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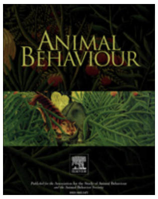

Male song structure predicts reproductive success in a wild zebra finch population

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The zebra finch is the model species for the study of the evolution of birdsong, female song preferences, song learning and the neural processes underlying song learning and production. Despite this, almost all work to date in these fields has focused on domesticated zebra finches in captivity and remarkably little is known about song preferences, or the reproductive success of males with different songs, in wild populations. In this study we tested, for the first time in a wild zebra finch population, whether a male's song structure predicts his reproductive success. We recorded male songs in a nestbox population. Males from this wild population sang longer songs, with a higher peak frequency, than domesticated males. The number of each male's offspring that survived until day 12 posthatching (a proxy for fledging success) was used as a measure of reproductive success. Nestlings were partially cross-fostered, allowing us to disentangle the indirect effects of male genetic quality or maternal effects from those of direct benefits such as parental care. Male song structure predicted the number of genetic offspring surviving, as well as hatching success, but not the number or size of eggs in a clutch. Song structure did not predict the number of unrelated foster-offspring that survived. These results provide the first evidence that differences in male song can predict differences in reproductive success in the zebra finch, and suggest that differences in genetic quality are responsible, rather than differences in parental care or maternal investment in the eggs.

Oscine song is a secondary sexual trait whose evolution is driven by both sexual and natural selection (Searcy & Andersson 1986; Catchpole & Slater 2008). It is supposed that traits such as ornamental birdsong advertise direct or indirect benefits to females choosing mates with the most attractive songs and that the honesty of these signals is mediated by their cost to the singer (Zahavi 1975; Grafen 1990). Birdsong is one of the best studied secondary sexual traits and studies across many species, notably of the zebra finch, *Taeniopygia guttata* (Riebel 2009; Griffith & Buchanan 2010a), have demonstrated that a number of male song traits are involved in attracting females (Marler & Slabbekoorn 2004; Catchpole & Slater 2008). Constraints on the development or production of some, but not all, of these traits have been identified, which maintain their honesty as signals of quality (Gil & Gahr 2002; Catchpole & Slater 2008).

Female preferences have been demonstrated, across a number of avian species, for several performance-related traits such as a high rate of singing (Houtman 1992; Nolan & Hill 2004), high-amplitude song (Searcy 1996; Ritschard et al. 2010), or longer songs or bouts of song. Female birds also show preferences for various structural song traits, including the presence of so-called 'sexy syllables' in the song of canaries, *Serinus canaria* (Vallet et al. 1998), or measures of performance quality in a number of songbird species, as defined by a trade-off between trill rate and frequency bandwidth (Podos 1996, 1997). The song trait for which female preferences have been most consistently demonstrated, in many species, is repertoire size, measured as either the number of syllables in a song or the number of different song types performed by a male, depending on the biology of individual species; furthermore, field studies have provided evidence from many species that the song repertoires of male birds are positively correlated with a number of measures of reproductive success (reviewed in Catchpole & Slater 2008).

The zebra finch has become the classic songbird species for studies of avian song (Griffith & Buchanan 2010a). In particular it has served as the main model species for understanding song

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learning (Clayton 1987a, b, 1988; Tchernichovski et al. 2001), the neural basis of both song learning and production (reviewed in Zann 1996; Brainard & Doupe 2002; London & Clayton 2010), and the effects of song on mate choice (reviewed in Riebel 2009). Zebra finches have also become an important model for research on avian mate choice and vision (Clayton 1990a; Bennett et al. 1996; Hunt et al. 1997; Roberts et al. 2007; Woodgate et al. 2010, 2011). The vast majority of studies, however, have been conducted under laboratory conditions using domesticated zebra finches. The structure, geographical variation and development of zebra finch song in wild populations have been extensively described (see Zann 1996), but almost nothing is known about the song preferences of wild females or whether male song is associated with reproductive success in the field.

Zebra finch males do not produce a repertoire of different song types, but rather a single, repeated, highly stereotyped song phrase, unique to the individual (Zann 1990; Nordeen & Nordeen 1992). A song phrase typically consists of 3–14 syllables produced in a fixed order and, in 73% of cases, contains one or more repeated syllables (Zann 1996). Zebra finches are closed-ended song learners, with a single sensitive phase for learning, extending from day 30 to 65 (Eales 1985, 1987; Roper & Zann 2006). The song preferences of female zebra finches, measured in laboratory audio experiments, predict their preferences for real, live males in mate choice chambers (Holveck & Riebel 2007), which in turn predict their choice of mates in aviary conditions (Clayton 1990b). Female zebra finches have been found by many studies to prefer complex songs with a larger repertoire of syllables (Neubauer 1999; Holveck & Riebel 2007; Vyas et al. 2009; Woodgate et al. 2011). Several studies have also indicated a preference for longer song phrases, but this is likely to reflect the confounding variable of syllable number (reviewed in Riebel 2009), and female preferences were better explained by syllable repertoire than phrase duration in operant and phonotaxis preference tests (Holveck & Riebel 2007). Female zebra finches also appear to prefer males that sing at a higher rate (ten Cate & Mug 1984; Houtman 1992; Collins et al. 1994; Pariser et al. 2010), although it remains unclear whether song rate is the cause or effect of female preference (reviewed in Riebel 2009). Other factors, including the proportion of sound versus silence within a song phrase and syllable syntax, may also play a role in female song preferences (reviewed in Riebel 2009), although few studies have yet addressed these directly.

