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Authors

Grunst, Melissa L
Rotenberry, John T
Grunst, Andrea S

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Elevating perceived predation risk modifies the relationship between parental effort and song complexity in the song sparrow *Melospiza melodia*

Melissa L. Grunst, John T. Rotenberry and Andrea S. Grunst

M. L. Grunst (mgrun002@ucr.edu) and A. S. Grunst, Dept of Biology, Univ. of California, Riverside, CA 92521, USA, and Dept of Biology, Indiana State Univ., Terre Haute, IN 47809, USA. – J. T. Rotenberry, College of Biological Sciences, Univ. of Minnesota, Saint Paul, MN 55108, USA.

Adult-directed predation risk elevates costs of parental care, and may modify relationships between sexually selected ornaments and parental effort by accentuating the tradeoff between survival and parental investment. We assessed multiple hypotheses regarding the relationship between maternal effort, paternal effort, and the sexually selected trait of male song complexity in the song sparrow *Melospiza melodia*. Further, we explored whether experimentally elevating perceived adult-directed predation risk near nests affected these relationships. We quantified two dimensions of song complexity: song repertoire size and residual syllable number (the relative number of syllables for a given song repertoire size). Under elevated perceived predation risk, but not in the absence of the predator stimuli, females mated to males with higher residual syllable number displayed higher nestling provisioning rates and performed a greater proportion of nestling provisioning trips. In other words, elevating perceived predation risk induced a pattern of maternal investment consistent with differential allocation. In contrast, under elevated perceived predation risk, only, females performed a lesser proportion of provisioning trips when mated to males with large song repertoire sizes. Further, consistent with the good parent hypothesis, males with large song repertoire sizes displayed lower latencies to return to the nest, independent of the predator stimuli. Results suggest that residual syllable number may reflect some aspect of male genetic quality, such that females are more willing to maintain maternal effort while facing heightened predation risk. On the other hand, females may gain paternal benefits when mated to males with large song repertoires. Our study supports the hypothesis that increased costs of parental care associated with predation risk may induce relationships between sexually selected traits and parental behavior, which may increase the strength of sexual selection. Additionally, results suggest that different aspects of song complexity may fulfill non-equivalent signaling roles.

Theoretical and empirical work supports variable relationships between the elaboration of male sexual displays and both paternal and maternal effort. With respect to paternal effort, the good parent hypothesis (Hoelzer 1989) proposes that elaborately ornamented males provide superior paternal services (Greig-Smith 1982, Hill 1991, Møller and Thornhill 1998, Buchanan and Catchpole 2000), whereas the tradeoff hypothesis proposes that males with elaborate sexual displays invest in mating effort over paternal care (Burley 1988, Møller and Thornhill 1998, Magrath and Komdeur 2003, Mitchell et al. 2007). With respect to maternal effort, the differential allocation hypothesis proposes that females increase maternal effort when paired with elaborately ornamented males to capitalize on offspring genetic quality (Burley 1986, 1988, Harris and Uller 2009), whereas the reproductive compensation hypothesis suggests that females increase maternal effort when paired to less ornamented males to ameliorate negative repercussions on offspring fitness (Bluhm and Gowaty 2004, Gowaty et al. 2007). Harris and Uller (2009) proposed that differential allocation should be more common than

reproductive compensation, and a recent meta-analysis in birds corroborated this conclusion (Horváthová et al. 2012). However, empirical studies support both hypotheses (Ratikainen and Kokko 2010 for review, Giraudeau et al. 2010, Garcia-Fernandez et al. 2013), as well as null relationships (Norris 1990, Lozano and Lemon 1996, Darolová et al. 2012).

Differing empirical relationships between the elaboration of sexually selected traits and paternal and maternal effort may, in part, derive from variation in the costs of parental care. Predation risk has potent effects on parental behavior, especially in birds (Ghalambor and Martin 2001, Peluc et al. 2008, Lima 2009, Tilgar et al. 2011). Adult-directed predation risk increases costs of parental care, accentuates the tradeoff between survival and reproduction (Ghalambor and Martin 2001), and may thus enhance or obscure relationships between ornaments and parental effort (Harris and Uller 2009). Further, considering maternal and paternal behavior in tandem is of paramount importance, since the costs and benefits of the parental behaviors of mated individuals are inter-dependent. For instance, if less ornamented males

provide poorer paternal services (good parent hypothesis), one might also expect reproductive compensation, since females mated with less ornamented males might up-regulate maternal effort to maintain offspring fitness.

We studied the relationship between song complexity and parental behavior in the song sparrow *Melospiza melodia*. Song complexity in the song sparrow is a well-studied sexually selected trait. Past studies report song repertoire sizes ranging from approximately 5 to 12 song types, and song repertoire size has been positively correlated with male fitness metrics including female choice (Searcy 1984, Hiebert et al. 1989, Reid et al. 2004), survival probability (Reid et al. 2005b), immunocompetence (Reid et al. 2005a), territorial defense (Reid et al. 2005b), number of offspring and grand-offspring recruited to future generations (Hiebert et al. 1989, Reid et al. 2005b) and offspring sex ratio at fledging (Potvin and MacDougall-Shackleton 2010). In addition to number of song types (song repertoire size), syllable repertoire size, or the number of distinct notes in a male's repertoire, may contribute additional information about male quality (MacDougall-Shackleton et al. 2009a, b). Male song sparrows do not modify their vocal phenotype later in life since song learning is close-ended in this species (Nordby et al. 2002). Thus, song complexity in the song sparrow is distinct from sexually selected ornaments that may plastically change to reflect current condition or energetic state. However, the developmental stress hypothesis proposes that only males of high phenotypic or genetic quality are able to afford costs of developing complex song early in life (e.g. producing neural structures to allow song learning), which promotes the reliability of this sexual signal (Nowicki et al. 1998, Spencer et al. 2003).

Our study had two primary objectives. First, we assessed whether song complexity in male song sparrows correlates with paternal or maternal effort under baseline conditions in a fashion consistent with one of the hypotheses presented above. Secondly, we evaluated whether increased costs of parental care associated with elevated predation risk alter correlations between paternal and maternal behavior and song complexity. To achieve these objectives, we measured parental behavior in the absence of any stimuli, and in the context of experimentally simulated adult-directed predation risk. To our knowledge, this is the first study to examine whether elevating perceived predation risk modifies relationships between song complexity and parental care.

