



Equivalent effects of bandwidth and trill rate: support for a performance constraint as a competitive signal



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Sexual signals that are physically limited can be reliable indicators of quality or motivation in male–male competition. One such example of a motor constraint in birds is the production of repeated notes, which are limited in the frequency bandwidth and trill rate at which notes can be produced, such that it is difficult to produce wide-bandwidth notes at fast rates. How well birds maximize frequency bandwidth and trill rate is one measure of vocal performance, commonly referred to as ‘vocal deviation’. In theory, fast songs with narrow bandwidths and slow songs with wide bandwidths should have similar values of vocal deviation. In many species, males respond to variation in vocal deviation, supporting the notion that it is a sexually selected signal. However, most studies test only one of these components, either trill rate or bandwidth, rather than both individually, when testing receiver response to vocal deviation. Therefore, a question remains as to whether songs with equivalent values of vocal deviation (e.g. fast songs with narrow bandwidths and slow songs with wide bandwidths) elicit similar levels of response from receivers. We tested whether receivers respond specifically to the trade-off between trill rate and bandwidth (i.e. vocal deviation) or only to variation in one of the component parts. Using territorial playback experiments with wild male white-crowned sparrows, *Zonotrichia leucophrys*, we found that males approached high-performance songs (fast trill, wide bandwidth) more closely than they did lower-performance songs (fast trill, narrow bandwidth; slow trill, wide bandwidth) and they did so regardless of whether performance varied because of differences in trill rate or bandwidth. Furthermore, we found that males gave similar responses to songs of similar vocal deviation. Our results empirically support the hypothesis that receivers respond specifically to the physical limitation on the production of repeated notes.

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Sexual signals are used to defend territories and attract mates, and it is generally thought that receivers should pay attention to sexual signals that accurately convey the quality or motivation of the signaller (Andersson, 1994; Searcy & Nowicki, 2005). Signal honesty can be maintained if there are constraints to producing the sexual signal (Maynard Smith & Harper, 2004; Zahavi, 1975). Well-studied examples of costs include developmental costs and performance limits. For instance, nutritional condition during signal development can affect signal expression, such as carotenoid-based coloration (fish: Frischknecht, 1993; birds: Hill & Montgomerie, 1994), ultraviolet (UV) coloration (birds: Delhey, Peters, Johnsen, & Kempenaers, 2006; insects: Lim & Li, 2007)

and repertoire size of vocal signals (birds: Nowicki, Peters, & Podos, 1998; Nowicki, Searcy, & Peters, 2002). Another example of production constraints is mechanical limits on ability to execute motor patterns, which can limit performance of a signal. Physically limited sexual signals, or index signals, are abundant across taxa (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 1995, 2004). For example, female collared lizards, *Crotaphytus collaris*, choose to mate with males that run the fastest (Husak, Fox, Lovern, & Van Den Bussche, 2006). Visual signals of weaponry, like antlers in roe deer, *Capreolus capreolus* (Vanpé et al., 2007) or horns in rhinoceros beetles, *Trypoxylus dichotomus* (Emlen, Warren, Johns, Dworkin, & Corley Lavin, 2012), are signals of overall body size or age and can indicate fighting ability. Low sound frequency in acoustic signals can also indicate body size and, therefore, competitive ability (Hall, Kingma, & Peters, 2013; Linhart & Fuchs, 2015). Sexual selection is expected to favour signallers that maximize signal expression or signalling skill for signals that are costly to produce.

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Performance limits on sound production are an example of index signals in animals that use acoustic communication (Cardoso & Mota, 2009; Nemeth et al., 2013; Podos, 1997). For example, in songbirds, there are multiple performance limits on vocalizations that contain rapidly repeated notes or trills (Podos, Lahti, & Moseley, 2009; Sockman, 2009; Sprau, Roth, Amrhein, & Naguib, 2013). One performance limit is a trade-off between the rate at which sounds are produced and the frequency bandwidth of those sounds. In songbirds, this trade-off may be the result of constraints on modulating beak gape, syringeal and oropharyngeal musculature to track the production of fundamental frequencies in the process of filtering out harmonic frequencies (Nowicki & Marler, 1988; Nowicki et al., 1998; Riede, Suthers, Fletcher, & Blevins, 2006; Westneat, Long, Hoese, & Nowicki, 1993). This trade-off results in a triangular distribution of trilled vocalizations, such that slowly produced trills have narrow or wide frequency bandwidths while rapidly produced trills are restricted to narrow bandwidths (Podos, 1997). An upper boundary on this triangular distribution is considered an estimate of the 'performance limit' (Podos, 2001), and deviation from this limit may be an indicator of performance of the motor constraint such that songs closer to the limit (smaller deviation) are of higher performance. Note that birds can achieve the same vocal deviation value in their songs by changing either trill rate or frequency bandwidth. Hereafter, we refer to vocal deviation as 'vocal performance', such that high-performance songs show smaller deviation and low-performance songs show larger deviation from an upper-bound regression line.

