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In a campus population of Northern Mockingbirds (*Mimus polyglottos*), male mating success depends on experience and timing

En una población de sinsontes norteños (*Mimus polyglottos*) de un campus universitario, el éxito de apareamiento de los machos depende de la experiencia y del momento

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ABSTRACT. Many birds are known for ornaments and behavior undertaken in the pursuit of finding and keeping a mate, but for many species, the specific factors that contribute to breeding success remain underexplored. In this study, we tracked the reproductive fates of a population of the Northern Mockingbird, *Mimus polyglottos*, on the Rice University campus in Houston, Texas. We related male mating success, total fecundity, offspring survival, and rates of extra-pair paternity to body size and condition, the timing of key reproductive events, and metrics of song and of territory quality. Our results indicate that heavier and more experienced males were significantly more likely to attract mates. Birds of both sexes that bred earlier in the season produced significantly more total offspring and enjoyed higher offspring survival. Surprisingly, although *M. polyglottos* is famous for the complexity of its song and for its high territorial aggression, we did not detect a significant effect of any metric of song or territory quality on mating success, although our song samples were short and exclusively collected early in the breeding season and other measurements might have been more successful. We also detected surprisingly few instances of extra-pair paternity or egg-dumping relative to other socially monogamous songbirds and other mockingbird studies. Our results underscore the variations in reproductive strategy that can exist between different bird species or across different environments.

RESUMEN. Muchas aves son conocidas por ornamentaciones y comportamientos emprendidos en la búsqueda de hallar o mantener una pareja, pero para muchas especies, los factores específicos que contribuyen al éxito reproductivo permaneces inexplorados. En este estudio, rastreamos el destino reproductivo de una población del Sinsonte norteño, *Mimus polyglottos*, en el campus de la Universidad Rice en Houston, Texas. Relacionamos el éxito de apareamiento de los machos, la fecundidad total, la supervivencia de la descendencia y las tasas de paternidad extrapareja con el tamaño y la condición corporal, el momento de eventos reproductivos clave y métricas del canto y de la calidad del territorio. Nuestros resultados indican que los machos más pesados y con mayor experiencia tuvieron una probabilidad significativamente mayor de atraer parejas. Las aves de ambos sexos que se reprodujeron más temprano en la temporada produjeron un número significativamente mayor de crías en total y presentaron una mayor supervivencia de la descendencia. Sorprendentemente, aunque *M. polyglottos* es famosa por la complejidad de su canto y por su alta agresividad territorial, no detectamos un efecto significativo de ninguna métrica del canto ni de la calidad del territorio sobre el éxito de apareamiento, aunque nuestras muestras de canto fueron breves y se recolectaron exclusivamente al inicio de la temporada reproductiva, por lo que otras mediciones podrían haber sido más exitosas. También detectamos sorprendentemente pocos casos de paternidad extrapareja o de puesta de huevos en nidos ajenos en comparación con otros paseriformes socialmente monógamos y con otros estudios sobre sinsontes. Nuestros resultados subrayan las variaciones en las estrategias reproductivas que pueden existir entre distintas especies de aves o a través de diferentes ambientes.

Key Words: *behavioral ecology; Mimus; mockingbird; reproductive strategies; song*

INTRODUCTION

Because of their very visible mating traits and behaviors and the need of their altricial young for extensive parental care, birds have long been model organisms for studying the evolution of reproductive strategies and sexual selection (Gill 1995, Kaiser et al. 2017, Brouwer and Griffith 2019, Maher and Lott 2000). Many birds are recognizable for flamboyant plumage (Møller and Birkhead 1994), courtship displays (Andrew 1961), song (Podos et al. 2004), or even building structures (Borgia 1995), all apparently in the name of attracting and competing for mates. Body size, morphology, age, past breeding experience, territory size and quality, courtship or song quality, timing, and many other factors are likely to play a role in determining which birds successfully reproduce and which do not, but the interplay between them is complex.

Many of the factors impacting a bird's chances of success are measurable traits of the individual birds themselves. Perhaps the most obvious is body size, with larger birds of either sex being more likely to successfully reproduce (Jensen et al. 2004). Larger males may have more mating opportunities, either because they are directly more appealing to potential mates or because they display greater dominance and can secure larger or higher quality

