several possible explanations.

Keywords
differential allocation, extra-pair paternity, male quality, nesting density, paternal investment, parental behaviour.
1. Introduction

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 extra-pair paternity is common because of frequent sexual relations outside of pair bonds (Westneat & Sherman, 1997; Griffith et al., 2002). This creates two dilemmas for males of species in which extra-pair paternity occurs frequently. First, parental investment is likely to come at the expense of reproductive investment (Magrath & Elgar, 1997; Raouf et al., 1997) and thus, selection may favour males that invest less with their social mate to seek mating opportunities with extra-pair (EP) females (Magrath & Komdeur, 2003). Second, and independently of a male’s response to the first dilemma, selection should favour males that assess the likelihood of loss of paternity in their nest and invest appropriately in the social mate’s brood. Evolutionary theory suggests that depreciable forms of parental care (i.e., those that cannot be shared; Westneat & Sherman, 1993) such as food deliveries should not be provided indiscriminately especially if current parental effort potentially compromises future adult survival and/or fecundity. This theoretical expectation (Queller, 1997) is supported by comparative interspecific studies that indicate that paternal care varies inversely with the frequency of extra-pair paternity (Møller & Birkhead, 1993; Møller & Cuervo, 2000).

It follows, all else being equal, that on a population level male energetic investment in parental care should also be contingent upon the proportion of young that he sired (Trivers, 1972; Queller, 1997; Kokko, 1999). Evidence from polygynandrous species supports this prediction (Davies et al., 1992; Briskie et al., 1998), but only a minority of studies of socially monogamous species have affirmed the predicted outcome (Dixon et al., 1994; Chuang-Dobbs et al., 2001; Suter et al., 2009; Perlut et al., 2012). In most studies of socially monogamous birds, paternity and paternal care are unrelated (Kempenaers et al., 1998; Peterson et al., 2001; Dickinson, 2003; Bouwman et al., 2005; Rytkönen et al., 2007; LaBarbera et al., 2012; reviewed by Whittingham & Dunn, 2001), and the most parsimonious explanation may be that males cannot reliably assess their share of paternity (Kempenaers & Sheldon, 1996). If this is the case, the best option for males of relatively short-lived species may be to deliver care in the expectation that he has sired at least a portion of the brood (Whittingham et al., 1992; Mauck et al., 1999).
However, other forces may influence paternal care. For instance, paternal care may persist when paternity has been lost if female preference for parental males, demonstrated by caring for young regardless of paternity, improves a male’s future prospects of siring young with his social mate (Freeman-Gallant, 1996, 1997; Rowe & Weatherhead, 2007). Also, sexual conflict over care is often substantial (Westneat & Stewart, 2003; Houston et al., 2005; 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). Low quality males may opt for high paternal investment (e.g., Sanz, 2001) in the face of potential loss of paternity if prospects of success outside the current pair bond are negligible (Grafen, 1980; Kokko, 1998). Similarly, females may choose to positively differentially allocate care (sensu Ratikainen & Kokko, 2010), in essence accepting 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 the quality of either sex, a dearth of fertile females, possibly as a consequence of a migrant’s late arrival to the breeding ground (e.g., Cooper et al., 2011), may be a determinant of paternal effort; without available females there is no conflict between mating and paternal effort (Magrath & Komdeur, 2003).

Eastern kingbirds (Tyrannus tyrannus; hereafter kingbirds) are socially monogamous, biparental, migratory tyrant flycatchers in which pair bonds can persist for multiple years (Murphy, 1996; Woodard & Murphy, 1999). Despite high mate fidelity, kingbirds exhibit one of the highest frequencies of extra-pair paternity known among socially monogamous passerines as 60% of broods have EP young (Rowe et al., 2001; Dolan et al., 2007). As a consequence, a significant opportunity for sexual selection exists through EP mating behaviour (Dolan et al., 2007). Intense parental effort in kingbirds has been shown to reduce both parental body condition (Maigret & Murphy, 1997), and future adult survival and fecundity (Murphy, 2000). Males in an eastern North American kingbird population provision young at lower rates than females and Woodard & Murphy (1999) attributed lower male effort to consistently high losses of paternity. While overall rates of EP paternity are high in kingbirds, there is consistently high among-male variation, with some (20% to 33%) losing all paternity and others (≥25%) securing all paternity in
their broods (Dolan et al., 2007; MTM unpubl. data). What remains unknown is whether this extreme intrapopulation variation in loss of paternity drives some males to invest more or less in parental care.