We evaluated specific predictions regarding how elevating perceived predation risk might affect the paternal behavior of male song sparrows differing in song complexity, given operation of either good parent or tradeoff processes. Given a good parent signaling function of song, we predicted that males with complex songs display higher paternal effort (Table 1a). Further, we predicted that predation risk might accentuate the positive relationship between song complexity and paternal effort by elevating costs of paternal care, and motivating greater decreases in paternal effort on the part of males with less complex songs (Table 1b). In contrast, males with complex songs might display lower paternal effort (Table 1d), especially under elevated predation risk (Table 1e), if these male invest in mating effort over paternal care, as proposed by the tradeoff hypothesis. However, elevating perceived predation pressure could also dampen positive or negative correlations between sexual ornamenta-

Table 1. Hypotheses and predictions regarding the direction of the correlation between male song complexity and parental effort, including how adult-directed predation risk may affect these relationships.

Hypothesis	Baseline conditions	Elevated predation risk
Paternal behavior		
a. Good parent	+	+
b. Good parent induced	0	+
c. Good parent dampened	+	0
d. Tradeoff	–	–
e. Tradeoff induced	0	–
f. Tradeoff dampened	–	0
Maternal behavior		
g. Differential allocation	+	+
h. Differential allocation induced	0	+
i. Differential allocation dampened	+	0
j. Reproductive compensation dampened	–	0

tion and paternal effort, if all males adopt relatively low paternal effort when costs of parental care are high (Table 1c, f).

Similarly, we made predictions regarding how elevating perceived predation risk might affect the maternal behavior of females mated to males differing in song complexity, given either differential allocation or reproductive compensation. Given differential allocation, we predicted that females mated to males with complex songs display higher maternal effort (Table 1g). Further, we predicted that perceived predation risk might accentuate the positive correlation between song complexity and maternal effort, by inducing females mated to males with less complex songs to greatly reduce maternal effort (Table 1h). Conversely, a recent model by Harris and Uller (2009) suggests that reproductive compensation may only be observed when increases in maternal effort have relatively small effects on offspring fitness. Given a direct threat to adult survival, the benefit of increasing parental effort to elevate the fitness of lower quality nestlings would be reduced relative to survival costs. Thus, in this case, we predicted that reproductive compensation would be less likely to occur under elevated adult-directed predation risk than in the absence of an acute predation threat (Table 1j).

Finally, we measured two dimensions of male song complexity, song repertoire size and residual syllable number (Fig. 1 and 2; see Methods). Residual syllable number is uncorrelated to song repertoire size, indicates whether a male has a large or small number of syllables given his song repertoire size, and reflects the complexity of a male's song types (Fig. 2). We were interested in whether these two dimensions of song complexity might convey distinct information about male quality, as proposed by the multiple messages hypothesis (Møller and Pomiankowski 1993, Johnstone 1996), and thus correlate differently with paternal and maternal behavior and responses to elevated predation risk.

Methods

Study species and site

We studied song sparrows breeding along Convict and McGee creeks, on the eastern slope of the Sierra Nevada
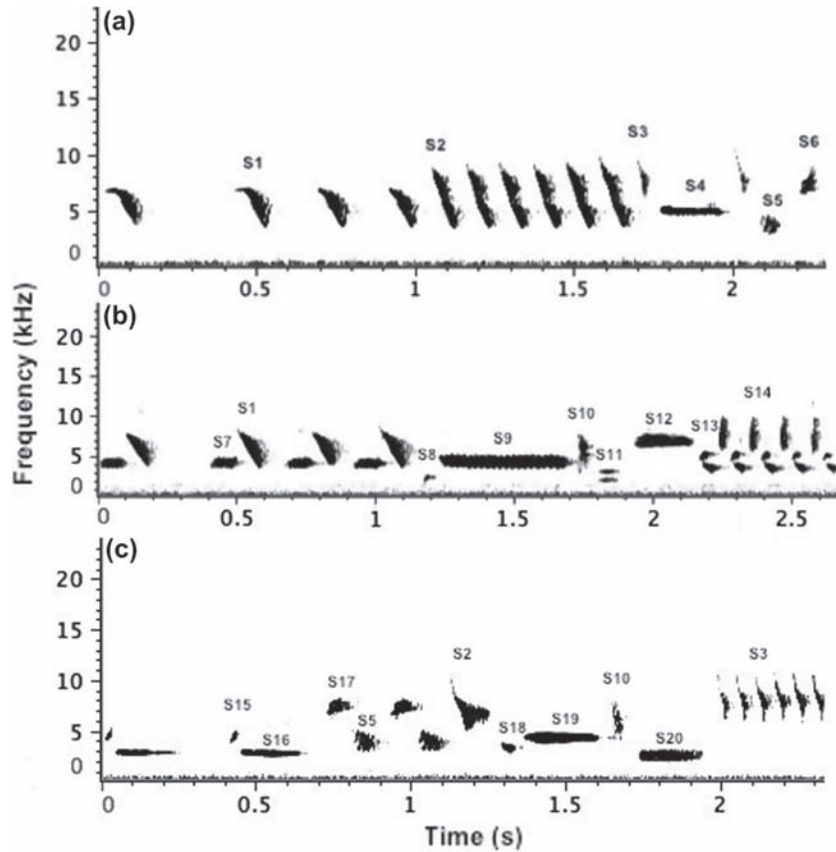
Figure 1. Sonograms of three song types (a–c) of a male song sparrow. Distinct song types differ in organization and type of syllables (notes). Different syllables (indicated within each song type) are represented by one or two traces on a sonogram. Syllable diversity was determined by counting the number of distinct syllable types across song types. These three song types contain 20 unique syllables, with some overlap in syllables between songs.

(Mono County, CA). Convict Creek flows through the Univ. of California's Sierra Nevada Aquatic Research Laboratory (SNARL; 37°36′51′N, 118°49′47′W). McGee Creek is located ~ 16 km south of SNARL in the Inyo National Forest (37°33′20′N, 118°47′35′W). We conducted research across three breeding seasons, from early May through early August, 2010–2012. Song sparrows are socially monogamous and exhibit biparental care (Arcese et al. 2002). Females are sole incubators of a 2- to 6-egg clutch, but both males and females provision nestlings (Arcese et al. 2002). Song sparrows in our population fledge multiple clutches per season and re-nest after clutch loss.