The studies described above relied almost entirely on birds that have been bred in captivity for many generations. It is far from clear, however, that wild and domesticated zebra finches will respond similarly in mate choice tests. Wild zebra finch females prefer wild males to domesticated ones, and vice versa (Rutstein et al. 2007), and wild and domesticated birds differ in nestling growth rate, adult mass and size, immune response (Tschirren et al. 2009) and the level of extrapair paternity (Griffith et al. 2010). Despite these differences, Tschirren et al. (2009) found no difference in song rate, and an experimental brood size manipulation appeared to affect life history trade-offs in similar ways, in wild and domesticated zebra finches. Forstmeier et al. (2007) found that all domesticated populations of zebra finches they tested had reduced genetic variability compared to wild populations, but that there was no evidence for any severe genetic bottlenecks.

Laboratory studies on captive populations may not reveal the selection pressures at work in the field so it is important to understand better the relationship between male song, female choice and reproductive success in wild populations. In this study we recorded the songs of male zebra finches in a wild population, in western New South Wales, Australia, and investigated whether song structure predicted reproductive success. Partial cross-fostering of the offspring of these males allowed us to disentangle the contributions of genetic quality (indirect benefits) and parental care (direct benefits) to reproductive success, providing evidence on which aspects of male quality might be signalled by male song structure. We also tested whether song structure is related to a male's morphology or predicts the morphology of his mate, as might be expected if males with more complex songs attracted higher quality females. In line with sexual selection theory, we predicted that males with longer or more complex songs, composed of a greater number of syllables, would produce more surviving offspring than those with simpler songs.

METHODS

Study Site

This study was conducted between September and December 2008 at the University of New South Wales Arid Zone Research Station, Fowlers Gap, NSW, Australia (31°05′S, 142°42′E). The station is located in the semiarid zone of far western New South Wales, experiencing seasonally highly variable temperatures with cold winters and hot summers, and receiving a mean annual rainfall of 240 mm (Griffith et al. 2008). Breeding attempts were monitored during this period in nestboxes at the Gap Hills site on the station. A total of 199 plywood nestboxes (140 × 93 mm and 120–180 mm high) were mounted on steel poles, 1.0–1.85 m above ground level (Griffith et al. 2008).

Nestling Survival and Parent Morphology

Clutch size, egg volume and hatching success rates were recorded. The volume of each egg was calculated using the formula $V = 0.57LB^2$, where L = length and B = maximum breadth of the egg (Hoyt 1979). Nestlings were banded at day 12 and care was taken not to disturb the nest after this date as doing so can provoke premature fledging (Zann 1996). Survival to day 12 was therefore used as a proxy for fledging success (fledging usually occurring at 16–18 days, Zann 1996). Hatchlings were cross-fostered between nests to separate direct and indirect effects of male quality on fledging success. The cross-fostering process was also used to manipulate brood size as part of a concurrent study. Nestlings from each brood were cross-fostered at 2 (±1) days after hatching, across up to three nests with chick age differences of no more than 1 day. We transferred 30–50% of the nestlings to another nest; the others stayed in their original nest. Brood sizes were either increased or decreased by one or two chicks. Nestlings were chosen at random for cross-fostering to other nests, and allocated at random to enlarged or reduced broods. Each experimental brood therefore consisted of nestlings from two to three different nests, including both genetic and foster offspring, and siblings were split equally between enlarged and reduced broods. Premanipulation brood size was two to six chicks (median = 4 chicks) and postmanipulation brood size one to seven chicks (median = 5). Four broods were not cross-fostered because of the unavailability of any other broods of suitable age. The brood size manipulation was performed independently to male song recording and by a different experimenter to ensure that experimental brood size was independent of male song characteristics. We confirmed that there was no significant relationship between male song and the brood size manipulation using a series of seven one-way ANOVAs in which the five song parameters, and the first two principal components of those song parameters, were the dependent variables and the number of chicks by which each brood was enlarged or reduced was a random factor (all $P > 0.1$).

Attempts were made to catch the parent birds attending each nest using nestbox traps. When caught, adults were banded with

Table 1
Definitions of five song structure parameters used in acoustic analysis of male songs

Parameter	Definition
Syllable number	The total number of syllables that make up the song phrase, excluding introductory syllables
Phrase length (s)	Duration of the song phrase from the start of the first to the end of the last syllable
Peak frequency (kHz)	The frequency of maximum power in the phrase
Frequency bandwidth (kHz)	The difference between the minimum and maximum frequency of the syllable with the greatest frequency range
Proportion unique	Number of unique syllable types in the song/Syllable number

a metal band (supplied by the Australian Bird and Bat Banding Scheme) and a unique combination of coloured plastic bands for visual identification. A number of morphological measures were taken, including mass, tarsus length (measured from the right tarsus) and wing cord length (measured from the right wing). Females caught on the nestbox during the rearing period were assumed to be the mate of the male observed at the box. This was confirmed in many cases by subsequent observation of the coloured leg bands.

Note that although we use the term genetic offspring throughout this manuscript to refer to nestlings originating in a male's nest, no attempt was made to establish paternity for each chick. None the less, extrapair paternity in wild zebra finches has been found to be as low as 1.7% (Birkhead et al. 1990), and Griffith et al. (2010) found that only 2.4% of nestlings in this population at Fowlers Gap were extrapair offspring, suggesting that it is unlikely to confound our analyses significantly. There is evidence that conspecific brood parasitism may occur in 17.5–21% of broods in both wild and domesticated zebra finch populations (Griffith et al. 2010; Schielzeth & Bolund 2010), and 5.4% of all nestlings studied at Fowlers Gap were unrelated to either 'parent' (Griffith et al. 2010). Brood parasitism could thus constitute a source of random noise in our data but is unlikely to introduce significant bias to the analyses.