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territories (Weatherhead and Boag 1995, Fiske et al. 1998, Desrosiers et al. 2021). Larger females are likely to be more fecund, capable of producing and supporting larger clutch sizes (Drent and Daan 1980). Larger parents of either sex may also be more capable of providing for offspring. Many morphological features like bright plumage are likely to have less direct benefits, but rather indirectly advertise health or quality (Møller and Birkhead 1994). Although early mortality is high for many songbird species, many individuals will participate in multiple breeding seasons in their lifetime (and, for many species, multiple clutches within a single breeding season) and are likely to gain useful experience from each attempt. Older or more experienced birds have been shown to be better at attracting or competing for mates, defending territories, or successfully protecting and providing for offspring (Pyle et al. 1991, Blas et al. 2009, Lv et al. 2016, Lifjeld et al. 2022). Male birds may additionally advertise their quality or experience through song or courtship displays, with more elaborate displays or expansive repertoires making for more attractive mates (Nowicki and Searcy 2005, Pfaff et al. 2007, Robinson and Creanza 2019). Courtship traits, being very costly in terms of energy or time spent, may be so-called honest signals of body condition and quality, such that low quality males are not capable of misrepresenting themselves.

Other factors impacting mating success are not properties of an individual bird, but rather of the territory or circumstance in which they breed. Many birds compete fiercely over territories (Hinde 1956, Niederhauser et al. 2021), and individuals that can secure the largest or best territories are likely to be more capable of providing food for offspring or protecting them from predation (Catchpole 1986, Flockhart et al. 2016, Poorboy et al. 2018). Another, subtler factor may be timing—the early bird may get the worm, and similarly, the earliest birds to begin attracting a mate may achieve some advantage over the laggards by maximizing mating opportunities or raising more clutches within a single breeding season (Verhulst and Nilsson 2008). However, synchronizing breeding with food availability and the intensity of competition may also be important, such that sometimes delaying reproduction may be a fruitful strategy as well (Sutton and Freeman 2023).

Studies of these factors and many others have advanced biologists' understanding of the reproductive strategies and fates of birds, but the interplay between factors is complicated. Many factors influencing mating success correlate—the largest males may be the most experienced and have the largest territories—making dissecting which factors matter when a non-trivial challenge. When birds advertise their quality, it is not clear exactly what information is being advertised. Which factors are about directly advertising quality, and which are more indirect and impact success through competition for territories or breeding opportunities? Many bird species also engage in extensive extra-parental couplings, such that there are multiple mating strategies in play at once—potentially favoring different characteristics for success (Brouwer and Griffith 2019). Most importantly, variation across taxa and geography means that some factors and strategies may not be in play at all times, making studies across different taxa and across different environments important to understanding the costs and benefits of different strategies.

To that end, in this study, we investigated an urban population of the Northern Mockingbird (*Mimus polyglottos*), a common but understudied North American songbird. Although mockingbirds appear drab, they stand out to the ear for the nearly unrivaled complexity of their songs, which often incorporate elements lifted from the songs of other bird species. Male mockingbirds are fiercely territorial and sing and employ fluttering, wing-flashing displays early in the breeding season when territories are being established and mate choices being made (Logan 1983, Merritt 1985, Derrickson 1987, 1988). Mockingbirds are socially monogamous, but likely to engage in extra pair fertilizations, like many other songbirds (Locklear 2016, Brouwer and Griffith 2019).

In this study, we explored the factors affecting the mating success, fecundity, and degree of extra-pair paternity experienced by Northern Mockingbirds living in an urban environment in Houston, Texas. We examined the relationships of mockingbird fitness components to bird size, male song properties, male territory attributes, and timing and demographic characteristics to uncover the criteria that female mockingbirds may use to choose their mates and the factors that most contribute to reproductive success.

METHODS

Study site

The study site comprised a large area of the Rice University campus in Houston, Texas, USA (29°40′ N, 95°20′ W). The site included 68.8 ha (170 acres) of lawns, hedges, and nearly 4,000 trees and contained up to 47 non-overlapping Northern Mockingbird territories. The most common tree was the Virginia live oak, *Quercus virginiana*. We collected the data reported here from 1991 to 1993, although most come from 1993 (DeLoach 1997).

Capture, bleeding, and banding

We caught adult birds with top-entry Potter traps mounted on platforms 1.5 m above ground and baited with red grapes. We were able to trap and handle all birds on 30 territories in 2 wks using eight Potter traps. Each bird received a U.S. Fish and Wildlife Service aluminum band (federal bird banding master personal permit no 22484, scientific collecting permit no. PRT-756809, Texas scientific permit no. SPR-0291-353, and permission from the Rice University Animal Care and Use Committee). We banded each bird with three colored plastic leg bands in a unique sequence, two on one leg and one on the leg with the aluminum band. We also collected 200 µL of blood for genetic analyses. At 8 d old, we weighed, color banded, and collected 200 µL of blood from nestlings.

We measured mating success only for male birds, which can be identified—whether they ultimately succeed in finding a mate or not—by the singing they do while establishing territories early in the season. Female birds that did not find mates were not identified in our study. For other, downstream fitness components, like total offspring produced, offspring survival, and parentage (due to extra-pair parentage or egg dumping), we were able to track both males and females.

