



## The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*

Barbara Ballentine\*

Biology Department, Duke University, Durham, NC, U.S.A.

### ARTICLE INFO

#### Article history:

Received 4 April 2008

Initial acceptance 30 May 2008

Final acceptance 18 December 2008

Published online 27 February 2009

MS. number: A08-00219

#### Keywords:

female choice

male quality

*Melospiza georgiana*

reliable signal

sexual selection

song

swamp sparrow

vocal performance

Selection should favour female preferences for reliable signals of male quality when such preferences result in benefits to females. Research on bird song suggests that, because song is costly to produce or sustain, females are obtaining accurate information about male quality through song preferences. Females have been shown to express mating preferences for three general categories of costly song features: song output, song complexity and geographical variation. A novel mechanism for the reliability of song is suggested by constraints on the ability to produce rapid, broadband trills (i.e. 'vocal performance'). In several species of birds, females show a preference for superior vocal performance, supporting a key prediction of the hypothesis that vocal performance, like other features of song, may be a reliable indicator of male quality. In this study, I further test this hypothesis by investigating whether female swamp sparrows' preference for vocal performance is favoured by selection because it reliably reflects male quality. I found that vocal performance in male swamp sparrows was correlated with age and size, measured as mass. By preferring males with superior vocal performance, female swamp sparrows may obtain direct and indirect benefits by mating with older larger males. These results support the hypothesis that vocal performance in swamps sparrows is a reliable indicator of male quality. © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Theory predicts that selection should favour female preferences for exaggerated male traits that are costly to produce or maintain such that the degree to which the trait is expressed is correlated with male quality (Grafen 1990; Andersson 1994). By preferring extreme versions of a trait, females are likely mating with superior males that provide them with fitness benefits directly through superior resources or care for offspring and/or indirectly through a superior genotype for offspring (Kirkpatrick & Ryan 1991; Andersson 1994). There is a growing body of empirical evidence that supports this mechanism for the evolution of female preferences for features of song in birds (Andersson 1994; Catchpole & Slater 1995; Searcy & Nowicki 2005). Female songbirds attend to three general categories of song features: song output, song complexity and local song features (Searcy & Nowicki 2000, 2005). Because it may cost something in terms of time and energy, song output can reflect a male's current physiological state (Radesäter & Jakobsson 1989; Eberhardt 1994; Oberweger & Goller 2001). Learning large repertoires and local dialects requires proper brain

development during a critical period of passerine life history that often overlaps with very stressful conditions; thus, these features of song may reflect the capacity of males to cope with periods of stress (Nowicki et al. 1998b, 2000, 2002; Buchanan 2000; Buchanan et al. 2003; Spencer et al. 2003; Searcy & Nowicki 2005). Recent studies on song production mechanisms suggest that the act of singing some types of songs might be more physically demanding than others (Nowicki et al. 1992; Lambrechts 1996; Podos 1997; Suthers & Goller 1997; ten Cate et al. 2002). Thus, constraints on song production may provide a novel perspective from which to ask what other features of song could reliably indicate male quality.

One limitation on song production involves the relationship between trill rate and frequency bandwidth (Westneat et al. 1993; Podos 1997; Hoese et al. 2000; Podos & Nowicki 2004) and suggests a mechanism by which song can reflect male quality. To produce pure tone sounds, birds must modify vocal tract resonances. One way to modify vocal tract resonance is by changing bill gape, with an open bill favouring high-frequency sounds and a closed bill favouring low-frequency sounds (Westneat et al. 1993; Hoese et al. 2000; Podos et al. 2004; but see Nelson et al. 2005; Riede et al. 2006). When birds are producing very broad-frequency sweeps, their bills are moving through a broad range of motion, thus imposing a constraint on the speed at which broad-frequency sweeps can be repeated. Consequently, trilled songs with

\* Correspondence and present address: B. Ballentine, Smithsonian Migratory Bird Center, National Zoological Park, 3001 Connecticut Avenue NW, Washington, D.C. 20008, U.S.A.

E-mail address: [ballentineb@si.edu](mailto:ballentineb@si.edu) (B. Ballentine)

narrow-frequency sweeps can be produced with either slow or fast repetitions, whereas trilled songs with broad-frequency sweeps can be produced only at slower repetition rates. That is, for a given frequency sweep, there is a limit to the speed at which sounds can be repeated, resulting in some songs being at or near physical limitation and other songs (i.e. those with both narrow bandwidth and slow repetition rates) being far from physical limitations (Podos & Nowicki 2004). The ability of males to produce trilled songs that meet these physical limitations is referred to as 'vocal performance' (Podos & Nowicki 2004). Because vocal performance is physically limited, other physically limiting traits such as aerobic capacity or endurance that have important consequences for fitness (Thomas et al. 2007) may correspond with variation in vocal performance. Thus, females may gain pertinent and accurate information about male quality when assessing males based on vocal performance.