Song Recording and Analysis

The songs of male parents were recorded opportunistically at the nestboxes, using a Marantz PMD670 solid state recorder (Marantz, Kanagawa, Japan) and a Sennheiser MKE 2P condenser tie-clip microphone (Sennheiser electronic GmbH, Wedemark, Germany). Recordings had a sampling rate of 44.1 kHz at 16-bit resolution. The microphone, connected to a 20 m cable, was attached to the base of the pole on which a nestbox was mounted and the experimenter was located in a hide 15–20 m from the nestbox. In total, recordings were obtained of the songs of 48 males whose identity could be verified either from their coloured leg band combination or, in the case of unbanded birds (24 males), whose behaviour confirmed ownership of the nestbox (e.g. nest building or feeding chicks). Raven 1.2 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.) was used to analyse all song recordings (Hann weighting, 1024 point DFT size, 140 Hz filter bandwidth). The spectrogram of each male's recording was examined to determine the composition of the stereotyped song phrase and accurate measures of five song parameters (summarized in Table 1) were made from five phrases selected at random. Fewer than five complete phrases were recorded for 12 males (the smallest number of phrases recorded was two), and in these cases all the recorded phrases were measured. It was not possible in this study to gather meaningful data on singing rate owing to the extremely sporadic singing behaviour of the zebra finches in this population.

Statistical Analysis

All statistical analyses were performed using Minitab 15 (Minitab Inc., State College, PA, U.S.A.). A number of the measures of song structure were correlated strongly with one another (Table 2) and consequently were nonorthogonal. Principal components analysis (PCA) was therefore used to transform the data and extract components that explained more of the variation in song structure between males than any single song parameter. Two principal components (PCs) had eigenvalues greater than one, and together they explained 72% of the variance (Table 3). Song PC1 explained 50% of the variance in male song structure, and loaded positively on the number of syllables and length of the song phrase and negatively on the proportion of unique syllables in the song phrase. PC2 loaded mainly on peak frequency, frequency bandwidth and the proportion of unique syllables in the song phrase.

Mass, tarsus length and wing length measurements were obtained for 24 males for which we also had song recordings. The same measurements were obtained for the mates of 17 of the males for which we had recordings. PCA on these morphological measures yielded a single principal component with an eigenvalue exceeding one. This component explained 45% of the variance and was used as a single index of male and female body size. We investigated whether a male's song structure predicted either his own size or that of his mate using two regressions in which the principal component of body size was entered as the dependent variable and the first two song structure components constituted the predictors.

Breeding attempts were made by 42 of the males we recorded. We took four main measures of reproductive success: clutch size, mean volume of the eggs in each clutch, initial brood size (the number of eggs that successfully hatched) and number of offspring surviving to day 12 posthatching. Eight breeding attempts failed at the egg stage because of predation or parental abandonment and only the 34 nests in which at least at least one egg hatched were used in the analysis of chick survival. Offspring were partially cross-fostered to separate the effects of genetic quality and parental care on offspring success. Consequently we analysed two measures of

Table 2
Correlation matrix of five song parameters measured from recordings of 48 adult male zebra finches

Variable	Phrase length	Peak frequency	Frequency bandwidth	Proportion unique
Syllable number	0.844 (**<0.001**)	0.097 (0.513)	0.289 (**0.047**)	−0.607 (**<0.001**)
Phrase length		−0.036 (0.806)	0.385 (**0.007**)	−0.602 (**<0.001**)
Peak frequency			0.082 (0.582)	0.055 (0.711)
Frequency bandwidth				−0.041 (0.780)

Each cell shows the Pearson correlation coefficient (*r*) with the associated *P* value in parentheses. Significant *P* values are indicated in bold type.

Table 3
Rotated component matrices, eigenvalues and percentages of explained variance of principal components analyses on five song structure parameters

Parameter	PC1	PC2
Syllable number	0.58	0.02
Phrase length	0.59	−0.03
Peak frequency	0.02	0.78
Frequency bandwidth	0.28	0.53
Proportion unique	−0.48	0.33
Eigenvalue	2.50	1.08
Explained variance (%)	50.0	21.7
Cumulative explained variance (%)	50.0	71.6

nestling survival: the number of genetic offspring of each male that survived to day 12, regardless of which nest they were reared in, providing a measure of the genetic fitness of the male; and the number of unrelated foster-offspring within each male's nest that survived until ringing.

Each of the dependent variables (clutch size, mean egg volume, initial brood size, overall number of genetic offspring surviving, and number of foster-offspring surviving in each male's nest) was tested in a multiple regression with the two principal components of song structure as predictors. A correlation between survival and the initial clutch size is to be expected. To control for this, clutch size was used as a covariate in the analyses of initial brood size and genetic offspring survival. Both the number of unrelated nestlings fostered into the nest and the total number of nestlings in the nest after cross-fostering were used as covariates in the analysis of survival within the nest. The initial model for each analysis also included, as a random factor, the number of nestlings by which each brood was enlarged or reduced. This factor had no significant effects (all $P > 0.1$), however, and was removed from the final models, Constraining the final model to retain this factor had no qualitative effect on the results.