To address this unanswered question, we documented paternity and recorded parental behaviour of kingbirds breeding at Malheur National Wildlife Refuge (MNWR) in southeastern, Oregon, USA. Our first prediction was that losses of paternity would result in reduced paternal care. However, because this hinges on the potentially suspect assumption that males can accurately assess paternity, we also tested for the possibility that paternal behaviour varied instead with a potential proxy of paternity loss. High breeding density equates to many potential EP suitors and a high potential for loss of paternity in some species (Westneat & Sherman, 1997; Møller & Ninni, 1999). Therefore, our second prediction was that males in high nesting density environments would provide less care. Our third prediction was that paternal care would decline with the increasing availability of fertile females in the population at the time behaviour was recorded. Finally, a male kingbird’s EP success is positively related to his quality (Dolan et al., 2007). Thus, low-quality males, characterized by small size and/or relatively short flight feathers (Murphy et al., 2008), may have little to gain from the pursuit of EP copulations, and possibly much to gain by demonstrating their parental abilities (e.g., Freeman-Gallant, 1996). This led to our final prediction that paternal care would increase with decreasing male quality. The alternative is that low quality males are constrained to provide less care (Curio, 1982).

2. Methods

2.1. Study site and field methods

Our study was conducted on a kingbird population nesting in the riparian zone of the Donner und Blitzen River at MNWR (43°N, 119°W). Most of the surrounding area is high desert (1400 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. Kingbirds overwinter in South America (Jahn et al., 2013), and males return from migration approx. 1 week before females and older birds approx. 1 week earlier than younger birds (Cooper et al., 2009). Since the beginning of our study in 2002 kingbirds have been marked with unique combinations of one federal and three plastic colored leg bands.
Parental behaviour was studied in five years in the period between 2003 and 2010.

We 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 (± 15 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 young to nestling growth curves (Murphy, 1981). Nests were checked 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. Identical data were collected from replacement nests that followed nest failures.

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 basilic vein on a wing, and heparinized capillary tubes were used to draw approx. 50 μl of blood from adults and 5–6-day-old nestlings. Blood samples were transferred to microcentrifuge tubes containing 1.5 ml of Longmire’s buffer (Longmire et al., 1988), and refrigerated until processing. 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 calipers), and tail lengths (± 0.5 mm; wing ruler). Sex of adults was determined using differences in the emargination of the 9th and 10th primaries (Pyle, 1997), and the presence of cloacal protuberances in males and brood patches in females.

2.2. Behavioural observations

Many of the adults were banded prior to the initiation of our study, and none of the filmed pairs were captured at the nest in the year of filming prior to our observations. Hence, parental behaviour should not have been affected by our banding efforts. Young ranged between 4 and 12 days of age at filming (hatching = day 0), a range over which feeding rate changes little with
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Parental behaviour was recorded 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 filming commenced, and recordings were made on 4-h Hi8 video cassettes. Camera focus was adjusted to capture an area of approx. 30 cm radius around the nest. Recordings ranged from 1–4 h, began any time between 0600 PST and 1000 PST, and were made with the timestamp in the bottom right corner to aid later analysis. Behavioural data were only collected on clear days of no precipitation and low winds.

Video cassettes were digitized using a StarTech USB 2.0 video capture cable along with the GrabBee software provided by the manufacturer. This enabled us to save all visits to digital media for more efficient processing and reference. Only periods when an adult was at the nest were transferred to digital media. Kingbirds are single-prey provisioners, and at each nest visit we recorded the timestamps of arrival and departure, and documented whether the adult (1) fed young, (2) ingested faecal sacs, (3) transported faecal sacs away from the nest, (4) positioned its body over the young to brood or shade them from the sun (‘shelter’), (5) exhibited behaviours indicative of nest maintenance (‘housekeeping’), or (6) ‘harassed’ the other adult. 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 (we assume) forage. This was almost always accompanied by a vocal outburst from both birds.