Females of several species of songbirds show a preference for songs that are more challenging to produce, supporting a key prediction of the hypothesis that vocal performance functions in mate choice, because it reliably reflects male quality or condition. In laboratory experiments, Vallet and colleagues (Vallet & Kreuzer 1995; Vallet et al. 1998) found that phrases characterized by rapid repetition rates of frequency-modulated notes elicited the strongest female response in canaries. In later studies, Draganoiu et al. (2002) found that, when given a choice, female canaries preferred trilled phrases that were beyond physical limitations in terms of the trade-off between trill rate and frequency bandwidth. Together these studies suggest that female preferences for trilled portions of songs in canaries might be driven by female preferences for portions of songs that are difficult to produce. In a laboratory experiment, female swamp sparrows gave more copulation solicitation postures to natural songs that were closer to the performance limit (Ballentine et al. 2004). This empirical evidence of female preferences for physically challenging songs supports the general hypothesis that vocal performance is a reliable signal of male quality, but it does not rule out alternative hypotheses such as sensory biases (Ryan et al. 1990) or runaway selection (Fisher 1930). If female preferences for vocal performance represent adaptive female choice for high-quality males, because vocal performance is a reliable signal of male quality, then it is necessary to determine whether vocal performance correlates with male quality.

Age-dependent expression of secondary sex traits is reported in a wide variety of animal taxa (Johnstone 1995) and may be an important characteristic of reliable signals because females stand to benefit by mating with older males (Andersson 1994; Kokko & Lindström 1996; Kokko 1997). In general, age-dependent reproductive performance is reported in various taxa where younger individuals are less successful than older ones (Clutton-Brock 1988). This pattern could represent an overall improvement of breeding skills (i.e. parental competence or obtaining high-quality territories) (Pärt 2001a, b; Hyman et al. 2004), increasing reproductive effort with age (Pärt 1995), or heritable variation in survival (Mauck et al. 2004). Although it is not well understood whether genes or experience contribute more to age-related patterns of reproductive success (Forslund & Pärt 1995), theory suggests that genes for viability could be an indirect benefit of mating with older males (Kokko & Lindström 1996). In a recent experimental study, Hegyi et al. (2006) reported potential genetic benefits to the offspring of females that mate with older males. When males provide parental care, females are likely to gain direct benefits by mating with older males if experience and competence at reproduction increase reproductive success or result in optimization of reproductive effort (Forslund & Pärt 1995; Kokko & Lindström 1996). In swamp sparrows, where males provide some parental care (Mowbray 1997; personal observation), reproductive success

in males increases with age (Ballentine 2006b). Thus, by mating with an older male, a female swamp sparrow could gain both viability genes for her offspring and a mate with increased competence at obtaining high-quality resources for her and her offspring.

Body size and condition are good proxies for male phenotypic quality in vertebrates because they capture variation in a suite of traits that could benefit females. Body mass can be measured directly, and essentially encompasses both body size and body condition. Body size is typically estimated in birds by measuring the length of tarsus or wing, and represents skeletal size. Body condition is typically estimated by mass corrected for body size and represents the amount of available energetic reserves (Schulte-Hostedde et al. 2005). In birds, body mass, body size and condition are vulnerable to early nutritional stresses that persist into adulthood (Starck & Ricklefs 1998; Searcy et al. 2004;). While environmental conditions such as nutritional status influence development of body size, there is ample evidence that body size and weight are also influenced by genetic variation (Noordwijk & Marks 1998). Larger males may have an advantage in competition for high-quality territories (Searcy 1979; Andersson 1994). By mating with larger males, females probably gain direct benefits in resources and perhaps indirect benefits in the ability to withstand periods of nutritional stress during early development. A relationship between vocal performance and male age, body size or condition in swamp sparrows would support the hypothesis that vocal performance is a reliable indicator of male quality. In this study, I investigated whether phenotypic quality of males, measured as age, body size and condition, predicts vocal performance in swamp sparrows, a species in which females prefer songs of males that demonstrate superior vocal performance.

## METHODS

Data were collected during four breeding seasons beginning in April 2002 and ending in June 2005 at Conneaut Marsh in Crawford County, Pennsylvania, U.S.A. Adults were captured in mist nets and given a unique colour band combination for identification. Morphological measurements collected at the time of capture included the length of the tibiotarsus, unflattened wing chord length and mass. I used vernier calipers (Tajima) to the nearest 0.05 mm for all linear measurements (tarsus and wing) and measured mass with an Avinet spring scale to the nearest 0.5 g. Some males in the population were banded during a previous research project that began in May 2001, and banding continued through June 2005.

Age was estimated as either 'second year' (SY), for males in their first breeding season, or 'after second year' (ASY), for males in their second breeding season and beyond. Male swamp sparrows are highly philopatric, often occupying the same territory year after year (personal observation). All territorial males were banded, so males that returned in subsequent years were easily identified and assigned as ASY. Unbanded males that held a territory for the first time during the study were considered SY males. Because unbanded males could potentially move into the study area from elsewhere in the marsh, I used males only from territories that were thoroughly covered in the previous year and for which I had complete knowledge of all the surrounding neighbours. All males for 2002 and 2003 were assigned as either ASY or SY. In 2004 and 2005, 12 of 23 males were assigned an age.

