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Song length variation serves multiple functions in the white-crowned sparrow

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Abstract A wide variety of hypotheses has been proposed to explain the structural diversity in bird song repertoires. Song diversity is frequently described in terms of song "types" or within-type "variants." Male Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*, produce variants of their single adult song type by altering the number of repetitions of syllables in the terminal trill. We tested whether variation in trill length correlated with distance to the receiver and with signaling context as predicted by the eavesdropping avoidance hypothesis and the strategic signaling hypothesis. In accordance with the eavesdropping avoidance hypothesis, males sang variants with shorter trills, and sang quieter and less frequently when near their mate during the incubation phase than during spontaneous singing while unpaired. Males also sang variants with short trills, but at a high rate and variable amplitude when within 10 m of an opponent during close male–male territorial interactions. In agreement with the strategic signaling hypothesis, males decreased trill length immediately before chasing an opponent, but did not change length consistently prior to flight. We conclude that the occurrence of short quiet songs sung near the mate agrees with predictions of the eavesdropping avoidance hypothesis, while short songs sung near other males are best explained by the strategic signaling hypothesis. Trill length variation may be a conventional signal of aggressive intentions in male–male contests stabilized by receiver-imposed retaliation costs.

Keywords Bird song · Puget sound · White-crowned sparrow · *Zonotrichia leucophrys pugetensis* · Song length · Song repertoire · Strategic signal · Conventional signal

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Introduction

Much research has focused on the function(s) of repertoires of song types in birds. An appreciable minority of species (~25%), however, sing but one song type (MacDougall-Shackleton 1997). To some degree, the definitions of song type and repertoire size are arbitrary, as there is always acoustic variation from one song token to the next, and researchers may disagree on whether they classify song variation into song types or variants, or instead consider song to vary along a continuum (Marler 1982; Podos et al. 1992). The recognition of song types implies a relatively discrete pattern of pronounced acoustic variation, while song variants are commonly thought to represent minor variations within types (Stoddard et al. 1988; Searcy et al. 1995).

The numerous hypotheses to explain repertoires of two or more song types differ in whether song types are assumed to convey the same or different information, whether song is addressed to male or female audiences, and whether songs are honest indicators of the signaler's quality (Nelson and Croner 1991; MacDougall-Shackleton 1997). Hypotheses developed for the function of song-type repertoires can also be applied to those species with one song type by examining when and where males produce variants within their single song type. Song-type variants may take the form of altering the number of repetitions of a song element and thereby altering song length [e.g., great tit, *Parus major* (Langemann et al. 2000); chiffchaff, *Phylloscopus collybita* (McGregor 1988)], or by changing the amplitude or frequency structure of songs [e.g., Kentucky warbler, *Oporornis formosus* (Morton and Young 1986); black-capped chickadee, *Poecile atricapilla* (Otter et al. 2002)]. Here, we examine factors that influence song variants in length and, to a lesser extent, amplitude, in the Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*.

Most adult white-crowned sparrow males sing a single song type consisting of a stereotyped sequence of phrases (Fig. 1). The order and structure of whistle, buzz, note complex, complex syllable, and trill phrases differs among geographic dialects, but is rigidly stereotyped within adult individuals (Marler and Tamura 1962; Baptista 1975). Given this stereotypy in sequencing of phrases within songs, one obvious way in which males can vary song structure is by altering the number of repetitions of simple syllables in the terminal trill.

Two factors that could influence the use of song variants that differ in length are the distance to receivers and the signaling context. When song is broadcast over long distances, as in advertisement of territory ownership to distant male neighbors and prospecting females, the frequency and temporal structure is degraded due to scattering and reverberation (Wiley and Richards 1982). Repetition, both of songs and of syllables within songs, will increase the probability of signal recognition (Brumm and Slater 2006). Increased signal amplitude at the source will also increase the distance over which song can be detected (Brenowitz 1982). In some short-distance signaling contexts, however, it may be advantageous to minimize the likelihood that the signal will be intercepted by individuals other than the intended receiver ("eavesdropping avoidance" hypothesis; Dabelsteen 2005). Such contexts may include agonistic interactions between males, courtship singing prior to copulation, and communication in the presence of predators (Dabelsteen et al. 1998). As predicted, several species produce quieter, shorter songs in these contexts than during broadcast advertising (Dabelsteen et al. 1998). The eavesdropping hypothesis makes no necessary prediction as to whether the basic message of short quiet song differs from that of broadcast song.