We also compared the structure of the male songs recorded at Fowlers Gap to the song of domesticated male zebra finches. Two of the song structure parameters we measured, syllable number and phrase length, were also measured by Forstmeier et al. (2009) in the largest study to date of zebra finch vocalizations. However, differences in the acoustic analysis mean that our measures of syllable number may not be comparable to those of Forstmeier et al. (2009). Because of this, and the fact that the other parameters we measured were not reported by Forstmeier et al. (2009), we also compared our data to the song of 24 male zebra finches from a domesticated population held at the Max Planck Institute for Ornithology, Seewiesen, Germany. With the exception of the frequency bandwidth, all the song structure parameters were available for these domesticated males and all acoustic analysis was carried out by the same experimenter (J. L. W.), allowing us to control for any observer bias in the acoustic analysis. Although both the domesticated populations we used are held in Seewiesen, they originate from different parts of Europe and can be considered distinct populations (Forstmeier et al. 2007). The birds reported by Forstmeier et al. (2009) belong to the population designated Seewiesen-GB by Forstmeier et al. (2007), whereas the other domesticated zebra finches originated from the Seewiesen-NL population. Two-sample *t* tests were used to compare each acoustic variable to the corresponding variable in the domesticated populations.

Ethical Note

This work was carried out under a scientific licence from New South Wales Parks and Wildlife Service (S11374) and approval from the Macquarie University Animal Ethics Committee 2007/2008.

RESULTS

Details of the males' song structure, clutch size and number of genetic and foster-offspring are given in the Appendix.

There was a significant positive relationship between the number of genetic offspring surviving to day 12 posthatching and the first principal component of the father's song (Fig. 1, Table 4). Together, song structure and clutch size predicted nearly 31% of the variance in the number of surviving chicks produced (Fig. 1, Table 4). The number of surviving chicks varied significantly with clutch size alone ($F_{1,32} = 4.93$, $P = 0.034$), but clutch size explained only 13.4% of the variance (Fig. 1c). Adding initial brood size (the number of eggs that successfully hatched) as a covariate in this analysis gives similar results although the effect of song PC1 becomes marginally nonsignificant ($P = 0.055$). A further regression analysis using a single measure of song complexity, syllable number, as a predictor of the number of genetic offspring surviving to day 12 showed a similar positive trend, when clutch size was controlled for, but this fell short of statistical significance ($F_{1,31} = 3.8$, $P = 0.060$, slope of regression equation = 0.21).

The survival of unrelated foster-offspring within a male's nest, however, did not correlate significantly with male song (Table 4). The number of foster-offspring surviving to day 12 posthatching was predicted by the number of unrelated nestlings fostered into each nest ($F_{1,29} = 18.35$, $P < 0.001$, $R^2 = 40.0\%$).

The second principal component of male song was predictive of the initial brood size, as was clutch size (Fig. 2, Table 4). However, male song did not predict the number of eggs laid in a clutch or the mean volume of those eggs (Table 4). In addition, song structure was not correlated either with a male's own body size or with that of his mate (Table 4).

To test whether nestlings are more likely to survive in nests with smaller than larger broods, we performed a Spearman rank-order correlation between the number of nestlings in each male's nest after cross-fostering (including both genetic and foster-siblings), and the proportion of those nestlings that survived to ringing. To test whether manipulating brood size affected the survival rate of nestlings, we performed a Spearman rank-order correlation between the number of nestlings by which each brood was enlarged or reduced and the proportion of nestlings that survived until ringing. There was no correlation between the proportion of nestlings that survived and either the postmanipulation brood size (Spearman $r_S = -0.073$, $N = 32$, $P = 0.575$) or the degree of brood size manipulation (Spearman $r_S = -0.263$, $N = 32$, $P = 0.741$).

The song phrases of male zebra finches at Fowlers Gap were significantly longer than those from either of the two domesticated populations (Table 5). The songs of wild males also contained more syllables than those reported by Forstmeier et al. (2009), but not those from the Seewiesen-NL population. The peak frequency of wild zebra finches was higher than that of captive birds but there was no difference in the proportion of syllables in the song phrase that was unique (Table 5). The body mass of wild males was significantly less than that of those from the Seewiesen-NL population ($t_{36} = 8.86$, $P = <0.001$).

DISCUSSION

This study is the first to test whether song structure predicts male reproductive success or morphology in any wild population of zebra finches. Two principal components of male song structure predicted different aspects of breeding success: initial brood size and nestling survival. The first principal component of song structure predicted the number of genetic offspring surviving to day 12 posthatching, when initial clutch size was controlled for. The principal component loaded most strongly on syllable number and