Songs were recorded using a Sony TCD-5000 EV recorder with either a Shure SM-57 microphone and a Sony Parabolic Reflector-330 or a Saul Mineroff SME Parabolic Reflector-1000. The same recording equipment was used throughout this study, and thus, differences between individuals or between years in acoustic

features of song were not due to differences in equipment, and when used in previous studies, this equipment resulted in highly repeatable acoustic measurements (Ballentine et al. 2004).

The method for quantifying vocal performance is described in detail elsewhere (Podos 2001; Ballentine et al. 2004; Ballentine 2006a). Briefly, I plotted trill rate (*X* axis) and frequency bandwidth (*Y* axis) of songs, then calculated an upper boundary regression, which estimates the performance limit on trill production (Podos 2001). Vocal performance was quantified as the orthogonal distance from the upper boundary such that very low numbers refer to songs that are close to the upper boundary and hence close to an estimated performance limit. Thus, high numbers for vocal performance represent songs with poor performance and low numbers represent songs with good performance. I digitized a mean of 8.7 exemplars for each song type in each male's repertoire (range 1–11 exemplars). Songs were digitized using RTSD (Engineering Design, Belmont, MA, U.S.A.) with 16-bit precision at 25 kilopoints/s. All acoustic analyses were performed using 'Signal' version 3.1 digital signal processing software (Engineering Design).

### Analyses

To examine the combined effects of body size and age on a male's ability to perform trills, I used a backward stepwise general linear model (GLM) with vocal performance as the response variable and age, tarsus length, wing length, mass, the residuals of mass on wing length and year as predictor variables. To account for the possibility of differential effects of age and size on vocal performance, I included an interaction term for mass and age in the model. Since mass was correlated with the other size measures, I chose mass for the interaction term. Variables were removed from the model if  $P > 0.15$ . I used the highest performance song in a male's repertoire to determine each male's vocal performance. All continuous variables were verified to be normally distributed using a one-sample Kolmogorov–Smirnov test. All statistical analyses were performed using SYSTAT 8.0 (SYSTAT Software, Inc., Richmond, CA, U.S.A.). I used individuals in the analysis only when I had complete data (mass, age, song) for a given year such that mass and song were collected in the same year and not across years. As a result, males were included only once, as I did not have repeated measures of mass on any individuals used in this analysis. In 2002, songs of 31 males were recorded, and of those, I took morphological measurements from 23; in 2003, songs of 21 males were recorded, and of those, I took morphological measurements from 15. In 2004 and 2005, sampling effort was reduced, resulting in smaller sample sizes. Therefore, I combined the data for these 2 years in statistical analyses: 23 males were measured, and of those, 22 were recorded.

### Ethical note

Care was taken to ensure the health and well-being of animals. Birds were captured in mist nests, banded if they were not already banded, measured and released at the point of capture usually within 5 min. Birds typically resumed normal activities immediately after release. Permits for these activities were obtained from the U.S. Fish and Wildlife Service and the Commonwealth of Pennsylvania. These methods were approved by the Institutional Animal Care and Use Committees of Duke University (protocol no. A063-04-02) and the University of Pittsburgh (protocol no. 0503186).

### RESULTS

Wing length was a better predictor of mass (Pearson correlation:  $r_{59} = 0.353$ ,  $P = 0.005$ ) than tarsus length ( $r_{59} = 0.256$ ,  $P = 0.05$ ), thus the residuals of mass on wing length as an estimate

of body condition were included as an independent variable in the GLM. In a backwards stepwise general linear model, the significant predictors of vocal performance were year, mass and age, while tarsus length, wing length, the residuals of mass on wing length did not meet the significance criteria and were removed from the model (GLM:  $R^2 = 0.32$ ,  $N = 49$ ,  $P = 0.001$ ; Table 1). There was no significant interaction between age and mass (Table 1). In the post hoc analysis, mass did not differ by age class (SY mass:  $\bar{X} \pm SD = 18.2 \pm 1.0$ ; ASY mass:  $\bar{X} \pm SD = 18.1 \pm 1.1$  unpaired *t* test:  $t_{47} = -0.3$ ,  $P = 0.77$ ). In summary, within a given breeding season, males with better vocal performance were older (Fig. 1) and larger (Fig. 2).