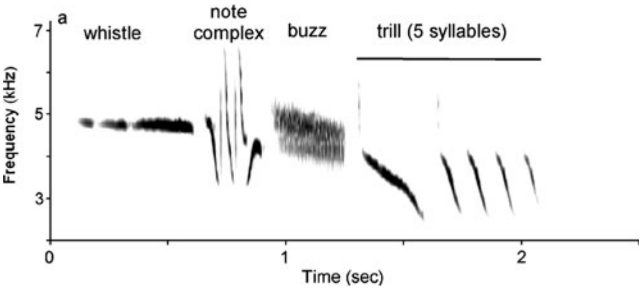

Fig. 1 Song of a male Puget Sound white-crowned sparrow illustrating song terminology. Spectrogram generated in Signal (Engineering Design) with a 256 point FFT from a file digitized at 25 kHz, step size 3 ms (frequency resolution=98 Hz, temporal=10 ms)

Other hypotheses do assume that different signals convey different messages. One, the "strategic signaling" hypothesis states that signals can be used by any contestant irrespective of quality or ability (Hurd and Enquist 2005; Searcy and Beecher 2009), and signal honesty is maintained either by production costs or the cost of evoking retaliation from receivers (Vehrencamp 2000). This hypothesis predicts that different song variants should be reliably associated with different subsequent behaviors by the signaler (attack, flee, etc.). Song length is one feature, along with song rate, song-type matching, switching or song overlapping that can potentially vary on a short time scale (Todt and Naguib 2000) and thus could be used to communicate information about a signaler's intentions. Variation in song length has been studied in several bird species and has been linked to signaling variation in aggressive tendencies in most of these studies [willow warbler, *Phylloscopus trochilus* (Järvi et al. 1980); coal tit, *Parus ater* (Adhikerana and Slater 1993); great reed warbler, *Acrocephalus arundinaceus*, (Catchpole 1983); bobolink, *Dolichonyx oryzivora* (Capp and Searcy 1990); blue tit, *Cyanistes caeruleus* (Poesel et al. 2004)], but has also been suggested to signal male quality in the great tit (Lambrechts and Dhondt 1987) and blue tit (Kempenaers et al. 1997; Poesel et al. 2001).

Here, we investigate how song length varies with distance from the receiver and context in a species with a single song type. We also compared song rates in different contexts, as a decrease in song rate should minimize detection by eavesdroppers in certain contexts. We observed singing males while unpaired early in the breeding season, when singing near their mate, and during close-range singing interactions between two males at territory borders. This allowed us to test the eavesdropping avoidance hypothesis in male–male and male–female signaling contexts. We also tested the strategic signal hypothesis in male–male interactions by examining whether variation in song length contains information about the signaler's immediate aggressive intentions.

Materials and methods

Field methods

We studied a population of Puget Sound white-crowned sparrows at Bullard's Beach State Park, Bandon, OR, USA, in April 2004 and between late March and June in 2005 to 2008. The study site consisted of a 3.5-km-long sand spit at the mouth of the Coquille River. Most territories were in coastal dune habitat with European beach grass, *Ammophila arenaria*, as the dominant ground cover. Males favored shore pine, *Pinus contorta*, and gorse, *Ulex europaeus*, as song perches (Baptista 1977) most of which were less than 2 m high. About 12 males bred in a picnic area with a grass lawn. Male *Z. leucophrys pugetensis* arrived from their winter quarters in California beginning in late March. Females and yearling males arrived on average about 2 weeks after adult males (Nelson and Poesel 2009).

We mapped song posts with a Magellan 315 GPS unit. We calculated the approximate center of each territory using the averaging tool in GPSUtility (GPS Utility Ltd.), and then calculated the average distance to the center of each immediate neighbor's territory. Because territory boundaries changed little from year to year, we present the average distance between territories for 65 males in 2005 only.

We caught males usually within 1 week after their arrival in mist nets or Potter traps and color-banded them. Banded males that had held a territory at the site in a previous year are termed "returns;" unbanded males that occupied a territory for the first time are termed "recruits," which were most likely yearlings (Nelson and Poesel 2009). We estimated clutch initiation date by searching for nests, aged nestlings (Banks 1959) and calculated hatching date by subtracting the 12-day incubation period plus 1 day for each egg, from chick age.