Morphological measures and sex determination

We measured the right-wing chord and mass of each bird (Pyle 1997). In 1993, we also measured the left-wing chord and both tarsus lengths. We also categorized the amount of visible body fat in the furcular (wishbone) depression, as well as abdominal fat (Rogers 1991).

After brooding had begun, we distinguished male and female adult birds using the presence of a brood patch. For birds we had banded earlier, we also used behavioral observations to identify sex—only males establish new territories early and sing regularly. Territorial defense is primarily within sex, so a bird attacking a known female is also likely to be a female. In addition, only females incubate eggs and brood nestlings (Breitwisch 1988, Breitwisch et al. 1989).

Territory characteristics

We defined a mockingbird territory as the area defended by one mockingbird against others of the same sex (Farnsworth et al. 2020). As mockingbird breeding territories are first established and subsequently defended by males (Laskey 1935, Logan and Rulli 1981), we identified those male territories by noting their singing and perching locations during the breeding season. We checked each territory every day from mid-February through mid-August, except on rainy days, when the birds took shelter and did not sing. Each day, we observed each territory for 10 min and plotted on a detailed map of the study area exactly where each bird was sighted during that observation period. We then used the minimum convex polygon (MCP) method for estimating territory boundaries and area (Worton 1987). We chose the MCP method because mockingbirds defend unconstrained, three-dimensional territories, and this method creates inclusive boundaries that are not constrained by geographical obstacles, as are mammals' territories (DeLoach 1997).

Hedges or bushes are crucial for fledgling survival and are thus a key variable of territory quality (Joern and Jackson 1983, Means and Goertz 1983, DeLoach 1997). In 1993, we measured the volume and linear feet of all hedges (primarily *Ligustrum* spp.) for all mockingbird territories.

Song characteristics

In early 1993, we recorded up to three song samples each from 29 males using normal bias audio cassettes, a Marantz PMD221 recorder, and a Sennheiser ME88 spot shotgun microphone. Recording sessions ended when the male stopped singing, when he left the area, when background noise overpowered the singer, or when he had sung at least 100 distinct continuous songs. The recordings we used all came from the pre-egg laying stage (Derrickson 1987).

We used a Spectral Innovations MacDSP KNI Signal Processor board in a Mac II computer and Spectral Innovations MacDSP Analysis Software V.1.8beta to digitize and view real time sonagraphs of mockingbird song. Samples were trimmed down to 50 contiguous songs to better compare between birds that sang for different lengths of time. We had at least 50 songs for each bird to analyze.

We scored each sample sonogram for measures of song quality (Kroodsma and Verner 1978, d'Agincourt and Falls 1983, Logan 1983, Merritt 1985, Derrickson 1988) as follows. We counted the number of bouts (sets of repeated identical songs) within each sample and the number of songs (a single expression of a distinct, acoustically separate vocal motif) per bout. We also scored each sample's versatility, including song versatility (number of song types per 50 contiguous songs), transition versatility (number of transitions between song types per 50 contiguous songs), and total versatility (product of song and transition versatility).

Additionally, on each daily observation, we noted whether each male was singing. We then calculated the total number of days singing over total days observed during the breeding season. More details are available in DeLoach (1997).

Genetic relatedness, paternity and maternity assessment

To determine parentage, we used two DNA microsatellites developed for this study (Hughes and Moralez Deloach 1997), MpAAT26 (heterozygosity 0.92, 19 alleles), and MpAAT95 (heterozygosity 0.94, 13 alleles). We extracted DNA, PCR amplified, and sequenced the MpAAT26 and MpAAT95 loci for each sample (Hughes and Queller 1993, Queller et al. 1993).

If a nestling matched the female parent at both loci but not the male, we attributed it to an extra-pair mating. If a nestling matched the male parent at both loci but not the female, we assumed another female had laid an egg in the nest (egg dumping). All nestlings were able to be matched to at least one parent.

Statistical methods

We performed statistics in R version 4.1.2 (R CoreTeam 2013). Before analyzing the data, we converted dates of first sighting, singing, nests, and eggs into days after 1 January to simplify comparisons across years. Some individual birds were missing values for certain traits. To include these birds in our analysis, we imputed missing traits by replacing them with the mean value of the trait. We imputed traits separately for males and females because we expected them to differ systematically in many characteristics. Using the median instead of the mean for imputation did not change our results. Using more complex multivariate imputation by chained equations or imputation with PCA did not change our results.

We had territory measures and song measures only for birds observed in 1993. For this reason, we performed the bulk of the analyses using data from 1993 only. When possible, we test conclusions derived from the 1993 data on the full data set, including data from 1993 and 1992. In these analyses, individual birds may appear multiple times.