We used the timestamps of arrival and departure to calculate the duration of each visit, and the sum of these visit durations was compared to the total recording length to determine proportion of time the nest was attended (‘attendance’). We assumed a nestling was fed any time a newly arrived adult dipped its bill into the mouth of a begging nestling. Feeding and non-feeding visits, and faecal sac ingestions and faecal sac transports away from the nest (i.e., faecal sac in bird’s bill as it flew from the nest) were combined into total visits and total faecal sac disposals, respectively. All behavioural variables were calculated as hourly rates except for nest attendance, which was calculated as a proportion of total time observed.

2.3. Sex of the feeding parent

Kingbirds are sexually monochromatic and, although size and morphology differ (Murphy, 2007), differences are not obvious without the bird in hand.
We nonetheless unambiguously determined sex of the parent at most nest visits because at least one member of a pair was banded in all cases. However, bands were not always visible and in those cases we used a combination of visual and behavioural cues to sex the adults. These included known differences in call, posture (male being more vertical), approach angle (individuals reliably approached and left the nest from the same direction; see Lessells et al., 2006), missing feathers, and strongly sex-biased behaviours such as female sheltering (Woodard & Murphy, 1999). It was also often possible to sex adults on the basis of sequence of visits; when the visit of an adult we could not sex overlapped a visit from its known-sex mate, which occurred often when adults fed at high rates, we could assign sex unambiguously. Confidence in the identification of sex at each nest visit was given a value between 0 and 100%, which we then averaged for each nest. Only nests with high average confidence were included in our analyses (93.5 ± 1.17% SE, N = 49 pairs).

2.4. Assignment of paternity

Detailed methods for the determination of nestling parentage are described elsewhere (Dolan et al., 2007). Briefly, we compared nestling and adult genotypes at seven microsatellite loci that amplified a total of 80 alleles. We 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 non-amplifying alleles were rare or absent. We 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. For some analyses we categorized males into three groups on the basis of their share of paternity within the nest of their social partner. Males in paternity class ‘none’ sired none of the young in their nest, those in class ‘some’ tended broods with a mix of within-pair and extra-pair young, while class ‘all’ males sired all the young in the nest.

2.5. Nesting density, number of fertile females and male quality

To quantify nesting density, we used universal transverse Mercator coordinates read from a Garmin GPS 76 to measure distance between a focal
nest where observations were made and its two nearest neighbours (‘nearest neighbour distance’, NND). The inverse of the average of the two NNDs yielded a quotient for which high values represented short NND (i.e., high density). The log_{10} transformed value of the inverse of average NND was distributed normally, and we refer to this value (log_{10}(NDD^{-1})) as ‘nesting density’. We performed identical calculations for the nearest neighbour and nearest three neighbours, and in the analyses described below, distance to two nearest neighbours performed best.

Although kingbirds are highly seasonal breeders and raise only a single brood per year, fertile females are available throughout the breeding season because of renesting after frequent nest failure (>60% of initial nests failed in all years). Renesting occurs on the same territory and requires 7 to 10 days. We assumed that a female’s fertile period ran from four days before the laying of the first egg until the laying of the penultimate egg. Extra-pair mates in kingbirds are often not immediate neighbours and are commonly separated by several and up to 15 km (Dolan et al., 2007). We thus used the number of fertile females from the entire population on the day of filming as our index of the availability of fertile females.