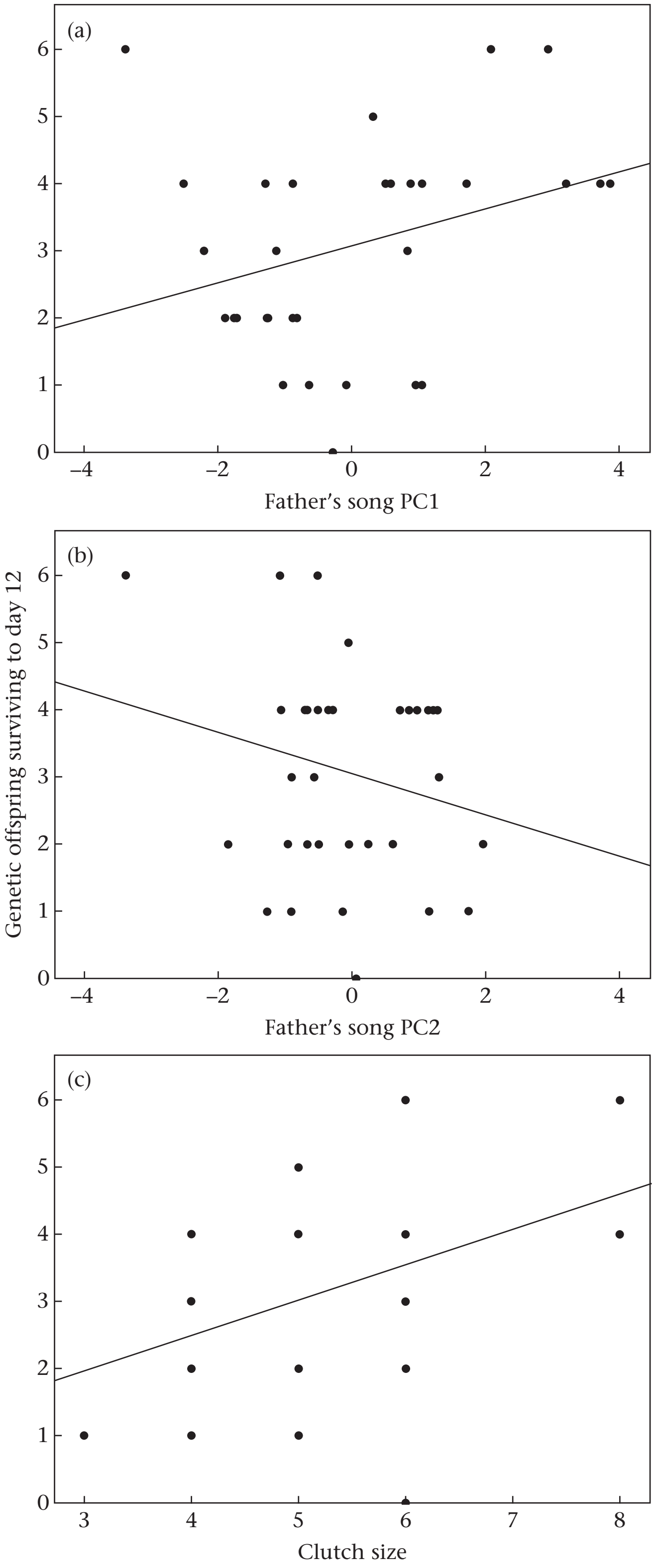

Figure 1. Regressions of the number of genetic offspring surviving to 12 days post-hatching on (a) and (b) two principal components of their father's song structure, and (c) clutch size.

phrase length, suggesting that individuals with longer, more complex songs had greater reproductive success. Song structure and clutch size accounted for roughly 31% of the variance in offspring survival, considerably more than could be explained by

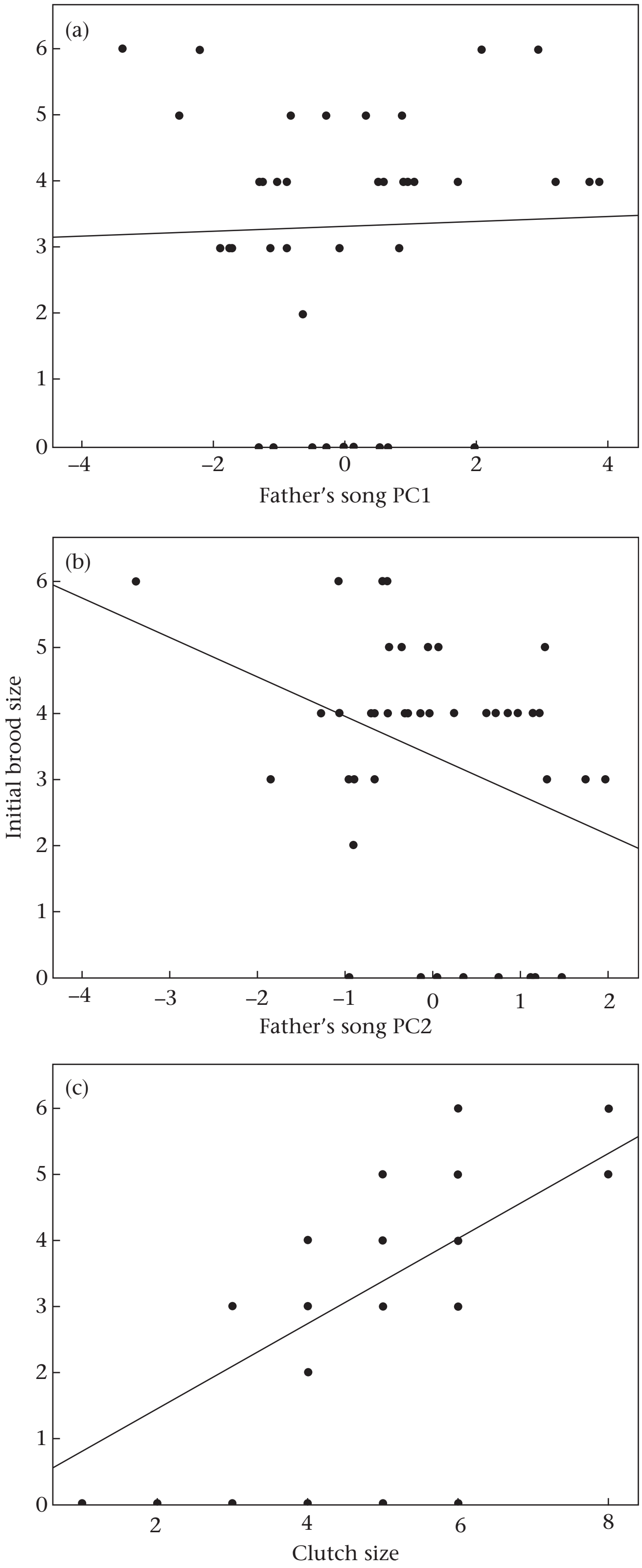

Figure 2. Regressions of the initial brood size (number of eggs that hatched successfully) on (a) and (b) two principal components of their father's song structure, and (c) clutch size.