Marking focal individuals and locating nests

We identified focal individuals (n = 25 unique males mated to 28 unique females, for which we determined song complexity and conducted predator presentation experiments; n = 47 males for measurements of song complexity) by locating singing males early in the breeding season during the period of territory establishment. We obtained repeated measures for behavioral data on seven males and four females, and single behavioral measurements on all other individuals. Our sample includes three more females than males because some of the males for which we had repeated
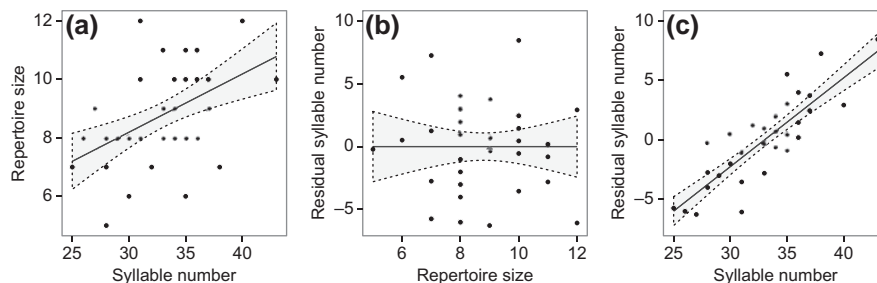

Figure 2. Linear relationships between song repertoire size and syllable diversity (a), residual syllable number and repertoire size (b), and residual syllable number and syllable diversity (c). Shaded regions show 95% confidence intervals.

behavioral measurements were mated to different females in different years of our study. Whenever possible, we target-netted birds using conspecific playback (n = 19 males and 5 females for individuals included in behavioral analyses), but we captured a smaller number of males, and the majority of females at nests during the nestling stage (n = 6 males and 13 females for individuals included in behavioral analyses). We marked individuals with an aluminum band from the United States Geological Survey and an additional combination of three colored leg bands. All males used in our behavioral analyses were banded. We were unable to capture and band 10 females. However, since all males were banded, unbanded females did not pose a problem in identifying sex when determining parental behavior. We located nests using a combination of systematic searching and behavioral observation. We monitored nests via nest checks every 2 to 3 d until the nest was depredated or fledged.

Characterizing song complexity

We recorded male song using Canon ZR800 series camcorders, simultaneously used to record baseline nesting behavior. The singing male was not visible at all time points during recordings. However, in all cases used, we could clearly distinguish the focal individual due to the louder magnitude of songs produced by the male singing near the nest. Neighboring males occasionally intruded onto territories, but we sampled an adequate number of songs to differentiate these cases. This method provides an efficient means of obtaining audio files containing long strings of male vocalizations (up to 124 min recording time). We extracted audio files from mini DV tapes and visualized .wav files via sonograms created in the acoustical analysis program 'Raven Pro' (Cornell Lab of Ornithology), with a sampling rate of 44 100 Hz. Spectrogram parameters gave a frequency resolution of 172 Hz and a temporal resolution of 2.9 ms (Hann window, DFT = 256, overlap = 50%). To sample repertoires, we viewed at least 300 consecutive songs or 450 total songs (Pfaff et al. 2007, MacDougall-Shackleton et al. 2009a) for 44 out of 47 individuals. However, since all song repertoires proved to be entirely sampled after at least 150 songs or fewer, we incorporated three males for which we had recorded 174, 176, and 188 songs. Neither song repertoire size (Linear model (LM): $F_{1,45} = 0.44$, $R^2 = 0.01$, $\beta = 0.002 \pm 0.003$, p = 0.51) nor syllable repertoire size (LM: $F_{1,42} = 0.58$, $R^2 = 0.01$, $\beta = -0.005 \pm 0.007$, p = 0.45) was predicted by the number of songs counted. Song sparrows sing with eventual variety, producing a number of sequential renditions of a single song type before switching to a different song type (Searcy et al. 2014). We determined song types via visual inspection of sonograms, with new song types identified upon song-type switching in strings of vocalizations (Fig. 1). In contrast to different song types, variants of a single song type are often produced in an interspersed fashion within a single consecutive string of songs, are more similar than different song types, and are especially likely to share introductory notes (Searcy et al. 2014). To standardize across males, a single observer (MLG) performed all song complexity determination.

After song repertoire size was established, we determined the total number of different syllable types in each male's repertoire by counting the number of distinct syllables across all song types (Fig. 1). Syllables are represented by one or two traces on a sonogram, and always occur together (Podos et al. 1992, Stewart and MacDougall-Shackleton 2008). We did not determine syllable repertoire size for 3 males because of low-quality recordings that precluded definitive determination of syllable types. We were interested in examining the potential for syllable diversity to convey information beyond that which is signaled by song repertoire size. However, although not entirely redundant, song repertoire size and syllable repertoire size are positively correlated metrics of song complexity (see Results). Thus, to derive a metric that is strongly related to syllable repertoire size, but uncorrelated with song repertoire size, we took the residuals of a regression predicting syllable repertoire size from song repertoire size (Fig. 2). We refer to this metric as 'residual syllable number'. Residual syllable number reflects the relative number of syllables in a male's repertoire for a given song repertoire size, and is related to the relative complexity of a male's song types. In other words, a male with a large song repertoire size but few notes per song type has a low residual syllable number, whereas a male with a small song repertoire size but many notes per song type has a high residual syllable number.