Numerous studies have tested whether this measure of vocal performance is an index signal. These experiments demonstrate that females prefer high-performance songs over low-performance songs (canaries, *Serinus canaria*: Drăgănoiu, Nagle, & Kreuzer, 2002; swamp sparrows, *Melospiza georgiana*: Ballentine, Hyman, & Nowicki, 2004; Lincoln's sparrows, *Melospiza lincolnii*: Caro, Sewall, Salvante, & Sockman, 2010; banded wrens, *Thryophilus pleurostictus*: Cramer, Hall, de Kort, Lovette, & Vehrencamp, 2011; singing mice (*Scotinomys* spp.): Pasch, George, Campbell, & Phelps, 2011). Additionally, males respond to variation in vocal performance during competition (Cramer & Price, 2007; Dubois, Nowicki, & Searcy, 2011; Illes, Hall, & Vehrencamp, 2006; de Kort, Eldermire, Cramer, & Vehrencamp, 2009; Moseley, Lahti, & Podos, 2013), at least in some species (but see Cramer, 2013a, 2013b). Vocal performance also correlates with male quality or motivation in some species. For example, in banded wrens, vocal performance increases with age (Vehrencamp, Yantachka, Hall, & de Kort, 2013) and males with high vocal performance attain more extrapair copulations (Cramer et al., 2011). In swamp sparrows, males with higher vocal performance tend to be older and bigger (Ballentine, 2009). Trill rate also tends to indicate motivation in both of these species (DuBois, Nowicki, & Searcy, 2009; Vehrencamp et al., 2013). Although there is support for the function of performance as measured by vocal deviation in sexual selection, there are differences in the methodological approaches used to test the function of vocal deviation, presenting some unanswered questions (Cardoso, 2017; Kroodsma, 2017; Podos, 2017; Vehrencamp, de Kort, & Illes, 2017).

Most experimental tests of the salience of vocal deviation in male–male competition and female choice maximize one component: either the rate of note production, or the bandwidth of the notes. The majority of these studies found support for a stronger response by receivers to either faster production of notes or to wider bandwidth notes (reviewed in Podos et al., 2009). In studies manipulating trill rate, males respond with more soft songs or an initial approach to high-performance trills (Illes et al., 2006; Moseley et al., 2013) and females prefer fast trills (Pasch et al.,

2011). In studies manipulating bandwidth, males respond more to wide-bandwidth songs either by approaching more closely (Luther, Phillips, & Derryberry, 2016) or by singing more (de Kort et al., 2009). In studies that manipulate both bandwidth and trill rate simultaneously, males respond more strongly to high-performance songs (Dubois et al., 2011) and females prefer high-performance males (Ballentine et al., 2004). In Drăgănoiu et al. (2002), female canaries were presented with three types of trilled songs with varying bandwidth and trill rates. Females performed more copulation solicitation displays to a superstimulus, with a fast trill and wide bandwidth beyond the natural range, but they responded generally equally to lower-performance songs, suggesting that females give equal responses to songs of equal performance, although this was not explicitly tested (Drăgănoiu et al., 2002). Therefore, an empirical question remains as to whether receivers, and specifically male receivers, are responding to the trade-off between trill rate and bandwidth (i.e. vocal deviation), or only to variation in one of the component parts.

Here, we test the hypothesis that trill rate and bandwidth are both important components in the assessment of vocal performance in male–male competition using white-crowned sparrows, *Zonotrichia leucophrys*, as our study organism. Previous work indicates that male white-crowned sparrows respond more strongly to wide-bandwidth songs compared to narrower-bandwidth songs (Luther et al., 2016) and to higher-performance songs than to lower-performance songs when both trill rate and frequency bandwidth are manipulated concurrently (Phillips & Derryberry, 2017). The question remains in white-crowned sparrows, as in other taxa, whether males respond specifically to variation in vocal deviation, or to variation in trill rate or bandwidth alone. Using a repeated measures design, we tested males' responses to songs with a fast trill and wide bandwidth (high performance), a fast trill and narrow bandwidth (mid-performance) and a slow trill and wide bandwidth (mid-performance). We predicted that males would (1) respond more strongly to songs with a fast trill rate compared to a slower trill rate, (2) respond more strongly to songs with a wide bandwidth compared to narrower bandwidth and (3) respond similarly to songs with similar vocal deviation values (fast trill and narrow bandwidth versus slow trill and wide bandwidth).

METHODS

Location and Subjects

We tested territorial males at the Abbott's Lagoon and Kehoe Beach region in Point Reyes National Seashore, California, U.S.A., during June (mid-breeding season) in 2015 and 2016. The habitat is coastal scrub, which consists of low-lying shrubs, dominated by coyote bush, *Baccharis pilularis*, various lupines (*Lupinus* spp.) and poison oak, *Toxicodendron diversilobum*. In this species, males in the same location tend to produce the same song type, known as a 'dialect' (Marler & Tamura, 1962, 1964). All males sang one song type, which was the 'McClure dialect' as described in Baker and Thompson (1985).

Recording Birdsongs in the Wild

In 2014 and 2015, we recorded songs from the McClure dialect in Point Reyes with a digital Marantz PMD 661 and a Sennheiser ME-62 omnidirectional microphone with windscreen mounted onto a Saul Mineroff SME-100 Parabola. Songs were recorded at 44.1 kHz and stored in uncompressed Wave format. We drew from these recordings to create stimuli for playbacks.

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