The effect of age on vocal performance could arise either because males that performed better had increased survival, or because vocal performance improves with age. I compared the vocal performance of males that did and did not return, assuming that those that did not return did not survive. There was no difference in vocal performance of males that returned ( $\bar{X} \pm SD = 5.5 \pm 6.1$ ) and males that did not return ( $\bar{X} \pm SD = 5.2 \pm 5.2$ ; unpaired *t* test:  $t_{28} = -0.156$ ,  $P = 0.877$ ). However, vocal performance of males increased from their first breeding year to their second breeding year (paired *t* test:  $t_{10} = 2.2$ ,  $P = 0.050$ ; Fig. 3a). Males in their second breeding season and beyond showed no such improvement in vocal performance in subsequent years (paired *t* test:  $t_{16} = 0.05$ ,  $P = 0.62$ ; Fig. 3b). However, vocal performance was repeatable from one year to the next (Pearson correlation:  $r_{27} = 0.70$ ,  $P = 0.0001$ ). In summary, songs of males were generally repeatable from one year to the next, but males tended to improve their vocal performance only after their first breeding year, after which their vocal performance remained stable.

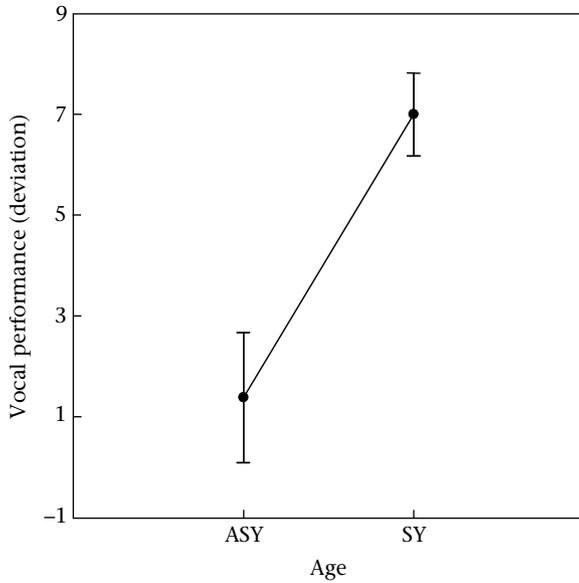
### DISCUSSION

Results of this study support the hypothesis that vocal performance of trilled songs in swamp sparrows is a reliable indicator of male quality. Within a given breeding season, mass and age explained 32% of the variation in vocal performance, with older and heavier males having higher vocal performance. Thus, if females are assessing males based on vocal performance, they are likely to be mating with older, heavier males. Although the general understanding of what aspects of male quality females are attempting to assess when choosing a mate is relatively poor (Searcy & Nowicki 2005), reliable signals of age and size are likely to provide valuable information to females both in terms of heritable variation in viability as well as the ability of males to provide high-quality resources to females and offspring (Andersson 1994; Kokko & Lindström 1996; Kokko 1997).

**Table 1**

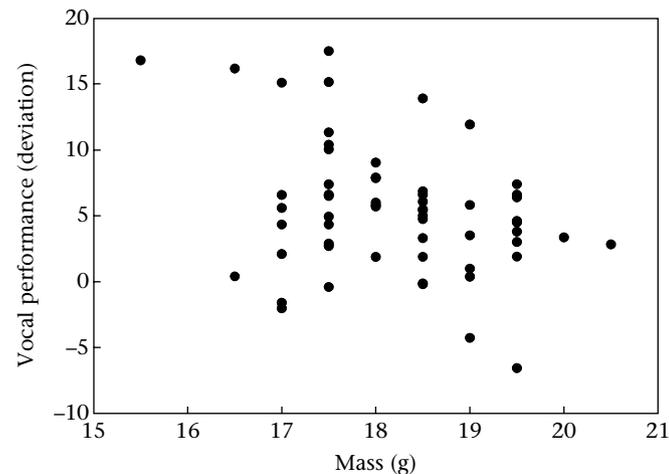
Results of backward stepwise general linear model with vocal performance of male swamp sparrows as the dependent variable

Effect	Coefficient	Standard error	Standard coefficient	Tolerance	df	F	P
<b>In</b>							
Age	-2.808	0.787	-0.513	0.747	1	12.724	0.001
Mass	-1.317	0.615	-0.270	0.974	1	4.582	0.038
Year				0.673	2	4.117	0.023
<b>Out</b>							
Tarsus	0.088			0.928	1	0.335	0.566
Wing	-0.025			0.667	1	0.027	0.869
Residuals	0.025			0.082	1	0.027	0.869
mass on wing							
Mass×age	0.161			0.003	1	1.139	0.292