Predator presentation experiment

We experimentally elevated perceived adult-directed predation risk using taxidermic mounts and recordings of sharp-shinned hawks *Accipiter striatus*. House finch *Haemorhous mexicanus* decoys and recordings served as negative controls, and we also recorded baseline behavior in the absence of any stimuli. We obtained recordings of hawk and finch vocalizations from the Bird songs of California, vol. 1 (Keller 2009; Cornell Lab of Ornithology, Macaulay Library). We performed hawk, finch and baseline (no stimuli) recordings of ~ 1.5 h duration (mean: 1.71 ± 0.04 h) between 06:00 and 16:00 Pacific Daylight Time, on day 4 to 9 of the nestling period. To avoid confounding effects of elevated predation risk with time of day or nestling age, we performed all treatments on a single nesting pair on the same day in randomly determined order, with ~ 10 min between treatments. Camcorders were concealed 3 to 6 m from nests. We placed decoys 6 to 10 m from nests, 0.5 to 2 m off the ground (Ghalambor and Martin 2001, Peluc et al. 2008), and projected recordings of vocalizations using a MP3 player placed on the ground below decoys. Hawk and finch decoys were present during the entire duration of the recording period. However, to help prevent habituation, we manually compiled recordings of vocalizations to include an equal proportion of calling versus silence (3 min of vocalizations followed by 3 min of silence). We used the same vocalization recordings for all experiments, but randomly choose one of three different hawk decoys and one of three different finch decoys per pair.

Following the field season, we viewed video-recordings to determine nestling provisioning rates over the entire recording period and the latency of each parent to return to the nest. Latency to return to the nest is a one-time measurement, following the initial disturbance of setting up the video-recorder and, in the case of the predation and negative control treatments, initiating the experimental stimuli.

Latency to return to the nest was negatively correlated to provisioning rate in both males (Spearman rank correlation: $r_s = -0.61$, n = 86, p < 0.001) and females ($r_s = -0.34$, n = 86, p = 0.002). We interpret lower latencies to return to the nest as reflecting higher parental motivation (Dale et al. 1996, Ghalambor and Martin 2000, Michl et al. 2000). Since song sparrows are monomorphic, we used colored leg bands to identify the sexes, in combination with behavioral cues such as female brooding (sitting on nestlings) and male song production.

Statistical analysis

Since repeated measures were taken for the parental behavior of individual males and females under baseline conditions and under elevated predation risk, we used linear mixed effects models (LMM) in the lme4 package (Bates et al. 2012) of R 2.15.2 (R Core Team) to analyze data. We fit models with reduced maximum likelihood, and reduced models via a step-wise reduction procedure, which entailed sequentially removing the term with the largest p-value until all terms retained were significant at the $\alpha = 0.05$ level, or were included in a significant interaction term. In addition, when song traits were retained in models as predictor variables, we confirmed that the final model had a lower Akaike information criteria (AIC) score than the model without the song traits but including highly predictive covariates. We specified maximum likelihood when calculating AIC scores. We used Satterthwaite approximations (implemented by R package lmerTest; Kuznetsova et al. 2013) to calculate degrees of freedom for final F tests in linear mixed effects models, and specified Helmert contrasts so that beta estimates for main effects were estimated across treatments.

We ran preliminary analyses to determine if the baseline, predator (sharp-shinned hawk), and negative control (house finch) treatments affected parental behaviors. The house finch (negative control) treatment was not significantly different from the baseline treatment in the models predicting paternal and maternal provisioning rates or latency to return to the nest (LMM: p > 0.40 in all cases; Supplementary material Appendix 1, Table A1). Thus, we recoded finch trials as baseline for final analyses, such that there were two levels across the categorical variable of treatment, rather than three.

We then assessed the relationship between song traits, nestling provisioning rates and latencies to return to the nest, and whether elevating adult-directed predation risk modified these relationships. Further, to help clarify how song complexity related to the relative provisioning contributions made by the male versus the female, we evaluated whether elevated predation risk modified the relationship between song traits and the proportion of provisioning visits performed by the female. We constructed models predicting provisioning rates, latencies to return to the nest, and the proportion of provisioning visits performed by the female, from the interactions between treatment (hawk, baseline) and song characteristics. We included brood size, nestling age, time of recording, date of recording, recording length and presentation order (whether the predation treatment was performed before or after the baseline treatment) in models as covariates. We did not include interaction terms between these covariates and treatment because our primary question

involved whether elevating perceived predation risk modified the relationship between song complexity and parental behavior, and we wanted to avoid constructing overly complex models. We included nest ID, male and female ID, and year in the models as random effects. We log transformed paternal latency to return to the nest and square root transformed maternal latency to return to the nest to normalize model residuals.

After initial analyses, we sought to clarify the effect of elevated perceived predation risk on the relationship between male song complexity, maternal nestling provisioning rates and the proportion of provisioning visits performed by the female by re-running models (minus the treatment term and associated interaction terms) within the baseline and predation treatment separately.

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.s6tn3 > (Grunst et al. 2015).

Results

Male song characteristics

Song repertoire size ranged from 5 to 12 song types with a mean of 8.87 ± 0.24 and syllable repertoire size ranged from 25 to 43 syllable types with a mean of 33.02 ± 0.62. Songs contained a mean of 7.34 ± 0.19 distinct syllable types, with a range of 5 to 12. Song repertoire size and syllable repertoire size were positively correlated (Spearman rank correlation: $r_s = 0.51$, n = 44, p < 0.001; LM: $F_{1, 42} = 14.15$, $\beta = 0.20 \pm 0.05$, p < 0.001; Fig. 2a). Residual syllable number ranged from –6.28 to 8.45. Residual syllable number was strongly correlated with syllable repertoire size (Spearman rank correlation: $r_s = 0.82$, n = 44, p < 0.001; Fig. 2c).

Paternal behavior and responses to predation risk

The mean provisioning rate of male song sparrows was 5.26 ± 0.65 (range: 0–14.03, median: 4.77) provisioning trips per hour in the baseline treatment and 3.71 ± 0.56 (range: 0–10.77, median: 3.38) provisioning trips per hour in the predation treatment. Males reduced nestling provisioning rates in response to adult-directed predation risk and provisioned larger broods at higher rates (Table 2). However, males differing in repertoire size (LMM: $F_{1, 26} = 0.06$, $\beta = 0.39 \pm 0.39$, p = 0.34, n = 74 observations, 37 nests, 28 females, 25 males) and residual syllable number ($F_{1, 17} = 0.22$, $\beta = -0.11 \pm 0.11$, p = 0.33) did not provision nestlings at significantly different rates, and the interactions between repertoire size ($F_{1, 26} = 2.17$, $\beta = 0.24 \pm 0.19$, p = 0.22), residual syllable number ($F_{1, 26} = 0.15$, $\beta = 0.02 \pm 0.05$, p = 0.65) and treatment were also non-significant. Time, date and duration of recording were unrelated to paternal nestling provisioning rates (p > 0.30 in all cases; Supplementary material Appendix 1, Table A2). Presentation order was not significantly correlated with paternal nestling provisioning rate ($F_{1, 43} = 2.31$, $\beta = 1.14 \pm 0.67$, p = 0.10).