‘Dawn song’ occurs in the predawn darkness, which is the primary display period for kingbirds (Smith, 1966; Sexton et al., 2007). To our knowledge, this is when essentially all copulations occur. The earliest singing male kingbirds are large (i.e., long tarsi), have the longest flight feathers (Murphy et al., 2008), and have the highest extra-pair and total reproductive success (i.e., within-pair + extra-pair young; Dolan et al., 2007). Our assumption therefore was that high quality individuals were of large overall size and had relatively long flight feathers. Body mass and morphometric data (wing chord, and tail, bill, and tarsus length) 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 (unpubl. data) very closely mirrored the earlier results. All variables loaded positively on principal component (PC) 1 (Table 1) indicating that PC1 represented a measure of ‘body size’. Wing chord and especially tail length loaded positively on PC2 while tarsus length loaded negatively (Table 1); high scores on PC2 were characteristic of birds that had long flight feathers and short tarsi. Hence, PC2 represented an index of ‘relative flight feather length’ (especially tail length).
Table 1.
Factor loadings from the principal component analysis of the five morphometric measurements taken from male eastern kingbirds captured at Malheur National Wildlife Refuge, Princeton, OR, USA between 2002 and 2011.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>0.487</td>
<td>−0.044</td>
<td>−0.605</td>
</tr>
<tr>
<td>Wing chord</td>
<td>0.518</td>
<td>0.336</td>
<td>−0.124</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>0.467</td>
<td>−0.587</td>
<td>−0.06</td>
</tr>
<tr>
<td>Bill length</td>
<td>0.415</td>
<td>−0.247</td>
<td>0.747</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.323</td>
<td>0.692</td>
<td>0.237</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>1.703</td>
<td>1.219</td>
<td>0.944</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>34.1</td>
<td>24.3</td>
<td>18.9</td>
</tr>
</tbody>
</table>

Percentage of the total morphological variation accounted for by the three top principal components (PC), along with their eigenvalues, are reported.

2.6. Analysis of paternal behaviour

We used the 49 pairs that were left after eliminating nests with low confidence of assignment of sex to adults feeding young to characterize general parental behaviour of both sexes. To evaluate paternal behaviour in relation to paternity, we used the 45 nests for which paternity was known. Male feeding rate was used as a measure of paternal effort, but for some analyses we also used the proportion of the total number of trips that were made by males. Parental effort is ‘multidimensional’ (i.e., more than just feeding young; Houston et al., 2005) and therefore we also conducted a PCA of male behaviour to characterize the major axes of behaviour that could serve as a more comprehensive measure of paternal care. We did not include total visit rate and total faecal sac disposal rate in the PCA because they were highly correlated with feeding rate ($r = 0.993$, $p < 0.001$) and faecal sac transport rate ($r = 0.797$, $p < 0.001$), respectively. Sheltering rate was also excluded because males essentially never exhibited this behaviour (Table 2).

Among-male variation in both feeding rate and PC1 of behaviour (see below) were examined 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) as nesting density increased, (3) as number of fertile females at the time of the recording increased and (4) as male quality increased. We assume that large size (high PC1 score) and/or relatively long flight feathers (high PC2 score) were representative of high male quality. Dif-
Paternal care by kingbirds

Table 2.
Comparison of female and male eastern kingbirds parental behaviour (N = 49 pairs) observed at Malheur National Wildlife Refuge, Princeton, OR, USA, between 2003 and 2010.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Females (mean (SE))</th>
<th>Males (mean (SE))</th>
<th>t (p)b</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>PC1</td>
</tr>
<tr>
<td>Nest attendance (%)</td>
<td>38.35 (3.456)</td>
<td>4.95 (0.745)</td>
<td>9.60 (0.000)</td>
<td>0.350</td>
</tr>
<tr>
<td>Visit ratea</td>
<td>6.21 (0.285)</td>
<td>5.18 (0.423)</td>
<td>3.33 (0.002)</td>
<td>–</td>
</tr>
<tr>
<td>Feeding ratea</td>
<td>5.35 (0.307)</td>
<td>4.94 (0.424)</td>
<td>1.20 (0.236)</td>
<td>0.564</td>
</tr>
<tr>
<td>FS ingestion ratea</td>
<td>0.54 (0.107)</td>
<td>0.29 (0.073)</td>
<td>2.30 (0.026)</td>
<td>0.191</td>
</tr>
<tr>
<td>FS transport ratea</td>
<td>0.96 (0.115)</td>
<td>0.92 (0.093)</td>
<td>0.32 (0.747)</td>
<td>0.462</td>
</tr>
<tr>
<td>Total FS disposal ratea</td>
<td>1.50 (0.147)</td>
<td>1.20 (0.121)</td>
<td>1.67 (0.102)</td>
<td>–</td>
</tr>
<tr>
<td>Housekeeping ratea</td>
<td>1.69 (0.232)</td>
<td>0.07 (0.020)</td>
<td>7.22 (0.000)</td>
<td>0.132</td>
</tr>
<tr>
<td>Shelter ratea</td>
<td>2.33 (0.251)</td>
<td>0.03 (0.017)</td>
<td>9.17 (0.000)</td>
<td>–</td>
</tr>
<tr>
<td>Harass ratea</td>
<td>0.64 (0.130)</td>
<td>1.84 (0.272)</td>
<td>4.95 (0.000)</td>
<td>0.540</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.418</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>40.3</td>
</tr>
</tbody>
</table>