To compare the traits of mated and unmated males, we used permutation multivariate analysis of variance or PERMANOVA (Anderson 2014) on 13 male traits. We used Euclidean distances and performed the analysis using the "adonis2" function in the vegan package (Dixon 2003). Because PERMANOVAs are sensitive to groups that have different dispersions (a measure of multivariate variance), we ruled out different dispersions using the "betadisper" function. Dispersion tests and PERMANOVA were performed with 10,000 permutations. To visualize differences in male traits, we performed principal components analysis (PCA) on the 13 traits.

To determine which traits best predicted whether a male mated or not, we used logistic regression (LR). Some sets of variables, such as song traits, represented similar traits and were highly correlated. To avoid problems of model overfitting and multicollinearity, we combined sets of correlated variables into compound variables using principal components. Our compound variable "territory size" was the first principal component of the correlated variables of territory area, hedge linear area, and hedge volume. Our compound variable "song quality" was the first principal component of the correlated variables of mean number of songs per bout, the proportion of days spent singing, song versatility, transition versatility, and total versatility. Our compound variable "timing of key events" was the first principal component of the correlated variables of dates of first sighting and of first singing. We fit all possible models using these three compound principal component traits, mass, fat scores, wing chord length, and categorical variables for whether males had mated in the previous year or were bigamists. To differentiate between prior mating experience and mating with the same female across years, we also included a categorical variable for whether males mated with the same female. In each model, ID was included as a random effect. To compare between different models, we used AICc and selected the best predictors from models with the lowest AICc values (Burnham and Anderson 2004). We considered models within 2 AICc units as equivalent for the purposes of model selection. To check for multicollinearity, we calculated variance inflation factors for final models using the "performance" package (Lüdecke et al. 2021). We tested our 1993 results for robustness by also fitting the same top logistic regression model with data from 1992 and 1993.

To identify male traits associated with fitness, we fit generalized linear models (GLMs) using the lme4 package (Bates et al. 2015) and linear models in R. As fitness measures, we used the total number of 24-d-old offspring and offspring survival from day 8 to 24. Because these fitness data involve offspring counts of the total number of 24-d offspring, we used a Poisson link function to account for the non-normality of the counts. For the proportion of chicks that survived from day 8 to 24, we used linear models. We included the same variables during model selection as for logistic regression, except that the principal component capturing the timing of key events now includes the date of first nests and eggs. To identify top models, we again used model selection with AICc. We tested for robustness across years by fitting the top model to the years 1992 and 1993 with band ID as a random effect.

We fit similar GLM and linear models using the same factors (as applicable) to understand female traits associated with female fitness. Female fitness was also measured as the total number of 24-d-old offspring and offspring survival from day 8 to 24. Because we did not record female song, we did not include a song quality compound variable, and the timing of key events principal component for females did not include the date of first singing. We initially fit models of female fitness using only birds from 1993 for which we had measurements of territory size. Because these models indicated that territory size was not associated with female fitness, we thereafter dropped territory size from the models so we could include birds from 1992 lacking territory size data. To understand the role of extra-pair copulation in female fitness, we included the number of extra-pair offspring that did not match males as an additional predictor variable. Overall, these models of female fitness included mass, the timing of key events, prior mating experience, and the number of offspring that did not match males, as well as a random effect of band ID for females that were present in 1992 and 1993.

RESULTS

Population, body size, song, and territory characteristics

The mockingbird population that we studied consisted of 36 males and 34 females in 1992 and 34 males and 25 females in 1993. All of the studied females obtained mates and made at least one breeding attempt in both years and produced between 0 and 6 young that survived to independence across all their nesting attempts. Although all studied males successfully established territories, only 81.6% and 70.6% of the males obtained mates in 1992 and 1993, respectively.

Male mass averaged 51.94 ± 2.94 g, $N = 32$ in 1993. Wing chord lengths averaged 113 ± 2.74 mm, $N = 33$ in 1993. Males had an average fat score of 0.59 ± 0.68, where fat score is scored both on the breastbone and the abdomen, in 1993 (Rogers 1991).

We measured five male song attributes in 1993. Males sang during the monitoring period on about a third of all days (0.32 ± 0.20, $N = 34$ d). Males averaged 3.4 ± 0.89 $N = 27$ songs per bout. Average song versatility was 0.22 ± 0.05, $N = 27$. Average transition versatility was 0.22 ± 0.05, $N = 27$. Average total versatility was 0.05 ± 0.02, $N = 27$.

Male territories averaged 1.39 ± SD 0.66 ha, $N = 30$ in 1993. Those territories contained 150.57 ± SD 125.69 LM of hedges, $N = 30$ in 1993.