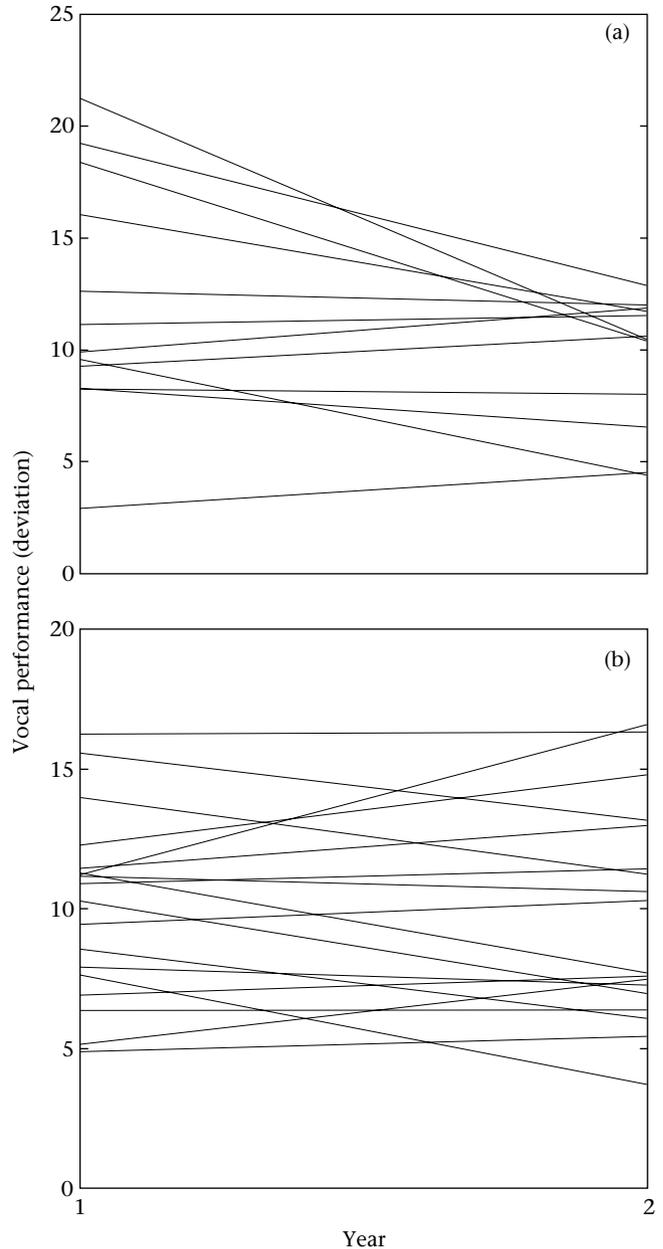


**Figure 1.** Least means squares  $\pm$  SE from the GLM for highest vocal performance for male swamp sparrows in each age group. Lower deviation indicates a better vocal performance.

Signals of male quality are particularly useful to females when they cannot directly assess aspects of male quality that could benefit them (Zahavi 1975, 1977; Kodric-Brown & Brown 1984). In swamp sparrows, it would be difficult for females to assess male age directly without some other cues such as plumage or song characteristics. Swamp sparrows do not show delayed plumage maturation and there is little evidence to suggest that plumage characteristics change substantially over time (unpublished data). However, the results of this study suggest that vocal performance does change with age, supporting the hypothesis that vocal performance, and in this case, male age, could function as an indicator of male quality. In a model that included age and body size as independent predictors of vocal performance, the strongest predictor of male vocal performance was age (Table 1). Thus, female preferences for vocal performance could result in females mating with older males. By mating with older males, females probably gain important fitness benefits. As in many other bird species (Forslund & Pärt 1995; Johnstone 1995), male swamp sparrows experience increased reproductive success with age (Ballentine 2006b). Although it is



**Figure 2.** Scatterplot of the relationship between mass and vocal performance of male swamp sparrows. Lower deviation values indicate better vocal performance.



**Figure 3.** (a) Change in vocal performance of second-year male swamp sparrows in their first breeding year and in the subsequent year. (b) Change in vocal performance of male swamp sparrows beyond their first breeding season in two subsequent years.

unknown why older male swamp sparrows have higher reproductive success, in other species, older males gain access to high-quality territories (Hasselquist 1998) and show increased competence at reproductive performance or foraging (Forslund & Pärt 1995). Older male swamp sparrows could increase female fitness directly by providing females and offspring with access to more or higher-quality resources. Furthermore, genetic models support the hypothesis that female preferences for traits that indicate age should offer females indirect benefits through genes for general viability (Kokko & Lindström 1996; Kokko 1997).

Better vocal performance in older males could result if males with better vocal performance have increased survival or if males improve vocal performance with age. Using a longitudinal approach, I found support for the latter explanation in age-related patterns of vocal performance. Males improved vocal performance

between their first and second breeding year, after which vocal performance tended to remain constant from one year to the next. However, given the limited range of my study in terms of the amount of time and the number of individuals studied, it would be premature to rule out the survival hypothesis. For instance, in great reed warblers, *Acrocephalus arundinaceus*, long-term longitudinal studies in two populations found that a correlation between song complexity and age was explained by differential survival in one population and by increasing song complexity with age in another population (Forstmeier et al. 2006). While some male swamp sparrows improved between the first and second breeding season, improvement was limited such that the overall statistical relationship between vocal performance in one year and in the subsequent year for all males was significantly correlated (Fig. 3a, b). However, the results of the present study suggest that singing experience may be one factor explaining the improvement in a male's ability to meet the performance trade-off between frequency bandwidth and trill rate. Perhaps if improvement in vocal performance is the result of increased competence at singing, the ability to sing physically challenging songs, in turn, represents an overall increase in competency in general.