Factor loadings for the first two vectors (PC1 and PC2) derived from the principal component analysis of male eastern kingbird parental behaviour of the same data are also reported. Shelter rate was not included in the male analysis because of its extreme rarity, while visit rate and total faecal sac (FS) disposal rate were excluded from the principal component analysis because of high correlation with other variables.

a All rates calculated on an hourly basis.
b Statistics based on paired t-test

Differences in feeding effort among males might also be a consequence of other variables that, for our purposes, were of little concern except that they might have introduced noise that could make it difficult to test our hypotheses. We therefore included brood size, average age of nestling in the nest, and time and date of observation as predictor variables. We also included a female behaviour, sheltering rate, in the analysis because sheltering prevented a female from feeding young, and if feeding rate was to be maintained, males had to increase their effort independently of other factors.

The best subsets regression analysis was conducted using an information theoretic framework. We used Akaike’s Information Criterion adjusted for small sample size (AICc) to evaluate model fit, with the assumption that all models within two AICc units of the top model (ΔAICc = 0) were candidates of potential explanatory value. Following Burnham & Anderson (2002), we calculated model weights (wi), model averaged parameter
estimates, 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 (Burnham & Anderson, 2002; Arnold, 2010). To assist in model evaluation, we also report the 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 3–4 h in length (67% of filmed events), but a few were less than two hours (7%). Prior analyses indicated that one hour observation bouts adequately characterized a pair’s behaviour (Murphy et al., 2015), but the latter study also suggested that two or more hours would likely yield more accurate measurements. To account for the potential weakness of short observations periods we weighted analyses by observation length by distinguishing between short (<2 h; 7% of bouts) and longer (2–4 h; 93% of bouts) observation bouts. Five males were recorded more than once (never in the same year), but in only one case was it the same pair in different years. Neither the number ($r = 0.465, p = 0.353$) nor proportion ($r = 0.311, p = 0.611$) of male feeding trips in different years gave indications towards consistently high or low feeding effort (with one possible exception; Figure 1) and thus we treat the multiple observations of males in different years as independent.

All analyses were conducted using STATISTIX (Analytical Software, Tallahassee, FL, USA). Statistics are reported as means ± SE, and as statistically significant at $p \leq 0.05$.

3. Results

Males spent little time in nest attendance, rarely sheltered young, or tended to the nest (Table 2). All three behaviours were conducted almost solely by females, who also ingested more faecal sacs (Table 2). Absolute feeding rate of the sexes did not differ, but variance in male feeding rate exceeded that of females ($F$-test, $F = 1.92$, df = 44, 44, $p = 0.017$), and as a proportion of total feeding trips, females contributed more than males (median test,
X^2 = 5.15, df = 1, p = 0.023). Males were nearly three times more likely to exhibit ‘harassment’ behaviour (Table 2), and male harassment increased with his feeding rate (r = 0.695, N = 49, p < 0.001). At the same time, the proportion of feeding trips made by females declined when male harassment was high (r = −0.430, N = 49, p = 0.002). Harassment was thus most common in males that were feeding at high rates while their partner’s proportional contribution was declining.

Eigenvalues for the first two factors from the PCA of paternal behaviour accounted for 60% of total variance (Table 2). PC1 was related primarily to feeding effort as shown by the high loadings for male feeding rate and male harassment of his partner. Males that fed nestlings at high rates also transported more faecal sacs from the nest. PC2 was mainly about the disposition of faecal sacs. Males with high scores on PC2 spent the most time at the nest, and while there, tended to ingest more faecal sacs rather than remove them by transport from the nest.

3.1. Paternity

EP young were present in 26 of 45 nests (57.8%), 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). After using multiple regression to account for a tendency for a seasonal decline in the proportion of young within a brood to be sired by the within-pair male (β = −0.263, SE = 0.164, p = 0.115), the proportion of young sired by a within-pair male in his nest declined as nesting density increased (β = −0.318, SE = 0.154, p = 0.045;
A substantial proportion of males lost all paternity in their nest (20.0%; 9 of 45), while all paternity was secured by roughly twice as many males (42.2%; 19 of 45). Loss of paternity was thus common and more likely when nesting density was high.