Table 4

Results of regressions of six measures of male and female morphology, and reproductive success, on the principal components of male song structure

Dependent variable	Predictor	*F*	*df*	*P*	Slope	R^2 (%)
Number of genetic offspring surviving	Song PC1	4.84	1,30	**0.036**	0.29	30.7
	Song PC2	2.56	1,30	0.120	−0.34	
	Clutch size	7.08	1,30	**0.012**	0.58	
Number of foster-offspring surviving	Song PC1	0.05	1,25	0.822	−0.03	44.8
	Song PC2	2.34	1,25	0.138	−0.27	
	Number of foster-offspring in nest	10.21	1,25	**0.004**	0.90	
	Nestling number (after cross-fostering)	0.01	1,25	0.923	0.02	
Initial brood size	Song PC1	0.01	1,38	0.921	0.02	31.7
	Song PC2	5.64	1,38	**0.023**	−0.56	
	Clutch size	11.07	1,38	**0.002**	0.62	
Clutch size	Song PC1	<0.01	1,39	0.975	<0.01	0.3
	Song PC2	0.11	1,39	0.747	−0.06	
Mean egg volume (mm^3)	Song PC1	0.55	1,29	0.463	−5.99	4.2
	Song PC2	0.72	1,29	0.402	10.88	
Male body size PC1	Song PC1	1.09	1,21	0.308	0.15	5.4
	Song PC2	0.22	1,21	0.645	0.09	
Female body size PC1	Song PC1	0.22	1,14	0.650	−0.09	1.5
	Song PC2	0.01	1,14	0.941	−0.03	

Note that R^2 values refer to the variance accounted for by all predictors, rather than to individual predictor variables. Significant *P* values are indicated in bold type.

variation in clutch size alone. We were able to control for differences in social and rearing conditions by partially cross-fostering the nestlings, suggesting that differences in the genetic quality of males with differing song structure may account for the difference in their reproductive success. A similar positive relationship between repertoire size and annual reproductive success has previously been demonstrated in great reed warblers, *Acrocephalus arundinaceus* (Catchpole 1986; Hasselquist et al. 1996), song sparrows, *Melospiza melodia* (Hiebert et al. 1989; Reid et al. 2005), European starlings, *Sturnus vulgaris* (Eens et al. 1991) and willow warblers, *Phylloscopus trochilus* (Gil & Slater 2000), but none of these studies were able to distinguish between direct and indirect contributions of males to reproductive success.

The initial brood size (number of eggs that hatched successfully) was predicted by the second principal component of male song structure, which loaded primarily on peak frequency and frequency bandwidth. Differences in bandwidth were driven mostly by variation in the maximum frequency produced, so that individuals that reached higher frequencies in their song had larger bandwidths. This result suggests that males with higher frequency songs had a lower hatching success rate than those that produced lower pitched song. A relationship between song and hatching success could reflect differences in genetic quality of the males, maternal effects on the eggs or differences in incubation behaviour. Unfortunately, as cross-fostering was performed with hatched nestlings rather than eggs, we are unable to differentiate between these potential mechanisms. The frequency of calls has been shown to signal body size in some avian species (Hardouin et al. 2007; Mager et al. 2007), but vocal learning can disrupt this relationship (Williams et al. 1989; Forstmeier et al. 2009), and song PC2 did not predict body size in our analysis, suggesting that differences in size were not responsible for the relationship between song and hatching success.

Male song sparrows and great reed warblers with larger song repertoires enjoy greater lifetime and annual reproductive success (Hiebert et al. 1989; Hasselquist et al. 1996; Reid et al. 2005), and two studies on the great tit, *Parus major*, that found no effect of repertoire on annual reproduction found that repertoire size did predict lifetime reproductive success (McGregor et al. 1981; Lambrechts & Dhondt 1986), perhaps because males with larger repertoires survived longer. If there are comparable effects of song structure on survival or lifetime reproductive success in zebra finches, song structure may in fact predict even greater fitness benefits than those suggested by this study. Unfortunately, estimates of survival, lifetime reproductive success or postfledging offspring survival are very difficult to obtain in nomadic species such as zebra finches as they have very high dispersal rates (e.g. Zann 1996, reported that only 22% of adults in a colony were hatched there) and less than 10% of adults at Fowlers Gap have been recaptured in subsequent years (M. M. Mariette & S. C. Griffith, unpublished data).