We recorded songs using a Sony TCD-D10 Pro II digital tape recorder (Sony Corporation, Tokyo, Japan) or a Marantz PMD670 solid-state recorder (Marantz Professional, Kanagawa, Japan) sampling at 48 kHz, 16-bit amplitude resolution, and Sennheiser MKH70 or ME67 "shotgun" microphones (Sennheiser, Wedemark, Germany) and Rycote windscreens (Rycote Ltd, Stroud, U.K.). For analysis, songs were digitized at or resampled to 25 kHz with 16-bit amplitude resolution using the Signal software package (Engineering Design; Berkeley, CA, U.S.A.). Assistants viewed all songs in the recording using a program in Signal that displayed each song sequentially on the computer monitor using constant settings (screen width=3 s, frequency range= 2–8 kHz, time resolution=10 ms, frequency resolution= 98 Hz, as shown in Fig. 1). Each song was first high-pass filtered above 1,500 Hz to remove surf and wind noise. The amplitude gray scale was then set to range between−12 and−36 dB relative to peak amplitude in the displayed song, so that faint syllables would have a constant probability of being detected across recordings. These amplitude values were selected after a period of trial and error. The observer counted the number of trill syllables in each song and coded the bird's behavior after each song (chase, fly, feed, call, stay). Observers were not informed of the hypothesis under study. We also calculated song rate over the period of observation. To assess interobserver reliability, four observers viewed a set of 88 songs displayed as described above. Two songs were chosen without regard for recording quality or song length from each of 44 recordings of different males. We then calculated correlation coefficients between the trill syllable counts made by each observer (Martin and Bateson 2007), converted each to Z-scores, and calculated the average correlation back-transformed from the mean Z-score. The six correlations averaged 0.989 (n=88), indicating that syllable counts are highly reliable. We used the number of trill syllables in the song as a proxy for song length because the two measures are highly correlated and trill syllables are easy to count (r=0.77, P<0.001, n=88 songs, range of number of trill syllables=0 to 8).

Song contexts

We performed 20-min-long focal watches on 45 unpaired males in March or April from 2005 to 2007, on average 9.9± 9.4 days after the male's arrival on territory. In this set of focal watches, single males sang undisturbed on their territories, usually countersinging with one or more distant neighbor(s), and we refer to this set of observations as "spontaneous" singing. We excluded any focal watches that had a territory intrusion from this sample. Focal watches were conducted between 0600 and 1030 hours in all weather other than heavy rain. The subjects of each day's focal watches were chosen in advance, and focal watches began as soon as the observer was in position on the subject's territory. Twenty-five (55%) of the subjects were returning males.

Male white-crowned sparrows sang prior to pair formation, and fell silent once paired unless challenged by a territorial intrusion. During our daily field work, we noted when paired males resumed singing 2–4 weeks after pair formation around the time incubation began (median date of first egg=14 May, median silent interval from pairing to resuming song=24 days). Males resumed singing a median of 0.5 days prior to egg-laying, but the range was large (first quartile=6.75 days before, third=1.75 days after, n=20). Males continued to sing throughout the incubation, nestling and fledgling stages. To compare songs of males when unpaired and paired, we performed 20-min-long focal watches on the same 45 males later in the same year an average of 6 days after singing resumed in the 26 males that were paired (median date of all second focal watches=10 May; range=21 April to 1 June).

We also analyzed 23 observations of interactions between two males at shared territory boundaries in March and April. The 23 interactions were observed for a median of 10.5 min (quartiles=6.3, 20 min). In 16 of the 23 interactions at a shared territory boundary, one interactant was a territory resident and the other was a new arrival (within the past 3 days of the recording date). The other seven interactions had no clear asymmetry between the interactants: either both males were residents or both had arrived within the past 3 days. In the 23 close interactions, we also estimated the distance between birds as less than or greater than 10 m throughout the interaction. To test whether trill length varied with the distance to the receiver, we compared mean trill length of all songs sung within 10 m of a male receiver to songs sung more than 10 m in a within-male analysis.