The mean latency of male song sparrows to return to the nest was 22.29 ± 5.50 (range: 1.67–128.10, median:

Table 2. Final linear mixed effects models predicting paternal nestling provisioning rate and latency to return to the nest from male song characteristics and treatment (predator presence).

	n	Estimate ($\beta \pm SE$)	F	Denom (DF)	p ($> F$)
Paternal provisioning	86, 41, 31, 29[a]				
Intercept		0.59 ± 0.78			
Treatment		-0.66 ± 0.17[b]	14.96	45.49	< 0.001
Brood size		1.32 ± 0.27	23.92	34.30	< 0.001
Paternal latency to return	78, 37, 28, 25				
Intercept		2.89 ± 0.34			
Treatment		0.69 ± 0.21	9.11	40.81	0.002
Repertoire size		-0.32 ± 0.15	4.64	27.96	0.04
Brood size		-0.23 ± 0.11	4.02	24.99	0.04

[a]Number of observations, nests, females, males.
[b]Predator treatment relative to baseline.

17.85) min in the baseline treatment and 34.81 ± 6.97 (range: 1.01–123.80, median: 12.55) min in the predation treatment. Latency of males to return to the nest increased during the predator presentation and decreased with male repertoire size (Table 2; Fig. 3) and brood size (Table 2). On the other hand, paternal latency to return to the nest was unrelated to residual syllable number (LMM: $F_{1, 18} = 0.08$, $\beta = 0.01 \pm 0.05$, p = 0.78, n = 74 observations, 37 nests, 28 females, 25 males). Neither repertoire size ($F_{1, 36} = 0.58$, $\beta = -0.08 \pm 0.11$, p = 0.45) nor residual syllable number ($F_{1, 37} = 0.01$, $\beta = -0.003 \pm 0.03$, p = 0.92) interacted with the presence of the predator to predict paternal latency to return to the nest, and no other covariate had predictive power (p > 0.10 in all cases; Supplementary material Appendix 1, Table A3). Presentation order was unrelated to paternal latency to return to the nest ($F_{1, 24} = 2.08$, $\beta = 0.46 \pm 0.32$, p = 0.16). The model predicting male latency to return to the nest from song repertoire size and covariates (Table 2) had a lower AIC score (247.47) than the model excluding repertoire size (AIC = 276.47).

Maternal behavior and responses to predation risk

The mean provisioning rate of female song sparrows was 5.85 ± 0.52 (range: 0–11.02, median: 5.38) provisioning trips per hour in the baseline treatment and 4.50 ± 0.56 (range: 0–10.77, median: 3.81) provisioning trips per hour in the predation treatment. Females reduced nestling provisioning rates in response to adult-directed predation risk (Table 3). Moreover, females mated to males with larger residual syllable number reduced provisioning rates less in response to adult-directed predation risk than females paired with males with small residual syllable number (positive treatment × residual syllable number interaction; Table 3). Thus, although females mated to males with high residual syllable number did not provision nestlings at different rates than other females under baseline conditions (LMM within the baseline treatment: $F_{1, 15} = 0.0002$, $\beta = 0.002 \pm 0.12$, p = 0.99; Fig. 4a), these females had higher provisioning rates under adult-directed predation risk (LMM within predation treatment: $F_{1, 31} = 5.36$, $\beta = 0.24 \pm 0.10$, p = 0.02; Fig. 4b). Male song repertoire size was not related to maternal nestling provisioning rates across treatments (LMM: $F_{1, 24} = 0.16$, $\beta = -0.17 \pm 0.41$, p = 0.68, n = 74 observations, 35 nests, 28 females, 25 males), and the interaction between song repertoire size and treatment was also non-significant ($F_{1, 35} = 0.59$, $\beta = -0.13 \pm 0.17$, p = 0.44). The effect of presentation order on maternal provisioning rate was significant (Table 3), and suggested that females provisioned at higher rates when the predation treatment was performed first, with this effect being driven primarily by behavior within the baseline treatment. The final model predicting maternal provisioning rate also included positive effects of nestling age and brood size (Table 3). Time, date and duration of recording did not significantly affect maternal nestling provisioning rate (LMM: p > 0.10; Supplementary material Appendix 1, Table A4). The final model predicting maternal nestling provisioning rate from residual syllable number and covariates (Table 3), had a lower AIC score (327.31) than the model without residual syllable number (AIC = 383.47).

The mean latency of female song sparrows to return to the nest was 8.18 ± 1.89 (range: 0.70–50.62, median: 4.78) min in the baseline treatment and 20.58 ± 3.43 (range:
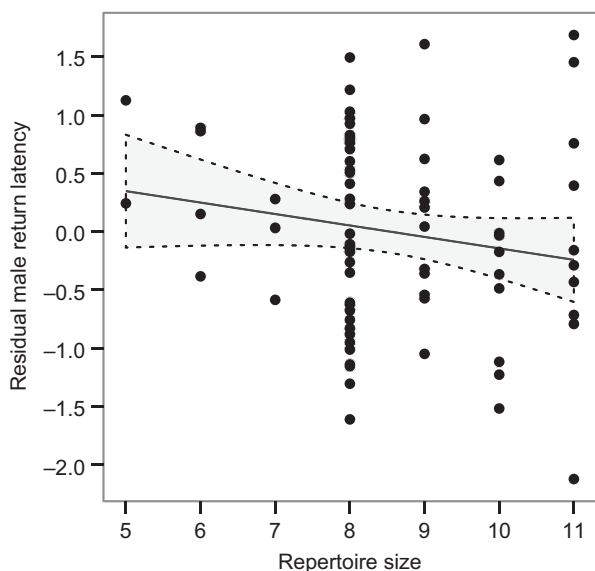

Figure 3. Linear regression between male song repertoire size and latency to return to the nest, across the baseline and predator treatments. This relationship existed across treatments. Thus, each male contributes three points to the figure (one point for each treatment). Residual latency to return to the nest reflects latency after controlling for the negative effect of brood size and higher latencies in the predation treatment. Shaded regions show 95% confidence intervals.