3.2. Variation in paternal effort

After eliminating uninformative models, our analyses of male feeding rate yielded three competitive models (Table 3). 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 variables just mentioned, start time of observation bout, number of fertile females, and paternity. Model averaged parameter estimates for the four variables in the top three models all excluded zero from their confidence intervals (Table 4), indicating that male feeding rate increased with brood size and female sheltering rate, but that young were also fed less by males who bred at high nesting density (Table 4) and by males with relatively long flight feathers (Table 4). When expressed as a proportion of total pair feeding effort, male effort declined as relative flight feather length increased (Figure 2). Between 30% and 35% of the variation in male feeding rate was accounted for by the three combinations of the four variables (Table 3).

Table 3.
Results of analysis of variation in the rate at which male eastern kingbirds fed young in nests located at Malheur National Wildlife Refuge, Princeton, OR, USA (N = 45 nests).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>RSS</th>
<th>AIC_C</th>
<th>ΔAIC_C</th>
<th>w_i</th>
<th>R^2</th>
</tr>
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<tbody>
<tr>
<td>BrSize + FemShelter + MalePC2 + Density</td>
<td>6</td>
<td>508.447</td>
<td>123.322</td>
<td>0.000</td>
<td>0.372</td>
<td>0.350</td>
</tr>
<tr>
<td>BrSize + FemShelter + MalePC2</td>
<td>5</td>
<td>542.954</td>
<td>123.605</td>
<td>0.283</td>
<td>0.323</td>
<td>0.306</td>
</tr>
<tr>
<td>BrSize + FemShelter + Density</td>
<td>5</td>
<td>544.395</td>
<td>123.724</td>
<td>0.402</td>
<td>0.304</td>
<td>0.304</td>
</tr>
</tbody>
</table>

Analyses weighted by duration of behavioral observation period. Predictor variables included 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 (FemShelter), and proportion of young in the nest sired by the male. Only models within 2 AIC_C units of the top model were included in the model set reported above. 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.
Table 4.
Importance weight of variables, model averaged parameter estimates and confidence intervals (85%) for variables included in the final model set emerging from the analysis of male eastern kingbird feeding rate of dependent young.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Importance weight</th>
<th>Parameter estimate (SE)</th>
<th>Confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brood size</td>
<td>1.000</td>
<td>1.116 (0.406)</td>
<td>0.522 – 1.710</td>
</tr>
<tr>
<td>Female sheltering rate</td>
<td>1.000</td>
<td>0.947 (0.419)</td>
<td>0.333 – 1.560</td>
</tr>
<tr>
<td>Relative flight feather length</td>
<td>0.696</td>
<td>−0.561 (0.339)</td>
<td>−1.058 – −0.064</td>
</tr>
<tr>
<td>Nesting density</td>
<td>0.677</td>
<td>−0.554 (0.346)</td>
<td>−1.061 – −0.048</td>
</tr>
</tbody>
</table>

Data collected at Malheur National Wildlife Refuge, Princeton, OR, USA between 2003 and 2010. Parameter estimates are directly comparable because all predictor variables were transformed to Z-scores before analysis.

Figure 2. Relationship between the proportion of trips to feed young and relative male flight feather length as measured by PC2 of the principal component analysis of male morphology for male eastern kingbirds breeding at Malheur National Wildlife Refuge, Princeton, OR, USA, between 2003 and 2010. Males with high positive scores on the abscissa had long remiges and rectrices in relation to tarsus length. The $r^2$ and $p$-value refer to the entire data set, but separate regression lines are shown for different categories of paternity: open circle and solid line denote males that lost all paternity in their nest; solid circle and dashed line denote males that gained some paternity in their nest; and half-filled diamond and dotted line denote males that retained all paternity in their nest.
Brood size did not differ among males that sired none, some, or all of the young in their brood (ANOVA: $F = 0.24$, df = 2, 42, $p = 0.786$). Likewise, the proportion of food deliveries by males did not differ among paternity classes (ANOVA: $F = 0.21$, df = 2, 42, $p = 0.813$). In addition, regression coefficients describing the decline in proportion of feeding trips with increasing relative flight feather length for males in different paternity classes did not differ (Figure 2; $F = 0.10$, df = 2, 39, $p = 0.909$). Overall, the proportion of feeding trips by males declined with increasing relative flight feather length (ANCOVA: $F = 8.32$, df = 1, 41, $p = 0.006$), but as before, elevation did not differ among paternity classes (ANCOVA: $F = 0.07$, df = 2, 41, $p = 0.929$). Comparison of mean and least squares mean (i.e., effects of variables in Table 4 removed) feeding rates confirmed that male feeding rate was independent of paternity class (Figure 3).