Statistical analyses

Sample sizes varied for different tests and individual males were only used once in a sample. We used mean trill length and mean song rate calculated for each male in each focal watch and *ad libitum* sample as the random variates in statistical comparisons. We compared song rates between contexts because the eavesdropping avoidance hypothesis predicts low song rates to minimize the probability of detection by eavesdroppers. The data on trill length and song rate could not be transformed to normal distributions, so we used nonparametric tests. We report exact two-tailed probability levels, and we used the Benjamini–Hochberg procedure to control the false discovery rate at 0.05 for the group of nine related tests used to test the eavesdropping avoidance hypothesis (Benjamini and Hochberg 1995). Statistical calculations were performed in SPSS 17. We present medians as the measure of central tendency with the first and third quartiles.

Strategic signaling

The strategic signaling hypothesis predicts that future signaler behavior should be predictable from song structure. In the sample of 23 interactions at territory borders, 20 interactions included chases or flights. To examine whether variation in trill length correlated with the singer's subsequent behavior, we counted the number of trill syllables in songs. We also noted behavior during the interaction, i.e., whether males chased ($n=16$ males), or flew from the opponent ($n = 14$ males) within 12 s of a song. Twelve seconds is approximately the average song period in close singing interactions (see below). We also recorded the interval between the song immediately preceding the behavior (Song-1) and the behavior. We did this to check whether the length of Song-1 was affected by the interval between singing and behaving (chase *versus* fly). A chase involved direct flight or movement at the other bird; a flight involved flying in any direction other than toward the other bird and was not preceded by chase initiated by the other bird. To control for possible individual differences in trill length and to test whether a change in trill length correlated with subsequent behavior by the singer (chase, flight), we subtracted the number of trill syllables in Song-1 from the number of trill syllables in the song two songs prior to the behavior (Song-2). Using a random number generator, we also randomly chose two consecutive songs for the same male in the interaction when the singer did not chase or fly after the last song in the pair, i.e., "stayed," and calculated the difference in trill length between these two songs. For interactions that included multiple attacks or flights by the same individual, we calculated the average number of trill syllables in each song for each male. We modeled the effect of one independent variable, change in trill length, on the relative probabilities of subsequent signaler behavior, either chase, flight or staying using multinomial logistic regression in SPSS 17. We set the probability of staying (P_{stay}) as the reference behavior and fit the model $\log(P_{\text{behavior}}/P_{\text{stay}})=\beta_0\pm\beta(\text{trill length change})$, where behavior was either chase or flight. We transformed the log-odds ratio for the β terms to the odds ratio by calculating e^{β} and present 95% confidence intervals. The odds ratio expresses the change in $P_{\text{behavior}}/P_{\text{stay}}$ for a unit change in trill length.

Results

Singing behavior

When countersinging with distant territory neighbors, or when (rarely) singing alone, unpaired males in March and April sang a median of four trill syllables per song (total of 2,206 songs measured for 45 males; quartiles=1, 4). These songs were usually delivered while perched above the ground in a tree or bush, but males occasionally sang while foraging on the ground. The median distance between territory centers in 2005 was 107 m ($n=64$ territories, quartiles=85, 123 m).

Across males, the frequency distribution of trill lengths was bimodal: 30% of songs had short trills, defined here as zero or one trill syllables, the remainder averaged four trill syllables (Fig. 2a). Very rarely, (<0.5%) songs lacked a buzz and/or note complex in addition to the trill. Within individual males, trill lengths also tended to occur in two variants or modal patterns: the frequency distribution of trill length was either unimodal with a peak at zero to one syllable or a peak at three to four syllables (long trills) or bimodal with both of these peaks. About half the males (23 of 45, 51%) sang long trills in 85% or more of their songs within the focal sample (Fig. 2b). Fourteen males (31%) mixed both long and short trills with neither category of trill lengths exceeding 85% of songs in the focal watch (Fig. 2c). Males that sang long and short trills tended to sing them in bouts of either variant rather than alternating between long and short trills. Eight males (18%) sang short trills in at least 85% of their songs (four of these males