Table 3. Final linear mixed effects models predicting maternal provisioning rate, maternal latency to return to the nest, and the proportion of provisioning trips performed by the female from male song characteristics and treatment (predator presence).

	n	Estimate (β ± SE)	F	Denom (DF)	p (> F)
Maternal provisioning	74, 37, 28, 25[a]				
Intercept		−2.47 ± 1.88			
Treatment		−0.67 ± 0.16[b]	18.56	36.00	<0.001
Residual syllable		0.10 ± 0.10	0.93	26.60	0.34
Nestling age		0.86 ± 0.31	7.57	30.56	0.009
Brood size		0.66 ± 0.29	5.40	28.73	0.02
Presentation order		1.61 ± 0.66[c]	5.97	51.96	0.01
Treatment × residual syllable		0.09 ± 0.04	4.32	35.88	0.04
Maternal latency to return	86, 41, 31, 29				
Intercept		2.88 ± 0.36			
Treatment		1.46 ± 0.34	18.85	57.69	<0.001
Presentation order		−1.04 ± 0.41	6.51	66.32	0.01
Proportion maternal provisioning	70, 35, 28, 25				
Intercept		0.81 ± 0.09			
Treatment[b]		0.008 ± 0.01	0.37	26.26	0.55
Repertoire size		−0.08 ± 0.02	12.47	24.65	0.002
Residual syllable diversity		0.02 ± 0.006	7.52	19.89	0.01
Duration		−0.14 ± 0.05	8.65	47.84	0.005
Treatment × repertoire		−0.05 ± 0.01	9.85	27.15	0.004
Treatment × residual syllable		0.01 ± 0.003	7.36	27.48	0.01

[a]Number of observations, nests, females, males.
[b]Predator treatment relative to baseline.
[c]Baseline treatment second relative to baseline treatment first.

1.38–80.18, median: 15.18) min in the predation treatment. Maternal latency to return to the nest increased in the predation treatment (LMM: $F_{1, 58} = 18.85$, $β = 1.46 ± 0.33$, $p < 0.001$, n = 86 observations, 41 nests, 31 females, 29 males) and was lower when the predation treatment was performed first ($F_{1, 58} = 18.85$, $β = −1.04 ± 0.41$, p = 0.01). However, females mated to males differing in song repertoire size (LMM: $F_{1, 26} = 1.35$, $β = 0.32 ± 0.28$, p = 0.26, n = 74 observations, 35 nests, 28 females, 25 males) and residual syllable number ($F_{1, 18} = 035$, $β = −0.04 ± 0.07$, p = 0.56) did not display differences in latency to return. Further, male song traits did not interact with treatment to predict maternal latency to return to the nest, and time and date of recording, brood size, and nestling age all lacked predictive power

(p > 0.10 in all cases; Supplementary material Appendix 1, Table A5).

Proportion of maternal provisioning trips

The mean proportion of provisioning trips performed by the female was 0.57 ± 0.03 (range: 0.20–1.00, median: 0.55) in the baseline treatment and 0.57 ± 0.04 (range: 0.05–1.00, median: 0.50) in the predation treatment. Repertoire size negatively interacted with treatment to predict the proportion of provisioning visits performed by the female (Table 3; Fig. 5a, b), whereas residual syllable number and treatment positively interacted (Table 3; Fig. 5c, d). Females mated to males with larger song repertoires performed a lower
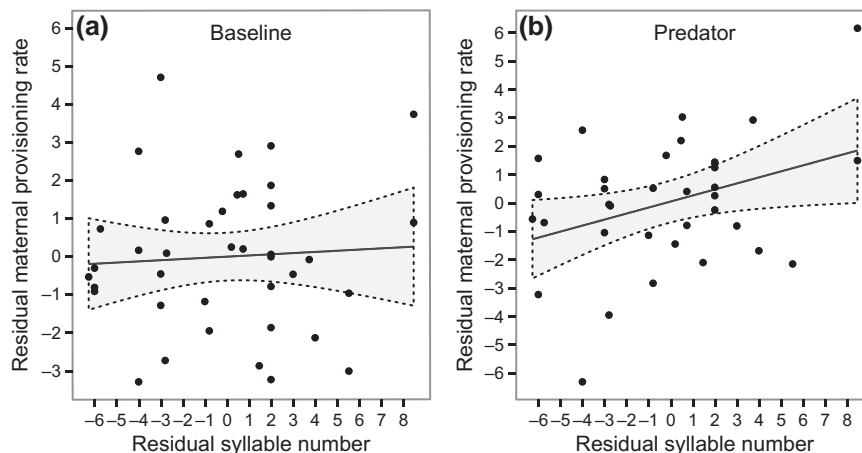
Figure 4. Linear regressions between male residual syllable number and maternal provisioning rate in the baseline treatment (a) and predator treatment (b). Residual maternal provisioning rate reflects provisioning rates after controlling for the positive effects of nestling age and brood size and higher provisioning rates when the predator presentation was performed first. Shaded regions show 95% confidence intervals.
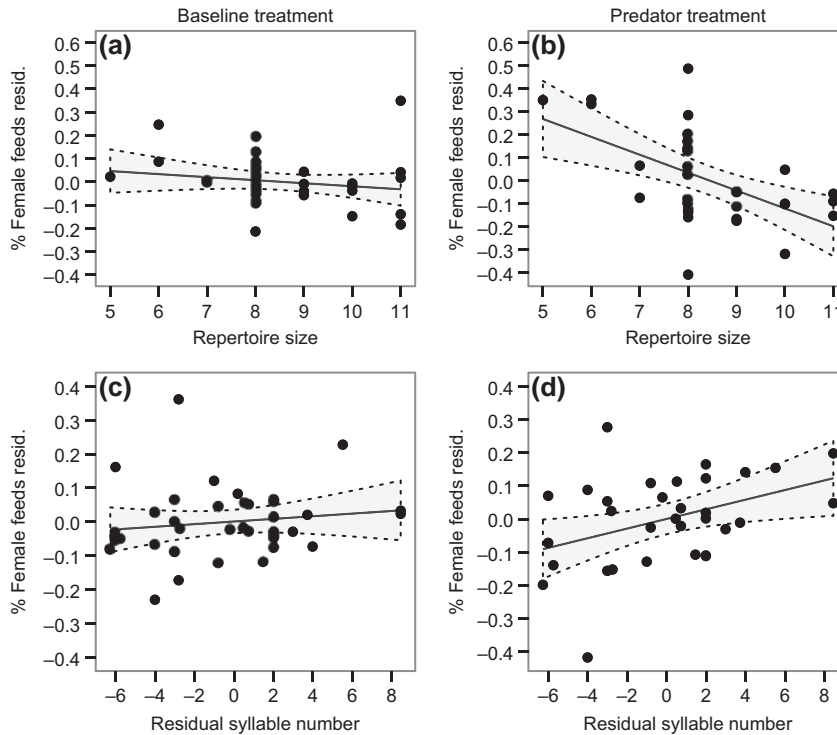
Figure 5. Linear regressions between song repertoire size (a, b) and residual syllable number (c, d) and the proportion of maternal provisioning trips in the baseline (a, c) and elevated predation risk (b, d) treatment. Residuals control for the positive effect of recording length and the effect of the other song complexity trait. Shaded regions show 95% confidence intervals.