Heavier and more experienced males were more likely to successfully find mates

We looked for male traits that predicted whether males would find mates or remain unmated. Females had distinct preferences, favoring larger and more experienced males. Mated ($N = 23$) and unmated ($N = 11$) males from 1993 tended to form distinct clusters across 13 continuous traits (PERMANOVA; R2 = 0.07, $p = 0.017$; Fig. 1A).

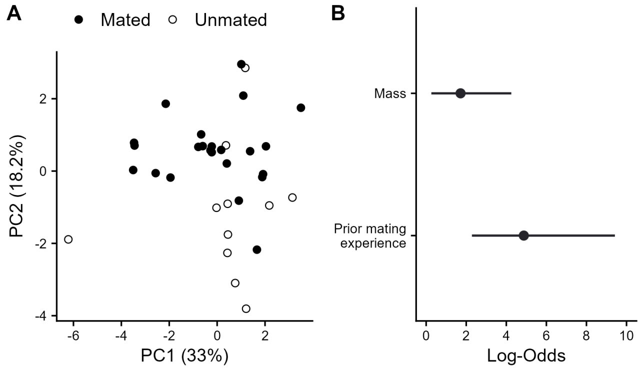
To identify specific male traits associated with male mating status, we used logistic regression models and selected important traits based on AICc (Append. 1). These models showed that mated males tended to have prior mating experience (LR; log-odds = 4.87; 95% CI = [2.28, 9.42]) and weighed more (LR; log-odds = 1.72; 95% CI = [0.26, 4.25]; Fig. 1B). Prior mating experience with the same female did not affect mating success.

We did not find that territory or song quality affected male mating status. To test whether these results were robust across years, we fit a mixed-effects logistic regression (MEL) model for males that were found in 1992 (31 mated and five unmated) and 1993. We again found that mated males weighed more (MEL; log-odds = 9.04; 95% CI = [-0.40, 18.49]) and had prior mating experience (MEL; log-odds = 15.05; 95% CI = [-4.46, 34.57]), although these estimated effects were more uncertain (Append. 1).

Males that acquired territories earlier had more surviving offspring

We measured the fitness of males that successfully found mates as the total number of their offspring that survived to day 24 (when chicks become independent) and as the proportion of chicks that survived from day 8 (when chicks were banded) until day 24. These fitness measures did not vary across the years 1992 and 1993 (GLMs; all 95% confidence intervals included 0). Because we lacked some male trait measures for 1992, we focused on males in 1993 to identify traits associated with male fitness.

Fig. 1. Mass and prior mating experience differentiate mated and unmated males - (A) First and second principal components of 13 male traits colored according to male mating status. (B) Estimated log-odd effects (and 95% confidence intervals) of mass and prior mating experience on mating status from the top logistic regression model. Because neither interval includes zero, both higher mass and prior mating experience can be interpreted as having had a positive effect on mating success. This figure represents only data collected in 1993, for which we had multiple metrics capturing different elements of bird size, timing, territory quality, song quality, etc. The loadings for PC1 and PC2 are complex (see Append. 3), but the data reveal some separation between the traits of mated vs. unmated males.



Males with earlier key breeding dates had higher fitness (Fig. 2). We calculated a compound measure of the timing of key events using PCs. This timing variable captures nesting dates from earlier to later (note positive loading on PC1). We found that PC1 was the best predictor of male fitness, whereas males breeding later had fewer total 24-d offspring (GLM; estimate = -0.30, 95% CI = [-0.57, -0.07]). This pattern of the timing of key dates being associated with male fitness was also found when we included data from 1992 (Append. 2).

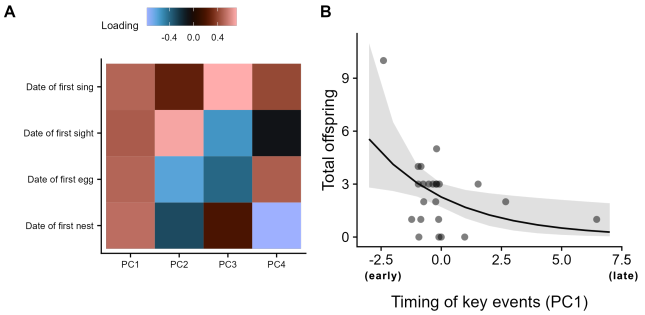
We did not find a relationship between any male traits (including mass) and the survival of offspring from day 8 to day 24.

Heavier females and females that nested earlier had more surviving offspring

We used the same fitness variables that we used for males to investigate female fitness (*N* = 58). As with male fitness, we did not find that female fitness varied from year to year (GLMs).