Regression coefficients describing the decline in ‘paternal care’, our composite measure of male behaviour (i.e., PC1 from Table 2), with relative flight feather length did not differ among males that sired none, some, or all young

**Figure 3.** Mean feeding rate ($\pm$ SE) for male eastern kingbirds 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 ($\text{means} \pm \text{SE}$) 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, Princeton, OR, USA.
Paternal care by kingbirds

\( (F = 0.08, \, df = 2, \, 39, \, p = 0.925). \) ANCOVA showed further that paternal effort declined with relative flight feather length \( (F = 6.43, \, df = 1, \, 41, \, p = 0.015) \) but did not differ among paternity classes \( (F = 0.43, \, df = 2, \, 41, \, p = 0.653). \) Results of the best subsets regression of paternal effort in relation to the full set of variables 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 \( (61.86; \, \Delta \text{AICc} = 0.00), \) but number of fertile females added nothing to the model because without it the AICc was virtually identical to the three-variable model of brood size, female sheltering rate, and relative flight feather length \( (61.87; \, \Delta \text{AICc} = 0.01). \) Moreover, the combination of brood size, female sheltering rate and number of fertile females was not competitive \( (\Delta \text{AICc} = 2.88). \) Thus, paternal effort declined as relative flight feather length increased \( (\beta = -0.518 \pm 0.202 \text{ SE}; \text{ Figure 4}), \) but was independent of the number of fertile females \( (\beta = 0.381 \pm 0.204 \text{ SE}). \)

![Figure 4](image)

**Figure 4.** Relationship between paternal effort (as measured by scores on the first axis of the principal component analysis of male parental behaviour) and relative flight feather length for eastern kingbirds breeding at Malheur National Wildlife Refuge, Princeton, OR, USA, between 2003 and 2010. Males with high positive scores on the abscissa had long remiges and rectrices in relation to tarsus length. The \( r^2 \) and \( p \)-value refer to the entire data set, but separate regression lines are shown for different categories of paternity: open circle and solid line = males that lost all paternity in their nest; solid circle and dashed line = males that gained some paternity in their nest; half-filled diamond and dotted line = males that retained all paternity in their nest.
4. Discussion

Although sexual differences in parental feeding rates were not as great as that reported for an eastern North American kingbird population (Woodard & Murphy, 1999), we detected pronounced sexual division of parental behaviour as females had nearly all responsibility for caring for nest and young, and provided a higher proportion of trips to feed young. Variance of male feeding rate was also higher than that of females. Consequently, female kingbirds provided a steadier and more consistent supply of food to the young. The proportion of broods that contained EP young (58%) was high compared to most species (see Griffith et al., 2002), but nearly identical to the long-term average of this western North American (Dolan et al., 2007; MTM unpubl. data) and an eastern North American population (Rowe et al., 2001). Our documentation of proportionately lower male effort is thus consistent with theoretical expectations given the frequent loss of paternity (e.g., Queller, 1997) and previous demonstration that kingbird parental care is costly to adult body condition (Maigret & Murphy, 1997), and survival and future fecundity (Murphy, 2000).