Although age predicted vocal performance in males, there was still considerable variation in vocal performance within age classes (Fig. 3a, b), suggesting that variation in other measures of phenotypic quality may also contribute to vocal performance. In a model including age with estimates of body size, condition and mass as dependent variables, mass was the only other phenotypic predictor of vocal performance. Although body size and condition did not improve the significance of the model, they are probably important factors to consider in future studies. Because body mass is basically a composite of body condition and body size, these phenotypic characteristics are likely to be biologically relevant. Both body size and condition were strongly correlated with body mass, perhaps resulting in their lack of explanatory power in the model. A larger sample size may have increased the power to detect independent effects of body size and condition on vocal performance. Nevertheless, larger, heavier birds had better vocal performance.

The relationship between body mass and vocal performance supports the hypothesis that vocal performance is a reliable indicator of male quality. Early developmental stages in birds are rapid and vulnerable to nutritional stress (Lack 1954; Weathers & Sullivan 1989). Nutritionally stressed birds are characterized by reduced body mass at fledging, a condition that is likely to persist into adulthood (Boag 1987; Starck & Ricklefs 1998; Searcy et al. 2004). Thus, low adult body mass might be indicative of birds that experience early developmental stress. Studies in mammals found that body size and mass were better predictors of phenotypic quality than body condition (Toigo et al. 2006). In breeding male birds, variation in energy stored as fat is very small. Male swamp sparrows carry little to no extraneous body fat during the breeding season (personal observation), possibly because of intense activity during the breeding season. Interestingly, body mass in swamp sparrows is repeatable between years (Pearson correlation:  $r_{23} = 0.62$ ,  $P = 0.001$ ; unpublished data), supporting the hypothesis that body mass represents a condition during development, whereas body condition might represent a more immediate and ephemeral state. Large adults either experience ideal conditions during development or are inherently superior, allowing them to overcome poor conditions during development. Larger males might confer fitness advantages to females directly through access to superior resources (Andersson 1994) or indirectly through inherent ability to overcome periods of stress and deprivation.

There is a direct relationship between body size and acoustic frequencies produced by birds such that increased body mass correlates with decreased fundamental frequencies (Ryan &

Brenowitz 1985; Wiley 1991). However, there is no reason to expect body size to influence frequency bandwidth. Thus, although body mass probably does not influence vocal performance directly, it may do so indirectly. If low adult mass is indicative of early developmental stress (Boag 1987; Starck & Ricklefs 1998; Searcy et al. 2004), costs of vocal performance could be explained in a manner similar to the costs associated with song complexity in birds (Nowicki et al. 1998a; Searcy & Nowicki 2005). Resources for brain growth and development may be sacrificed during these important developmental periods, resulting in reduced repertoire sizes of adult male songbirds (Nowicki et al. 1998a, 2000; Buchanan et al. 2003). Song control regions of the brain developing during this time are not only involved in song learning capacity but are also involved in other aspects of singing. For instance, portions of the motor pathway that control song production are also developing during this time (Nottebohm et al. 1976). Thus, song production pathways that are involved in the coordination of muscular activity with respiration may be negatively affected by early nutritional stress such that production of fast trills with wide-frequency bandwidths is compromised.

The model presented here for how bills constrain song production is incomplete since there are other constraints on production of broadband, rapid trills (Nelson et al. 2005; Riede et al. 2006). The vocal tract itself is also involved in dampening harmonic overtones by rapid changes in the oropharyngeal cavity (Riede et al. 2006), and bill movements may be important only in the production of frequencies produced above 4 kHz (Nelson et al. 2005; Riede et al. 2006). In the population of swamp sparrows that I studied, the average high frequency produced is about 7.7 kHz (Ballentine 2006a); thus, bill movements at least partly constrain song production in swamp sparrows (Westneat et al. 1993; Hoese et al. 2000). While the specific model for how constraints on the production of rapid, broadband trills presented here may be incomplete, the production of rapid, broadband trills is nevertheless physically limited, and vocal performance provides a framework for how song can be an accurate indicator of male quality.

Selection should favour female preferences for signals that reliably indicate male quality. This study supports the hypothesis that constraints on trill production provide a mechanism by which females can reliably assess male quality through male song. By choosing males based on vocal performance, female swamps sparrows gain information about male age and size. Thus, males with superior vocal performance are likely to positively influence female reproductive success directly and/or indirectly. This is the first study showing that female preference for vocal performance (Ballentine et al. 2004) in males may be an adaptive female choice for a reliable signal of male quality.