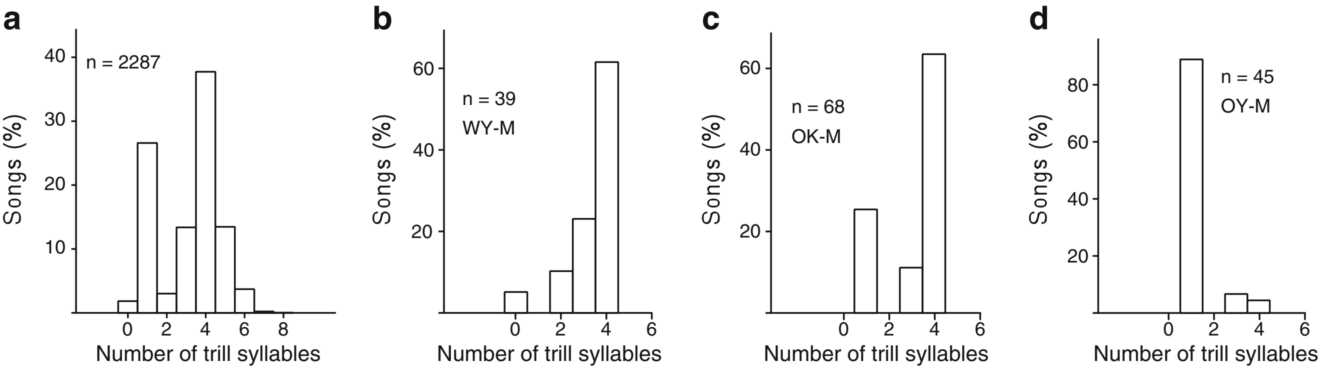

Fig. 2 **a** Distribution of trill lengths in 2,206 songs of 45 unpaired males singing alone on their territories early in the season in 20-min-long focal watches. **b–d** Trill length in songs of three different males during one focal watch each. See text for description

never sang trill syllables in our samples; Fig. 2d). Overall, males favored long trills when singing alone on their territories early in the year, but not uncommonly sang short trills as well.

Eavesdropping avoidance hypothesis

In accordance with the eavesdropping avoidance hypothesis, short trills were common in two contexts where the presumptive receiver was close to the singer. The first context was when paired males resumed singing about the time their mates began egg-laying and continued through incubation. In the analysis of focal watches, paired males sang shorter trills in May/June than when they were unpaired earlier in the season (Fig. 3a; Wilcoxon matched pairs, T=30.5, exact P<0.001, n=26 males, P_{critical}=0.028 for multiple comparisons). Males that never paired decreased trill length somewhat late in the breeding season, but not significantly so (Fig. 3a; Wilcoxon matched pairs, T=70.5, exact P=0.34, n=19 males;). We frequently observed paired males fly to a perch nearby the nest and start singing songs with short trills. These songs usually sounded quieter than broadcast songs, but we did not quantify song amplitude in this study. If the female came off the nest, the male then followed her as she fed.

Secondly, songs with short trills also commonly occurred in close territorial interactions. Trill lengths were significantly shorter in the 23 close male–male interactions (n=40 males) compared to spontaneous singing (n = 45 males) in March and April (Fig. 3b, U=576.5, exact P=

