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

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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.

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

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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 & Kreutzer 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 tibotarsus, 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