To capture the timing of key breeding dates in females, we again used PCA. In contrast to males, the female PC1 captured the timing of key events from late to early (the x-axis is flipped because of negative loadings; Fig. 3A). Similar to males, females produced more offspring when they had earlier key dates (GLMM; estimate = 0.17; 95% CI = [0.01, 0.34]). This top model that included only the timing of key events fit best according to AICc, but models that also included mass or the number of extra-pair offspring (both having a positive effect on total offspring) were within 2 AICc units of the top model. These models represent weak evidence of an effect. Earlier timing of key events weakly reduced offspring survival from day 8 to day 24 (LMM; estimate = -0.06; 95% CI = [-0.12, 0.00]), but this model was within 1 AICc unit of the null model fit to only the intercept.

Fig. 2. Earlier breeding males produce more total offspring—the males that produce the most total offspring breed early. (A) Loadings for principal components of dates of key breeding events. PC1 explains 75% of the variance and measures the timing of events from early to late. The timing variables are positively correlated only for PC1, suggesting the other PCs are less useful. (B) Effect of timing of key events (PC1 in A) on the total number of 24-d offspring from a generalized linear model. This figure represents only data collected in 1993, for which we had metrics of bird size, timing, territory quality, and song quality.



Extra-pair parentage accounts for only 3.1% of young

Over the 3 yr of the study, only 10 of 324 hatchlings (3.09%, 6.9% of the broods) had microsatellite alleles that did not match the resident male, indicating a low rate of extra-pair fertilization. In 1991, four offspring (4.7%) in two broods (7.1% of broods) did not match the resident female—both such instances were fathered by the resident male ("egg-dumping"). Cumulatively, the percentage of intraspecific brood parasitism over 3 yr was only 1.2% of offspring in 1.5% of the broods.

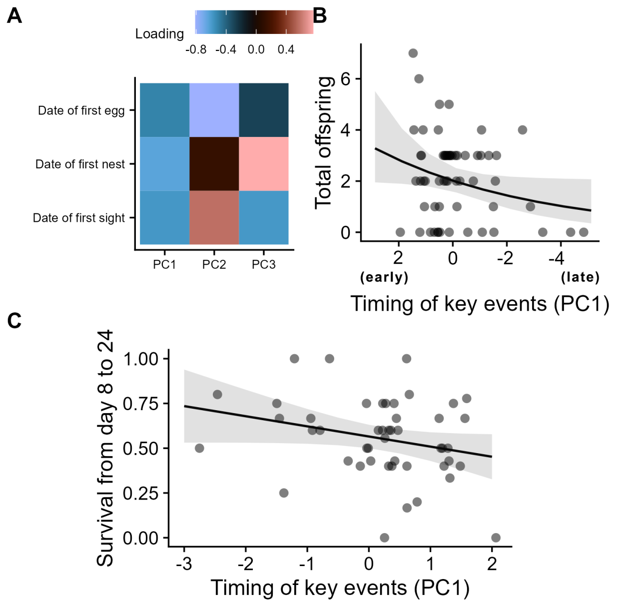
DISCUSSION

In this study, we sought to determine factors that impact mating success, fecundity, offspring survival, and rates of extra-pair parentage in an urban population of the Northern Mockingbird, *Mimus polyglottos*. We investigated measures of bird size, territory size, territory quality, song quality, and the timing of key reproductive events.

Our results suggest that the best predictors of whether or not a male mockingbird would successfully attract a mate were body mass and past experience (Fig. 1). Female mockingbirds may prefer mates with larger body size as a sign of fitness and good health (Hegner and Wingfield 1986, Barclay 1988), although interestingly we did not detect a relationship between male body size and total offspring produced. Larger body size might potentially also indirectly benefit a male's mating success by making it easier to outcompete other males for the choicest territories.

Males with previous mating experience (here defined as males observed successfully mating in earlier years reappearing in surveys of the same population in later years) were more likely to

Fig. 3. Earlier breeding females produce more total offspring but may experience a trade-off between fecundity and offspring survival. Timing of key events affects total offspring and offspring survival differently. (A) Loadings for principal components of dates of key breeding events. PC1 explains 63% of the variance of total offspring produced and measures timing from early to late (note that loadings for PC1 are negative). The timing variables are positively correlated only for PC1, suggesting the other PCs are less useful. (B) Effect of timing of key events (PC1 in A) on the total number of 24-d offspring from a generalized linear model. (C) Effect of timing of key events on survival of offspring from day 8 to day 24.



successfully attract a mate. The effect of past mating success was independent of whether or not the males in question paired with the same mate with which they had paired in previous years, suggesting that it is not the result of compatibility with particular mates as has been observed in some bird species (Bateson 1983). Given the extensive biparental care in *M. polyglottos* and similar birds, it is plausible that older, more experienced males may be better able to forage and care for their offspring (Lack 1968, Curio 1983, Clutton-Brock 1988). Additionally, some studies suggest that male mockingbirds accumulate increasingly broad repertoires of songs over their lives, such that females could select experienced mates based on their songs (Gammon 2020, Gammon and Tovsky 2021).