proportion of total nestling provisioning trips under predation risk than other females (LMM within the predator treatment: $F_{1, 27} = 28.96$, $\beta = -0.10 \pm 0.02$, $p < 0.001$), but not under baseline conditions (LMM within the baseline treatment: $F_{1, 28} = 1.72$, $\beta = -0.02 \pm 0.02$, $p = 0.20$) (Fig. 5a, b). Conversely, females mated to males with higher residual syllable number performed a higher proportion of provisioning visits under predation risk than other females (LMM within the predator treatment: $F_{1, 23} = 17.43$, $\beta = 0.03 \pm 0.007$, $p < 0.001$), but not under baseline conditions (LMM within the baseline treatment: $F_{1, 22} = 1.02$, $\beta = 0.007 \pm 0.007$, $p = 0.32$) (Fig. 5c, d). The presence of the predator stimuli did not induce an overall shift in the proportion of provisioning visits performed by females (Table 3). However, the proportion of maternal provisioning trips decreased with the duration of the recording (Table 3). This effect was driven by the fact that females displayed shorter latencies to return to the nest than males, regardless of treatment (Paired t-test: $t_{85} = -4.30$, $p < 0.001$). The proportion of provisioning visits performed by the female did not vary as a function of brood size, nestling age, date of recording, time of recording, or presentation order (LMM: $p > 0.10$; Supplementary material Appendix 1, Table A6). The model predicting the proportion of provisioning trips performed by the female from song traits (Table 3) had a lower AIC score (–56.85) than the model excluding song traits (AIC = –50.74).

Discussion

We hypothesized that elevated perceived predation risk might change associations between male song traits and paternal

or maternal behavior. Consistent with this hypothesis, our results suggest that female song sparrows paired to males with large residual syllable numbers display higher maternal effort than other females only under elevated perceived predation risk. Thus, a pattern consistent with differential allocation emerged only under elevated perceived predation risk (Table 1h). In addition, consistent with the good parent hypothesis, our results provide some evidence that male song sparrows with large song repertoire sizes may provide more paternal support, both in the presence and absence of the predator stimuli (Table 1a). We found no support for the reproductive compensation hypothesis for maternal behavior (Table 1j) or the tradeoff hypothesis for paternal behavior (Table 1d–f).

Our strongest result supported the differential allocation hypothesis (Burley 1986, 1988, Ratikainen and Kokko 2010) for the nestling provisioning behavior of female song sparrows under elevated perceived predation risk (Table 1h). Specifically, in the presence of the predator stimuli, females paired to males with higher residual syllable number provisioned nestlings at higher rates than other females and performed a higher proportion of overall provision trips. In contrast, no correlation existed between male song traits and maternal effort in the absence of the predator stimuli. This result supports the hypothesis that elevating costs of parental care may induce positive relationships between maternal behavior and the sexually selected ornaments of males (Matessi et al. 2009).

Females mated to males with higher residual syllable numbers may display higher maternal effort than other females only under elevated predation risk if increased costs of parental care induce females with lower quality mates to

reduce parental investment. Specifically, residual syllable number may reflect male genetic quality, such that the offspring of males with low residual syllable number have less reproductive value (Ratikainen and Kokko 2010). Thus, females mated to males with low residual syllable number may decrease maternal investment under predation risk and prioritize survival, whereas females mated to males with high residual syllable number may maintain relatively high levels of maternal effort (Darolová et al. 2012). In contrast, maternal provisioning behavior may be uncorrelated with residual syllable number in the absence of an acute predation threat because costs of caring for offspring are relatively low, such that females with lower quality mates do not benefit by reducing investment into reproduction. Similar to our results, male rock sparrows *Petronia petronia* differentially allocate with respect to female plumage pigmentation when defending nests against a weasel predator, but not when provisioning nestlings, which may entail lower risks to survival (Griggio et al. 2003, Matessi et al. 2009). Differential allocation has the potential to magnify fitness differences between males and increase the strength of sexual selection (Harris and Uller 2009). Thus, our results suggest that elevating predation risk may increase fitness differences between males differing in residual syllable number, which may increase the strength of sexual selection acting on this trait.

Unlike maternal provisioning behavior, the latency of female song sparrows to return to the nest after perturbation did not correlate with male song traits. Why one metric of maternal behavior would correlate to song characteristics, whereas another would not, is unclear. However, irrespective of male song traits, females may show strong parental motivation to return to the nest, but subsequently modify their provisioning behavior once risk at the nest has been more fully assessed.

With respect to paternal behavior, we found some support for males with large song repertoires providing superior paternal services. First, across the baseline and predation risk treatments, males with larger song repertoires displayed lower latencies to return to the nest. This result suggests that males with larger song repertoires display higher paternal motivation, and is consistent with the good parent hypothesis (Hoelzer 1989; Table 1a), and other studies that link song complexity to paternal services (Greig-Smith 1982, Buchanan and Catchpole 2000). Further, under elevated perceived predation risk, only, a negative correlation existed between the proportion of provisioning visits performed by the female and male song repertoire size, which again supports relatively high paternal effort by males with large song repertoires. However, the interpretation that females gain paternal benefits by mating with males with large song repertoires is weakened by the absence of a correlation between paternal nestling provisioning rates and song repertoire size.