4.1. Sources of variation in paternal effort

While lower male kingbird investment in parental care is consistent with frequent loss of paternity, our findings lend no support to the expectation (Trivers, 1972; Westneat & Sherman, 1993; Queller, 1997; Kokko, 1999) that individual males would respond directly to loss of paternity by reducing effort. Our results are consistent with findings from the majority of other socially monogamous species (see Introduction). Parental care is costly in kingbirds (Maigret & Murphy, 1997; Murphy, 2000) and therefore selection for an ability by males to discriminate between within- and extra-pair young would seem strong. However, that the parental effort of the 20% of males who sired no young was indistinguishable from other males with at least a share of paternity (Figure 3) suggests strongly that males do not have the capacity to assess paternity. Males of polygynandrous species appear to assess their probable paternity using the proportion of time spent with and copulating with a female (Davies et al., 1992; Briskie et al., 1998). We have almost never witnessed a kingbird copulation, be it within- or extra-pair. By default we have concluded that the ‘dawn song’ period, which is when males sing in the predawn darkness (Smith, 1966; Sexton et al., 2007), is when copulations occur. Females are likely able to surreptitiously move among
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territories to obtain extra-pair copulations, leaving males both literally and figuratively, in the dark.

However, perceptions of loss of paternity may still influence behaviour (e.g., Sheldon et al., 1997), and our detection of reduced male effort as nesting density increased is consistent with the possibility that males used nesting density as a proxy of the probability of having lost paternity. High nesting density might create uncertainty for males if the frequency of extra-pair copulations increases when females have multiple potential partners in close proximity (Westnest & Sherman, 1997; Møller & Ninni, 1999), and indeed, we found that the proportion of extra-pair young in a brood increased when nesting density increased. Thus, it may be that the threat of loss of paternity influenced paternal behaviour, although alternative explanations exist. For instance, habitats of high food abundance might support higher nesting density, and at the same time reduce the need for male assistance in feeding young. Given that loss of paternity is common and parental care is costly (see above), selection would favour males that reduced their effort when food was abundant. High nesting density could have also increased agonistic interactions among males or attracted nest predators, either of which could compromise male feeding effort (e.g., Qvarnström, 1997) as territory and nest defence are performed mainly by male kingbirds (Woodard & Murphy, 1999; Redmond et al., 2009).

Regardless of real or perceived loss 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). Earlier work on this kingbird population showed that the opportunity for sexual selection approached that of polygynous species because within- and extra-pair success covaried positively (Dolan et al., 2007). High quality males, who are likely to have the greatest extra-pair success, may thus conserve time and/or energy for seeking reproductive opportunities rather than being parental (e.g., Magrath & Elgar, 1997). However, restriction of copulations to the predawn period eliminates potential temporal conflicts between seeking copulations and providing food to young as an explanation for the reduced proportional feeding effort of males with relatively long flight feathers (Figures 2 and 4).

Male kingbirds with relatively long flight feathers sing the earliest in the dawn song period (Murphy et al., 2008) and such individuals have the highest extra-pair mating success (Dolan et al., 2007), suggesting that females
prefer these males as sires of their young. Thus, one possible explanation for the decline of male effort with increasing relative flight feather length is that, as predicted by theory (Burley, 1986; Sheldon, 2000; Harris & Uller, 2009), females may be more willing to bear a greater portion of parental care in exchange for the opportunity to pair with a male of high quality with whom to share high quality habitat and/or produce high quality young. However, alternative explanations again exist for the lower effort of males with relatively long flight feathers. 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 the possibility that older (or higher quality males) possess higher quality territories. If the latter, females may be able to carry a larger share of the feeding effort without cost to her future survival or fecundity (Murphy, 2000). Future work should seek to elucidate whether male and territory quality covary, and whether male behaviour is consistent across female partners or contingent on his partner’s overall quality.

Despite extreme variation in paternity and paternal care of young, we conclude that paternal investment by kingbirds was not affected directly by paternity. Nonetheless, equivalent levels of paternal feeding effort were not provided by all males, and those that provided less care nested in close proximity to neighbors where loss of paternity was more likely, or tended to be males of high apparent quality. Understanding why these patterns exist will not be solved easily because alternative explanations exist for each (see above). Our results also indicate, however, that the major threat to female participation in extra-pair mating behaviour, the withholding of paternal care (Arnqvist & Kirkpatrick, 2005), is weak and possibly non-existent in kingbirds. The absence of this potential cost frees females to pursue extra-pair copulations (see also Varian-Ramos et al., 2012), but also leaves open the question of what advantages, if any (Forstmeier et al., 2014), females gain from extra-pair copulations.

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References