Surprisingly, however, we did not detect any impact of any metric of song quality on mating success. Northern mockingbirds are famous for their aptitude for mimicry and the extensive repertoire of songs they sing (Farnsworth et al. 2020). Previously, the elaborateness of mockingbird song has been interpreted as the audible equivalent of a peacock's tail—a gaudy, costly signal intended to advertise a male's quality to prospective mates—and so the absence of any detectable effect on mating success in our experiment was unexpected. It is possible that reproductive success may be impacted by song characteristics not captured by the limited sampling and metrics in our study. Our song samples were brief enough that it is likely we only captured a small part of each male's repertoire, and thus may not have captured the full song behavior of each male. In addition, we only collected song data early in the mating season, but evidence exists that male song quality may change over the course of a season, especially later in a season when females are more exhausted and may only be swayed by particularly impressive performances (Logan and Donaghey 1997, Gammon 2014)—perhaps a study over a longer period would have detected significant impacts of song quality on reproductive success. Alternatively, our focus on measures of song versatility may not fully capture what makes a male's song attractive or unattractive to potential mates. Tellingly, we did not find much variation between males in our chosen song quality metrics. It may be that other metrics like repertoire size, morphing, stereotypy, or measures of mimicry might offer a more complete picture in a future study (Searcy 1992, Price 2013, Benedict and Najar 2019, Roeske et al. 2021).

We also did not detect any relationship between territory size or quality and mating success. In judging territory quality, we focused on the presence of hedges that shelter fledgling mockingbirds from predators, due to the high mortality suffered by birds during this stage of their lives, but we found no evidence that female mockingbirds prefer mates with either larger territories or territories with more abundant hedges. As with our metrics of song quality, it is also possible that male territories did differ in some important way that was not captured by our metrics of territory quality.

Another possible explanation for the lack of a significant effect of song or territory quality on mating success may relate to the urban environment in which we performed our study. Mockingbirds readily colonize and thrive in urban environments (Chamberlain et al. 2009, Stracey and Robinson 2012*a*), but it is likely that urban environments impose different selective pressures on birds than they would have experienced throughout the majority of their evolutionary history (Derryberry and Luo 2023). For example, city background noise is likely to influence the evolution of bird song—one study found that urban mockingbirds evolved to sing at higher pitches, presumably the better to stand against the low-frequency artificial noise of urban traffic (Walters et al. 2019). Urban environments are also likely to differ in the density and identity of nest predators (Stracey and Robinson 2012*b*). It may be that some aspect of urban life impacts the criteria by which female mockingbirds choose their mates. Future studies incorporating multiple mockingbird populations across different environments could explore this possibility.

Males that established territories earlier in the season had significantly more offspring survive to fledging (Fig. 2). Perhaps the early bird gets the (territory with the best) worms, although as before, we did not detect any effect of territory quality on offspring survival. We also did not detect an effect of male size or past experience on offspring survival.

Heavier females and females that nested earlier in the season had significantly more surviving offspring (Fig. 3). Heavier females likely can provision eggs more generously—or produce more eggs

—than lighter females, accounting for the significant effect of body size we detected in females but not males. We also found weak evidence of a possible trade-off between the number of offspring a female produced and the likelihood of those offspring surviving to fledging, as might be expected if a female is provisioning limited resources between her offspring.

In addition to mating success, fecundity, and offspring survival, we also measured the parentage of all offspring. It is now well known that extra-pair paternity and intraspecific nest parasitism likely strongly impact the fitness of many socially monogamous bird species. Rates of extra-pair paternity vary considerably across bird species, but are often high in passerines like *M. polyglottos*. Surprisingly, we detected only 3.1% (10 of 324 total) of all hatchlings not fathered by their nest's resident male—a notably lower rate than typically observed in mockingbirds and other socially monogamous birds (Ryder et al. 2012, Locklear 2016, Brouwer and Griffith 2019). We also detected two instances of conspecific brood parasitism resulting in hatchlings not mothered by the resident female (Lyon and Eadie 2008). In all cases, the mismatched offspring were fathered by the resident male, suggesting either that he had changed mates or that he had allowed a second mate to deposit eggs in his nest while his social mate was away, rather than egg-dumping by completely unrelated females.

Overall, our results suggest a key role of experience, timing, and body size in the reproductive fitness of *M. polyglottos*. We did not find the expected impact of male mockingbirds' elaborate songs on their ability to attract mates, nor an impact of territory size or quality. We also noted a surprisingly low degree of extra-pair paternity relative to other socially monogamous songbirds. Our results underscore the complexity of factors involved in mating decisions, and the need to study birds of different taxa and in different contexts to construct a full picture.