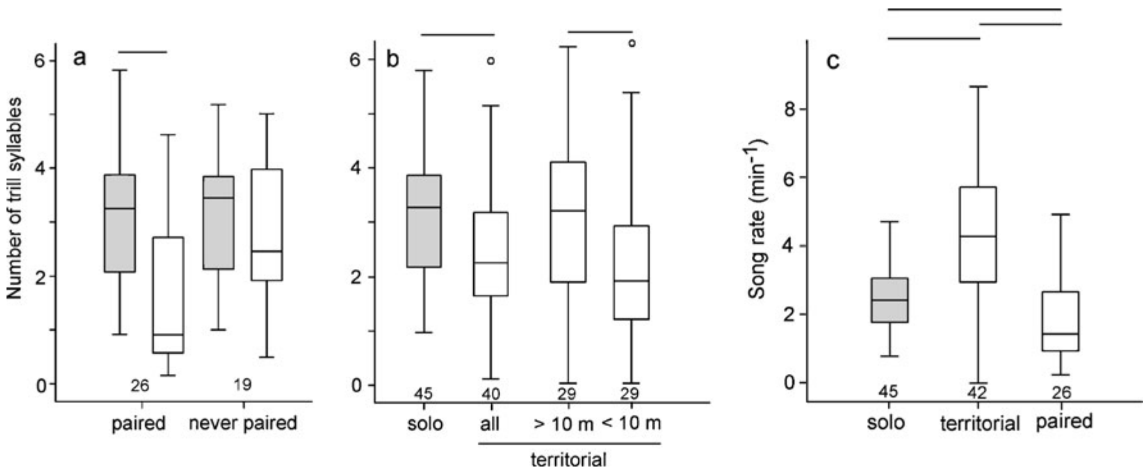

Fig. 3 Comparison of mean trill lengths (**a**, **b**) and mean song rates (**c**) in three contexts. **a** Songs of males that eventually paired and that never paired early in the season (*shaded bars*) and around the time incubation began in the population (*open bars*). **b** Spontaneous solo singing by unpaired males early in the season (*shaded bar*, the two shaded bars in **a** pooled), all songs in close interactions at a territory border pooled, and those songs in a subset of close interactions when <10 m or >10 m from opponent. **c** Song rates in spontaneous solo singing by unpaired males, in close territorial interactions by two males, and by paired males singing near their mate. The *lower* and *upper* edges of the boxes represent the first and third quartiles, the *horizontal line* within each box represents the median. The *vertical lines* (‘whiskers’) include the range of values within 1.5 times the interquartile range. Individual outliers are *small open circles*. Groups that differ significantly are connected by *horizontal lines* at the top. *N* males is given *below* each box

0.004). All but two males sang in these territorial interactions, in which both males typically walked along the ground usually within 1 m, alternating between apparent feeding and singing. In many cases, short songs in male–male interactions sounded quieter than broadcast song, especially when males were <10 m, but loud songs by one or both males also occurred. Within these close territorial interactions, trill length varied with the distance between interacting males: interactants sang significantly shorter trills within 10 m of an opponent compared to when the same male sang more than 10 m from the opponent (Wilcoxon matched pairs: $T=83$, $n=29$ males (13 of the 42 total males did not sing in both distance categories), exact $P=0.01$; Fig. 3b).

To minimize eavesdropping, males should also decrease song rates when the receiver is close by, but this prediction was true only in male–female signaling (Fig. 3c). There was no difference in song rate early in the season between males that later became paired ($n=26$) and those that did not ($n=19$), so we combined these males in the following comparisons (Mann–Whitney $U=197.5$, exact $P=0.26$). Song rates also did not differ between residents (median=4.7 songs/min) and new arrivals (median = 4.6) in close male–male interactions, so all chasing males were lumped in the following comparisons (Mann–Whitney $U=119.5$, exact $P=0.99$; $n=16$ interactions). Song rates by paired males when near their mates were significantly lower than when unpaired males sang earlier in the season (Mann–Whitney $U=372.5$, exact $P=0.011$, $n=26$, 45) and when males sang in close territorial interactions (Mann–Whitney $U=309$, exact $P<0.001$, $n=26$, 42; Fig. 3c). In contrast to the prediction from eavesdropping avoidance, song rates were significantly higher in close male–male interactions compared to spontaneous singing in March and April (Fig. 3c, Mann–Whitney $U=454$, exact $P<0.001$, $n=42$, 45).

Strategic signaling

If trill length provides reliable information about signaler intentions, future signaler behavior (chase, flight, or stay) should be predictable from variation in trill length. In the territorial interactions, the change in trill length from Song-2 to Song-1 was significantly related to variation in the relative probability of subsequent signaler behavior (Likelihood ratio test $\chi^2=11.34$, $df=2$, $P<0.003$). Males decreased trill length by an average of one syllable from one song (Song-2) to the next (Song-1) immediately prior to chasing the opponent (Fig. 4). The odds ratio of chase/stay $\beta=2.69$ (95% CI=1.24–5.53; $P<0.01$), indicates that the probability of chase relative to stay increased 1.69-fold as trill length decreased by one syllable from Song-2 to Song-1. Males did not significantly change trill length prior to a flight away from an opponent (flight/stay $\beta=1.09$ (95% CI=0.54–2.18, $P>0.80$). The change in trill length between Song-2 and Song-1, or the length of Song-1 itself, appeared to be the important predictor of future behavior, as the length of the trill in Song-2 did not vary among the three subsequent behaviors (Fig. 4, Kruskal–Wallis $\chi^2=0.10$, $df=2$, $P=0.95$). The median interval between Song-1 and chasing [6.2 s (quartiles=3, 9.5)] did not differ from the interval between Song-1 and flying [10.3 s (4, 12); Mann–Whitney $U=76$, exact $P=0.142$, $n=14$, 16]. Chasing or flying by the signaler might be contingent on the receiver's behavior, i.e., a retreat by the receiver may remove the need to follow-through with a chase (Nelson 1984), but in no case did we observe the receiver move toward or away from the signaler in the interval between the signaler's Song-2 and his chase or flight. Resident males performed 11 chases, newly arrived males performed the other five (binomial test, exact $P=0.21$). All but one chase ($n=16$) occurred when the birds were less than 10 m apart.