A relationship between song and reproductive success suggests that males with more attractive songs provide direct or indirect benefits to the female (Andersson 1994), or that females invest more in their offspring if their mate has an attractive song. Song complexity may act as a signal of direct benefits such as a male's ability to find and exploit sources of food (Boogert et al. 2008) or the level of parental care he provides (Yasukawa et al. 1980; Greig-Smith 1982; Buchanan & Catchpole 2000; Halupka & Borowiec 2006), although this last may be confounded by an association between song and territory quality. The most obvious direct benefit provided by male songbirds from many species is territory quality (Andersson 1994), but zebra finches are not territorial (except in the immediate vicinity of the nest, Zann 1996), so obtaining good genes for their offspring may be of more importance than direct

Table 5

Mean ± SD for five song structure parameters along with comparisons to the song structure of males from two domesticated populations, the first (Seewiesen-GB) as reported by Forstmeier et al. (2009) and the second (Seewiesen-NL) from a breeding population at the Max Planck Institute for Ornithology, Germany

Parameter	Wild (Fowlers Gap)	Domesticated (Seewiesen-GB)	*t*	*df*	*P*	Domesticated (Seewiesen-NL)	*t*	*df*	*P*
Syllable number	6.58±2.03	4.69±1.86	66.16	56	**<0.001**	6.52±2.16	00.11	43	0.910
Phrase length	0.92±0.28	0.81±0.32	22.61	61	**0.011**	0.74±0.25	22.77	51	**0.008**
Peak frequency	4.15±1.19					2.85±1.05	44.73	51	**<0.001**
Frequency bandwidth	11.98±4.93								
Proportion unique	0.81±0.15					0.82±0.16	00.26	43	0.800
N	48	413				24			

benefits for zebra finch females. In this study, the breeding population was subject to a partial cross-fostering manipulation and we found that there was a relationship between song PC1 and offspring survival across all genetic offspring, regardless of whether they were raised in their natal nest or a foster nest. By contrast, song structure was not predictive of the number of foster-offspring that survived within each nest, suggesting that the correlation between song and nestling survival did not reflect direct benefits provided by the male or increased parental effort by his mate. Our results probably indicate either that song predicts genetic quality and females obtain genetic benefits for their offspring by mating with males that produce attractive songs or that females invest more resources in their eggs when mated with attractive males.

Females might adjust their investment in the eggs by manipulating clutch size, egg size or the concentration of hormones within the egg yolk. Egg volume is probably related to offspring survival in the zebra finch (Rutkowska & Cichon 2005; Bolund et al. 2009), although these analyses may be confounded by female condition, among other factors (Griffith & Buchanan 2010b), and Bolund et al. (2009) found that females laid larger eggs when paired with low-quality rather than high-quality males. However, we found no relationship between male song structure and either the number of eggs in a clutch or the mean egg volume, implying that females did not manipulate these traits in response to the attractiveness of their partner's song. Gil et al. (1999) found that female zebra finches laid eggs with higher testosterone levels when the attractiveness of their mates was manipulated using coloured leg bands, but we did not collect data on egg hormone levels in this study. Future studies could address the possibility that females might manipulate hormone levels in their eggs in response to their partner's song structure.

Partial cross-fostering of nestlings between nests allowed us to distinguish whether male song structure predicted direct or indirect benefits for offspring survival, but it should be noted that it could introduce a potential confound. Brood sizes were manipulated, which is likely to affect both the quality of parental care and sibling interactions and could, therefore, constitute another factor affecting offspring survival separate from the effects of parental quality and maternal investment. None the less, the proportion of offspring that survived to day 12 was not correlated with the postmanipulation brood size, suggesting that the brood size manipulation did not confound our analysis.

A male's song structure did not predict the principal component used as an index of his body size. Kipper et al. (2006) found a relationship between repertoire and male size in the nightingale, *Luscinia megarhynchos*, but no such relationship was observed in several other species, despite song repertoire being predictive of reproductive success (McGregor et al. 1981; Catchpole 1986; Lambrechts & Dhondt 1986; Eens et al. 1991). In domesticated zebra finches Holveck & Riebel (2007) reported a relationship between song performance (a principal component of a number of song parameters loading primarily on syllable rate and sound density) and male mass and tarsus length, but these results were not replicated by Forstmeier et al. (2009). Developmental stress has been shown to have detrimental effects on song complexity, but not adult mass (Spencer et al. 2003; Zann & Cash 2008), further suggesting that song structure is not a reliable signal of male morphology or condition in the zebra finch. We also found that a male's song structure did not predict the body size of his mate.

In this study we used principal components analysis to describe the variation across a number of song structure parameters, rather than use a single measure of song complexity. Despite the widespread use of zebra finches as a model to investigate song and female choice, it remains unclear exactly what song traits are attractive to females or what is the relative importance of individual song traits in female choice (reviewed in Riebel 2009). Using PCs rather than individual traits might identify information regarding male quality signalled by song structure as a whole that is accessible to female zebra finches but not apparent in a single, reductive measure of song complexity. Individual variation in song PC1 and PC2 explains some of the variation between males in reproductive success, but it is important not to conflate these principal components with more complex or attractive songs. For this reason, we repeated the analysis on the number of genetic offspring surviving to day 12 posthatching using syllable number, a single measure of song complexity, as a predictor. Although falling short of statistical significance there was a trend towards males with a greater number of syllables in their song phrase having more surviving offspring, indicating that song complexity does play a role in signalling male quality.