Author Contributions:

DMDL, CRH, DCQ, and JES conceived of the study and guided the field work. DMDL did all the field work, the initial statistical analyses, and wrote the draft that was her dissertation as part of her PhD. CRH developed the DNA microsatellite markers and did the parentage lab work and analyses. TJS did the statistical analyses presented here. JES, TJS, and TJL wrote this paper, which all approved.

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Data Availability:

All data and code used in this project can be publicly accessed on Gitlab. Project ID: 41826377, https://gitlab.com/treyjscott/mockingbirds

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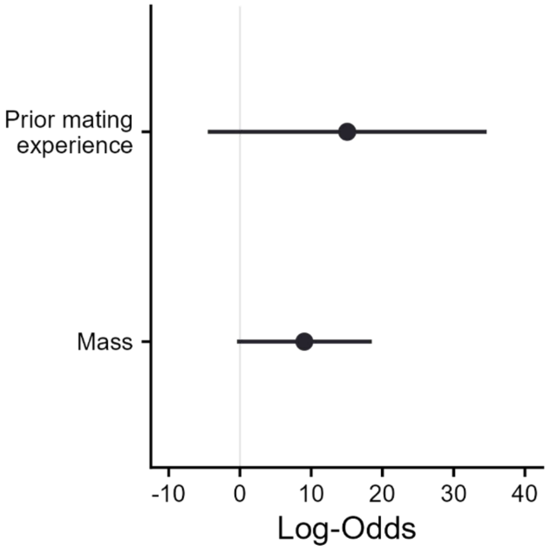
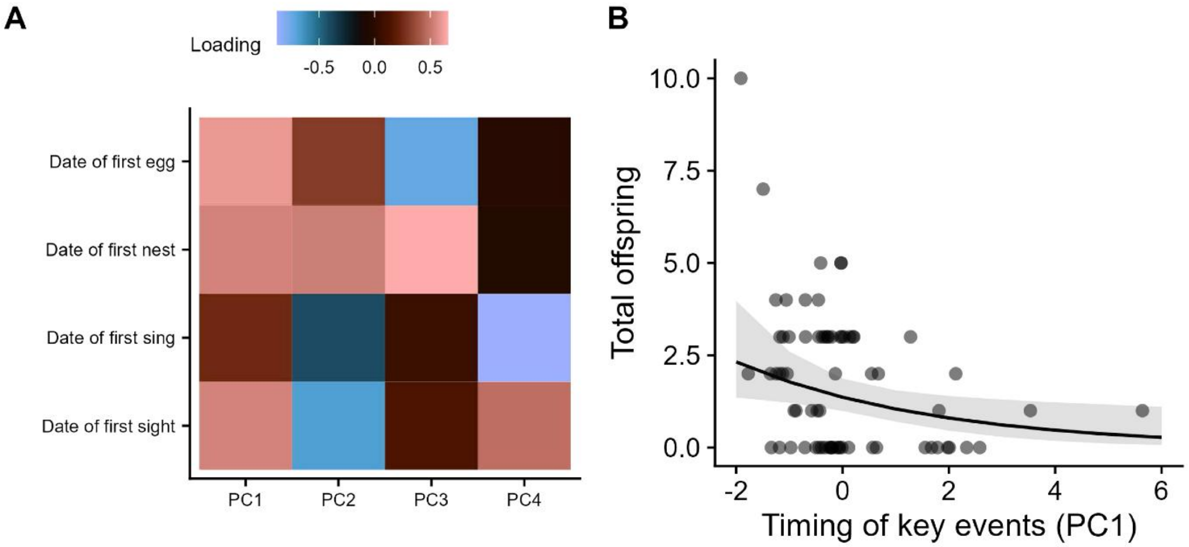
Appendix 1. Mass and prior mating experience differentiate mated and unmated males.

Estimated effects (and 95% CI) of prior mating experience and mass on male mating success from mixed-effect logistic regression. This figure corresponds to main paper Figure 1B, but incorporates data from both 1993 and 1992.



Appendix 2. Earlier breeding males produce more total offspring.

(A) Loadings for principal components of dates of key breeding events. PC1 explains 75% of the variance of total offspring produced. The timing variables are positively correlated only for PC1, suggesting the other PCs are less useful. (B) Effect of timing of key events (PC1 in A) on the total number of 24-day offspring from a generalized linear model. This figure corresponds to main paper Figure 2, but incorporates data from both 1993 and 1992.



Appendix 3. Loadings for principal components of morphological, song, and territory traits.