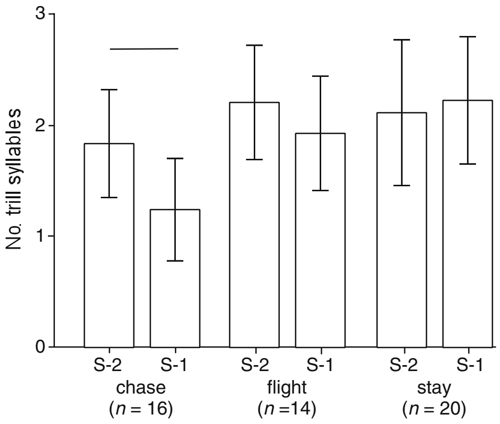

Fig. 4 Trill length of the two songs (S-2 and S-1) prior to chasing the receiver, flight, or staying in male–male territorial interactions. Males decreased trill length significantly prior to chasing. Means ± SE are shown

Discussion

Within the adult repertoire of a single song type, male Puget Sound white-crowned sparrows sang one or two song variants that differed in the length of the terminal trill (Fig. 2b–d). Males sang these variants depending on distance to the receiver and context. Consistent with predictions of the eavesdropping avoidance hypothesis, males sang shorter trills when the receiver, either male or female, was nearby than when broadcasting song over long distances. Males shortened their songs even more immediately prior to chasing an opponent, supporting the hypothesis that trill length is a conventional strategic signal of aggression.

Rather than choose trills from a continuously graded series of lengths, male white-crowned sparrows appear to emphasize either short or long trills, with minor variation within these variants or modal patterns (Fig. 2). Trill length can vary in either a continuous, graded fashion, or discontinuously if males favor a restricted set of trill lengths when singing. While a continuously graded signal is, in theory, capable of encoding more precise information than a set of discrete signals, discrete signals have the potential advantage of imposing fewer cognitive demands on receivers and perhaps are easier to discriminate in a noisy environment (Morris 1957; Green and Marler 1979). Because trill length falls into two natural categories (*sensu* Marler 1982), we suggest that white-crowned sparrows sing a repertoire of two song subtypes, variants, or modal forms within the single type that most adult males sing. Trill length does vary somewhat within each variant; perhaps most significantly in close singing interactions at territory borders (see below).

Prior to pairing when singing undisturbed on their territories, most males favor songs with long trills averaging four syllable repetitions (Figs. 2 and 3). Males sing a song variant with a shorter trill, even omitting the trill entirely, in two contexts: when singing near their mate several weeks after pair formation, and in male–male territorial boundary disputes (Fig. 3a, b). In close male–female interactions, the observations of shorter, and often quieter, songs support the eavesdropping avoidance hypothesis. Male white-crowned sparrows start to sing short songs when their mate is fertile and continue to sing during incubation. The function of songs may vary in these two contexts: During the fertile period, short songs may function in courtship and/or reproductive stimulation of the female. Here, the short quiet songs may restrict the signal to the female without alerting potential kleptogamists (Dabelsteen et al. 1998). The private nature of this singing argues against Møller's (1991) hypothesis that song at this time in the breeding cycle functions as a paternity guard.

The quiet short songs by paired males during the incubation phase may function as an "all-clear" signal to the incubating female, as has been described in other species (Stork 1971; Ziolkowski et al. 1997; Wingelmaier et al. 2007). Males usually sang within 10 m of the nest and so could probably be heard by the female, while not attracting distant predators such as American crows (*Corvus brachyrhynchos*) and possibly Steller's jays (*Cyanocitta stelleri*) to the nest. Crows are abundant at our study site and are probably the main avian nest predator. The short songs usually contain a note complex which differs between males and is used by males in individual recognition (Nelson and Poesel 2007). Possibly females use the note complex to recognize their mate as well since females often leave the nest after males begin singing nearby. We have not tested responses of incubating females to playback but have noted that females often leave the nest during playback directed to their mate (D.A. Nelson, pers. observation). It would be interesting to test if females leave the nest depending upon song length and amplitude and the identity of the singer (Blumenrath et al. 2007).