Male zebra finches recorded at Fowlers Gap had longer song phrases than captive males from two different populations, and their songs had higher peak frequencies than those from the Seewiesen-NL population. A number of morphological, ornamental and genetic traits have previously been found to differ between domesticated and wild populations of zebra finches (Forstmeier et al. 2007; Tschirren et al. 2009), and differences in song structure may result from the different selection pressures faced by wild and captive birds. It is not clear, however, how much variation in song structure exists between different zebra finch populations, both in captivity and in the wild, although Zann (1993a, b) reported differences between wild populations in several song structure parameters including phrase length. Indeed, the phrase lengths of the males from Fowlers Gap and both domesticated populations all fall within the range for wild males reported by Zann (1993b). The difference in peak frequency between wild and domesticated birds is likely to be at least partly explained by the fact that the wild birds were lighter than domesticated ones, frequency being largely determined by the resonant properties of the vocal tract, which are in turn correlated with body size (Forstmeier et al. 2009). The relatively larger size of domesticated than wild zebra finches is well established (Tschirren et al. 2009). Birds from Fowlers Gap also appeared to have a greater number of syllables in their song phrase than those in one captive population (Forstmeier et al. 2009). However, Forstmeier et al. (2009) used an automated process to measure syllable number (Sound Analysis Pro, Tchernichovski et al. 2004), which is known to give different estimates from those of some human observers, so this difference is likely to be an artefact rather than reflecting a true difference in song complexity. Indeed, there was no difference between the syllable number of males from Fowlers Gap and another domesticated population measured by the same experimenter.

Overall, this study provides the first evidence that song structure in the zebra finch predicts reproductive success in a wild population. It is not clear what mediates this relationship but our results suggest that differences in parental care are not responsible, and nor is maternal manipulation of clutch size or egg volume. The most likely explanation appears to be that male song structure reflects variation in heritable quality and may signal that a male carries good genes for offspring viability.

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Appendix

Table A1
Song structure parameters for 48 male zebra finches along with clutch sizes and the number of genetic and foster-offspring, both after hatching and surviving to day 12

Male number	Syllable number	Phrase length (s)	Peak frequency (kHz)	Frequency bandwidth (kHz)	Proportion unique	Clutch size	Initial brood size	Initial number of foster-offspring	Number of genetic offspring surviving	Number of foster-offspring surviving
1	9.0	1.11	3.55	15.74	0.56	6	6	4	6	4
2	3.0	0.29	2.94	5.29	1.00	8	6	2	6	2
3	8.0	1.60	1.14	8.04	0.38	6	6	2	6	2
4	4.0	0.65	3.46	7.09	1.00	6	6	2	3	1
5	6.0	0.79	4.13	6.88	0.83	5	5	2	2	2
6	5.8	0.82	5.30	7.85	0.69	6	5	3	0	0
7	4.0	0.54	3.98	5.77	1.00	5	5	1	4	1
8	7.0	1.18	4.97	18.12	0.86	8	5	3	4	3
9	8.0	0.83	4.45	10.53	0.75	5	5	2	5	2
10	4.8	0.63	4.58	9.12	0.79	5	4	1	2	0
11	13.0	1.66	4.84	8.75	0.62	6	4	3	4	2
12	7.0	1.21	4.75	18.37	0.86	5	4	3	1	0
13	7.0	1.16	3.91	6.49	0.57	5	4	1	1	1
14	6.2	0.84	4.99	19.94	0.68	6	4	3	4	2
15	5.0	0.83	3.94	11.76	1.00	6	4	4	2	4
16	8.0	1.16	3.42	11.16	0.75	5	4	1	4	1
17*	10.0	1.45	4.94	19.43	0.60	5	4	0	4	0
18	13.0	1.39	4.16	12.37	0.54	4	4	3	4	3
19	5.0	0.63	3.80	7.94	0.80	5	4	4	4	4
20	7.0	0.84	5.14	7.67	1.00	5	4	1	2	1
21	9.0	1.19	2.92	12.46	0.67	4	4	2	4	2
22	6.0	1.03	4.19	12.06	0.67	4	4	2	4	2
23*	5.0	0.86	4.57	17.08	1.00	5	4	0	4	0
24*	5.4	0.81	3.73	10.92	0.93	4	4	0	1	0
25	7.8	1.13	3.91	18.47	0.90	4	4	2	4	1
26	7.0	1.13	4.09	20.57	0.86	5	4	4	4	4
27	5.0	0.69	1.12	9.46	1.00	4	3	2	2	1
28	7.0	0.91	6.82	10.77	0.86	3	3	2	1	0
29	8.0	0.92	7.24	8.60	0.63	6	3	4	3	1
30	5.6	0.83	2.76	11.87	0.93	4	3	2	2	2
31	5.0	0.56	6.76	10.23	1.00	6	3	3	2	3
32	4.0	0.56	3.93	5.43	0.75	5	3	1	2	1
33*	5.0	0.77	3.84	5.66	0.80	4	3	0	3	0
34	7.0	0.80	3.53	6.17	0.86	4	2	2	1	0
35†	7.0	0.97	3.97	9.73	1.00	6	0	0	0	0
36†	7.0	0.95	3.71	15.22	0.71	3	0	0	0	0
37†	7.0	0.93	3.58	14.89	0.86	2	0	0	0	0
38†	4.6	0.82	6.58	9.64	0.87	1	0	0	0	0
39†	4.0	0.73	3.96	19.84	1.00	5	0	0	0	0
40†	7.0	0.93	4.03	19.75	1.00	4	0	0	0	0
41†	7.8	1.24	4.04	19.38	0.64	6	0	0	0	0
42†	7.0	0.98	3.84	19.88	0.86	6	0	0	0	0
43‡	6.4	0.78	5.58	9.00	0.84					
44‡	4.0	0.56	2.79	5.85	0.75					
45‡	7.6	0.77	4.10	20.01	0.61					
46‡	6.0	0.77	3.32	8.50	0.83					
47‡	7.0	1.03	4.24	12.00	0.86					
48‡	6.0	0.95	3.72	13.46	0.83					

* Four broods were not cross-fostered owing to the unavailability of any other broods of suitable age.

† No eggs hatched in eight nests.

‡ Six males whose songs were recorded did not make breeding attempts.