## Acknowledgments

I thank Steve Nowicki, Susan Peters, Kimberly Rosvall and Jeremy Hyman for their help in the lab and in the field. I thank Steve Nowicki, Jeremy Hyman, Susan Alberts, Dan McShea, Haven Wiley, Will Wilson and three anonymous referees for their comments on the manuscript. I thank the Pennsylvania Game Commission for permission to conduct this study in Pennsylvania Gamelands. I thank Pymatuning Laboratory of Ecology for support in the field. This project was funded by a National Science Foundation Doctoral Dissertation Improvement Grant IBN-0407966 to S. Nowicki and B. Ballentine.

## References

- Andersson, M. B. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

- Ballentine, B.** 2006a. Morphological adaptation influences the evolution of a mating signal. *Evolution*, **60**, 1936–1944.
- Ballentine, B.** 2006b. Production constraints on song production in swamp sparrows: implications for the function of song in mate choice. Ph.D. thesis, Duke University.
- Ballentine, B., Nowicki, S. & Hyman, J.** 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, **15**, 163–168.
- Boag, P. T.** 1987. Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). *Auk*, **104**, 155–166.
- Buchanan, K. L.** 2000. Stress and the evolution of condition-dependent signals. *Trends in Ecology & Evolution*, **15**, 156–160.
- Buchanan, K. L., Spencer, K. A., Goldsmith, A. R. & Catchpole, C. K.** 2003. Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). *Proceedings of the Royal Society of London, Series B*, **270**, 1149–1156.
- Catchpole, C. K. & Slater, P. J. B.** 1995. *Bird Song*. Cambridge: Cambridge University Press.
- Clutton-Brock, T.** 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago: University of Chicago Press.
- Draganoiu, T. L., Nagle, L. & Kreutzer, M.** 2002. Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. *Proceedings of the Royal Society of London, Series B*, **269**, 2525–2531.
- Eberhardt, L. S.** 1994. Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *Auk*, **111**, 124–130.
- Fisher, R. A.** 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon.
- Forslund, P. & Pärt, T.** 1995. Age and reproduction in birds: hypotheses and tests. *Trends in Ecology & Evolution*, **10**, 374–378.
- Forstmeier, W., Hasselquist, D., Bensch, S. & Leisler, B.** 2006. Does song reflect age and viability? A comparison between two populations of the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology*, **59**, 634–643.
- Grafen, A.** 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Hasselquist, D.** 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376–2390.
- Hegyvi, G., Rosivall, B. & Torok, J.** 2006. Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects. *Behavioral Ecology and Sociobiology*, **60**, 672–682.
- Hoese, W. J., Podos, J., Boetticher, N. C. & Nowicki, S.** 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. *Journal of Experimental Biology*, **203**, 1845–1855.
- Hyman, J., Hughes, M., Searcy, W. A. & Nowicki, S.** 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour*, **141**, 15–27.
- Johnstone, R. A.** 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews of the Cambridge Philosophical Society*, **70**, 1–65.
- Kirkpatrick, M. & Ryan, M. J.** 1991. The evolution of mating preferences and the paradox of the lek. *Nature*, **350**, 33–38.
- Kodric-Brown, A. & Brown, J. H.** 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist*, **124**, 309–323.
- Kokko, H.** 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology*, **41**, 99–107.
- Kokko, H. & Lindström, J.** 1996. Evolution of female preference for old mates. *Proceedings of the Royal Society of London, Series B*, **263**, 1533–1538.
- Lack, D.** 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.
- Lambrechts, M. M.** 1996. Organization of birdsong and constraints on performance. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 305–320. Ithaca, New York: Cornell University Press.
- Mauck, R. A., Huntington, C. E. & Grubb, T. C.** 2004. Age-specific reproductive success: evidence for the selection hypothesis. *Evolution*, **58**, 880–885.
- Mowbray, T. B.** 1997. Swamp sparrow. In: *The Birds of North America Online*. No. 279 (Ed. by A. Poole). Ithaca, New York: Cornell Lab of Ornithology, doi:10.2173/bna.279. <http://bna.birds.cornell.edu/bna/species/279>.
- Nelson, B. S., Beckers, G. J. L. & Suthers, R. A.** 2005. Vocal tract filtering and sound radiation in a songbird. *Journal of Experimental Biology*, **208**, 297–308.
- Noordwijk, A. J. v & Marks, H. L.** 1998. Genetic aspects of growth. In: *Avian Growth and Development* (Ed. by J. M. Starck & R. E. Ricklefs), pp. 305–323. New York: Oxford University Press.
- Nottebohm, F., Stokes, T. M. & Leonard, C. M.** 1976. Central control of song in the canary, *Serinus canarius*. *Journal of Comparative Neurology*, **165**, 457–486.
- Nowicki, S., Peters, S. & Podos, J.** 1998a. Song learning, early nutrition and sexual selection in songbirds. *American Zoologist*, **38**, 179–190.
- Nowicki, S., Searcy, W. A. & Hughes, M.** 1998b. The territory defenses function of song in song sparrows: a test with the speaker occupation design. *Behaviour*, **135**, 615–628.