Short songs also commonly occurred in close range male–male territorial disputes. In contrast to male–female singing, these songs were not always noticeably quieter than broadcast songs, which is in contrast to predictions of the eavesdropping avoidance hypothesis. Measuring the amplitude of song is difficult under field conditions (Dabelsteen 1981; Anderson et al. 2008; Patricelli et al. 2008), and we did not attempt it here because males move rapidly during territorial interactions. In song sparrows, the measured amplitudes of songs deemed "loud" and "soft" by an observer intergrade (Anderson et al. 2008). The elevated song rate in territorial encounters is also inconsistent with eavesdropping avoidance. The eavesdropping avoidance hypothesis predicts that quiet and/or short songs in a male–male agonistic context should have the benefits of not attracting territory intrusions by other males and of concealing information in the interaction from eavesdropping receivers (Dabelsteen 2005). However, experimental evidence in the song sparrow, *Melospiza melodia*, does not support this hypothesis: territory neighbors intruded more often, not less, after a simulated territory interaction included quiet song (Searcy and Nowicki 2006). We conclude that singing behavior in male–male interactions between white-crowned sparrows is partially consistent with the eavesdropping avoidance hypothesis, but is better explained by the strategic signaling hypothesis.

Immediately before a chase, males shortened their songs. The model of free-strategic signaling assumes that signals are freely chosen by contestants, and the costs inherent in that choice enforce signal reliability (Hurd and Enquist 2005). It is unlikely that shorter songs are energetically more costly to produce than longer songs (Oberweger and Goller 2001), so a handicap cost appears unlikely to apply in this case. It appears instead that variation in trill length most likely qualifies as a conventional signal, in which signal form is arbitrary, and reliability is maintained by receiver-dependent costs (Vehrencamp 2001). Because males sing shorter trills when less than 10 m from the opponent than when more than 10 m away, and all but one attack in our sample occurred when males were less than 10 m apart, an increased risk of receiver retaliation appears to be the likely cost associated with short trills (Vehrencamp 2000). Males appear to probe each other, and both residents and new arrivals attack each other. Differential risks of retaliation may be associated with long and short trill variants. However, just prior to attack males shortened their short trills even further without moving any closer to the opponent. As the males "negotiate" a long-term territory boundary, repeated probes and assessment over the interaction (some chasing bouts lasted 2 or 3 days), coupled with individual recognition by song could limit the ability of a weak male to acquire a larger territory by bluffing increased aggressive tendencies (Van Rhijn and Vodegel 1980).

Shortened trills appear to be honest indicators of impending aggressive behavior in the white-crowned sparrow. Shortened songs in agonistic contexts have been observed in some species [willow warbler, (Järvi et al. 1980), great reed warbler (Catchpole 1983); bobolink, (Capp and Searcy 1990), white-throated sparrow, *Zonotrichia albicollis* (Falls 1969), and chestnut-sided warbler, *Dendroica pensylvanica* (Lein 1978)], but longer songs occur in agonistic contexts in other species (indigo bunting, *Emberiza cyanea* (Emlen 1972), yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Cosens and Falls 1984), coal tit (Goller 1987), dark-eyed junco, *Junco hyemalis* (Titus 1998)). This lack of a uniform trend in song length variation across species supports the interpretation that song length variation is a conventional signal in which aggressive tendencies are coded arbitrarily in different species.

Short songs in white-crowned sparrows may convey a common message in both male–male and male–female signaling contexts indicating that the signaler is likely to interact with the recipient. The response different receivers make to short songs likely depends upon the context in which the signal occurs (Smith 1965). As suggested above, short songs may have several functions in male–female signaling that depend upon the stage of the reproductive cycle. In song-playback experiments, male white-crowned sparrows respond differently to long and short songs (Nelson and Poesel unpublished data). Taken together, the observations and experiments in the white-crowned sparrow suggest that short songs are an aggressive signal in male–male territorial encounters (Searcy and Beecher 2009).

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