Our results do not support the tradeoff hypothesis (Table 1d–f), which predicts negative relationships between the expression of sexually selected traits and paternal services. However, some sexually selected traits impair the maneuverability of ornamented males or make these males visually conspicuous (Martin and Badyaev 1996, Grunst et al. 2014). In these cases, a pattern consistent with the tradeoff hypothesis might be more likely to emerge, especially under conditions of elevated predation risk, and when providing

parental care involves confronting a predator near a stationary nest. Further, when sexually selected displays are visually conspicuous, female preference for highly ornamented males might also be dampened under elevated predation risk (Berglund 1993, Johnson and Basolo 2003).

Taken together, our results suggest that song repertoire size and residual syllable number may play non-equivalent signaling functions, as suggested by the multiple messages hypothesis for the information content of multifaceted sexually selected traits (Møller and Pomiankowski 1993, Johnstone 1996). Specifically, residual syllable number may communicate information about some aspect of male genetic quality, such that females use residual syllable number when making parental allocation decisions. Indeed, past research has reported that females increase solicitation behavior or reproductive investment when males demonstrate the ability to sing 'sexy syllables' or physically demanding songs, composed of particular syllable types (Vallet et al. 1998, Leitner et al. 2006, Cardoso et al. 2009). Further, during development, it may be more costly to produce the neural networks needed to learn complex songs, such that residual syllable number may more reliably indicate certain dimensions of male quality than song repertoire size alone. In contrast, although based on less conclusive results, song repertoire size may communicate information about paternal quality such that females gain paternal benefits by mating with males with large song repertoires (Hoelzer 1989). Nevertheless, song repertoire size and residual syllable number could also fulfill redundant signaling roles with respect to other aspects of male quality that we did not examine (Hebets and Papaj 2005).

To our knowledge, no previous study in the song sparrow has examined how different song traits relate to parental care. However, different correlations between song traits and other behavioral, quality and fitness metrics have been reported, which is consistent with the idea that song repertoire size and residual syllable number may play non-equivalent signaling roles (MacDougall-Shackleton et al. 2009b, Grunst and Grunst 2014). Further, past studies in other bird species have reported that one component of a sexually selected display positively reflects paternal effort while another does not, or that two sexually selected traits differentially reflect paternal services. For instance, in great tits *Parus major*, males with large black melanin-based breast stripes defend nests more vigorously, whereas carotenoid-based plumage coloration fails to predict nest defense, but does predict body condition and nestling provisioning rate (Senar et al. 2003, Quesada and Senar 2007).

As a caveat, our results are correlational. Thus, we cannot conclusively determine whether relationships between male song complexity and maternal behavior are a direct consequence of assessment of male song traits, a reaction to paternal behavior, or the outcome of some other correlated factor such as territory or female quality (Sheldon 2000). Indeed, males with certain song characteristics may secure higher-quality territories, which may affect optimal patterns of maternal behavior (Yasukawa et al. 1980). Similarly, males with certain song characteristics may secure mates of higher quality, such that variation in maternal behavior may reflect differences between females rather than female assessment of, and reaction to, male traits (Sheldon 2000). Moreover,

male song characteristics may be correlated with some other aspect of male quality, such as physiological condition, that was not measured in this study. If song serves as a signal of male quality, this would be expected. We cannot currently determine whether song serves as a signal of male quality, which females assess, or merely correlates with other aspects of male or female quality. Disentangling these alternatives would require experimental manipulation of song complexity, which would be difficult in a field study.

In addition, the challenging nature of our field experiment raised some difficulties with the control of covariates including presentation order and recording length, which could introduce noise into our data. However, these noise variables should theoretically reduce our ability to detect significant relationships between song traits and parental behavior, and significant correlations still emerged. Females provisioned nestlings at higher rates when the predation treatment was performed before the baseline treatment, potentially because females compensated for reduced provisioning rates in the predation treatment by increasing provisioning rates during the subsequent baseline recording. The effect of presentation order on the provisioning rate of males was non-significant, perhaps reflecting lower paternal motivation to compensate for reduced provisioning rates during the predator treatment, but the coefficient estimate was in the same direction. Retaining presentation order in the model predicting maternal provisioning rate should control for the effect of presentation order on maternal behavior, especially given that our experimental design was relatively balanced with respect to presentation order (baseline treatment performed first 44.7% of the time, second 55.3% of the time).

The proportion of provisioning visits performed by the female was the only metric of parental behavior affected by recording length. This effect was driven by the fact that females displayed shorter latencies to return to the nest than males, both in the presence and absence of elevated perceived predation risk. Shorter return latencies of females relative to males may suggest that females have higher parental motivation than their mates. Indeed, in songbirds with biparental care such as the song sparrow, females may have more invested in the social brood, since females alone incubate, and females have higher certainty of parentage (Møller and Thornhill 1998). We retained recording length in the model predicting the proportion of provisioning visits performed by the female to control for effects of this variable.

In summary, our results suggest that correlations between sexually selected traits and parental effort may be modified in the context of elevated adult-directed predation risk, or in response to other factors that affect the relative costs and benefits of investing parentally. In the case of maternal provisioning behavior, elevating perceived predation risk induced a pattern consistent with differential allocation with respect to residual syllable number. Thus, maternal allocation decisions may be modified under elevated predation risk, and the strength of sexual selection magnified. In the case of paternal behavior, results provided some support for the good parent hypothesis, specifically suggesting that males with larger song repertoire sizes may have higher paternal motivation. In combination, our results suggest that females exposed to elevated perceived predation risk differentially allocate nestling provisioning effort with respect to residual syllable number,

but that song repertoire size may communicate paternal benefits. Thus, song repertoire size and residual syllable number may fulfill non-equivalent messaging functions.

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Supplementary material (Appendix JAV-00758 at <www.avianbiology.org/appendix/jav-00758>). Appendix 1.