- Nowicki, S., Westneat, M. & Hoese, W.** 1992. Birdsong: motor function and the evolution of communication. *Seminars in the Neurosciences*, **4**, 385–390.
- Nowicki, S., Hasselquist, D., Bensch, S. & Peters, S.** 2000. Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London, Series B*, **267**, 2419–2424.
- Nowicki, S., Searcy, W. A. & Peters, S.** 2002. Brain development, song learning and mate choice: a review and experimental test of the 'nutritional stress hypothesis'. *Journal of Comparative Physiology A*, **188**, 1003–1014.
- Oberweger, K. & Goller, F.** 2001. The metabolic cost of birdsong production. *Journal of Experimental Biology*, **204**, 3379–3388.
- Pärt, T.** 1995. Does breeding experience explain increased reproductive success with age: an experiment. *Proceedings of the Royal Society of London, Series B*, **260**, 113–117.
- Pärt, T.** 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. *Animal Behaviour*, **62**, 379–388.
- Pärt, T.** 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. *Proceedings of the Royal Society of London, Series B*, **268**, 2267–2271.
- Podos, J.** 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, **51**, 537–551.
- Podos, J.** 2001. Correlated evolution of morphology and vocal signals in Darwin's finches. *Nature*, **409**, 185–188.
- Podos, J. & Nowicki, S.** 2004. Performance limits on birdsong production. In: *Nature's Music: the Science of Birdsong* (Ed. by P. Marler & H. Slabbekoorn), pp. 318–342. New York: Elsevier Academic Press.
- Podos, J., Southall, J. A. & Rossi-Santos, M. R.** 2004. Vocal mechanics in Darwin's finches: correlation of beak gape and song frequency. *Journal of Experimental Biology*, **207**, 607–619.
- Radesäter, T. & Jakobsson, S.** 1989. Song rate correlations of replacement territorial willow warblers *Phylloscopus trochilus*. *Ornis Scandinavica*, **20**, 71–73.
- Riede, T., Suthers, R. A., Fletcher, N. H. & Blevins, W. E.** 2006. Songbirds tune their vocal tract to the fundamental frequency of their song. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 5543–5548.
- Ryan, M. J. & Brenowitz, E. A.** 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, **126**, 87–100.
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S.** 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*, **343**, 66–67.
- Schulte-Hostedde, A. I., Zinner, B., Millar, J. S. & Hickling, G. J.** 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology*, **86**, 155–163.
- Searcy, W. A.** 1979. Morphological correlates of dominance in captive male red-winged blackbirds. *Condor*, **81**, 417–420.
- Searcy, W. A. & Nowicki, S.** 2000. Male–male competition and female choice in the evolution of vocal signaling. In: *Animal Signals* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 301–315. Trondheim: Tapir Academic.
- Searcy, W. A. & Nowicki, S.** 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, New Jersey: Princeton University Press.
- Searcy, W. A., Peters, S. & Nowicki, S.** 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. *Journal of Avian Biology*, **35**, 269–279.
- Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. & Catchpole, C. K.** 2003. Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). *Hormones and Behavior*, **44**, 132–139.
- Starck, J. M. & Ricklefs, R. E.** 1998. *Avian Growth and Development*. New York: Oxford University Press.
- Suthers, R. A. & Goller, F.** 1997. Motor correlates of vocal diversity in songbirds. In: *Current Ornithology* (Ed. by V. Nolan Jr), pp. 235–288. New York: Plenum.
- ten Cate, C., Slabbekoorn, H. & Ballintijn, M. R.** 2002. Birdsong and male–male competition: causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). In: *Advances in the Study of Behavior* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon & T. J. Roper), pp. 31–65. San Diego: Academic Press.
- Thomas, D. W., Shipley, B., Blondel, J., Perret, P., Simon, A. & Lambrechts, M. M.** 2007. Common paths link food abundance and ectoparasite loads to physiological performance and recruitment in nestling blue tits. *Functional Ecology*, **21**, 947–955.
- Toigo, C., Gaillard, J. M., Van Laere, G., Hewison, M. & Morellet, N.** 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography*, **29**, 301–308.
- Vallet, E., Beme, I. & Kreutzer, M.** 1998. Two-note syllables in canary songs elicit high levels of sexual display. *Animal Behaviour*, **55**, 291–297.
- Vallet, E. & Kreutzer, M.** 1995. Female canaries are sexually responsive to special song phrases. *Animal Behaviour*, **49**, 1603–1610.
- Weathers, W. W. & Sullivan, K. A.** 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs*, **59**, 223–246.
- Westneat, M. W., Long, J. H., Hoese, W. & Nowicki, S.** 1993. Kinematics of bird-song: functional correlations of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology*, **182**, 147–171.
- Wiley, R. H.** 1991. Association of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist*, **138**, 973–993.
- Zahavi, A.** 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A.** 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.