Etología, 8:1-7 (2000)

When a bird is tired from singing: a study of drift during the dawn chorus

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Received: 12 May 2000; accepted: 30 May 2000.

Abstract. Many songbirds are discontinuous singers with a relatively small repertoire of song types. They repeat each song type a variable number of times in a song bout with pauses between each strophe, before they switch to another song type. It was first described in great tits *Parus major* that song output declines over time when a male sings a particular song type. This phenomenon is referred to as drift and it is mainly caused by an increase in the pauses between strophes. Drift can be explained either by neuro-muscular exhaustion or by a decline in motivation to sing. We studied the occurrence of drift during a period of high song output (the dawn chorus) in the blue tit *P. caeruleus*. Drift occurred in 31% of 104 recorded song bouts. Most males significantly increased their song output again after switching to another song type. Some evidence suggests that drift in great and blue tits might be used by females as a cue reflecting male or territory quality. The anti-exhaustion hypothesis predicts that males that have a larger repertoire size should show less drift, because they can switch more frequently to other song types and thus avoid neuro-muscular exhaustion. Our data on 20 blue tit males provide at best weak evidence for this hypothesis. However, the prediction can also be tested at the interspecific level, although data on more species are needed. Great tits have the smallest repertoires and the highest levels of drift, while coal tits *P. ater* have the largest repertoires and drift is very rare.

Keywords: Song, Anti-exhaustion hypothesis, Motivation hypothesis, Sexual selection, Blue tit, *Parus caeruleus*.

Resumen. *Cuando un ave se cansa de cantar: un estudio del «decaimiento» durante el coro del alba.* Muchas aves canoras cantan de forma discontinua utilizando un repertorio vocal relativamente reducido. Dentro de cada canción repiten cada estrofa un número variable de veces intercalando pausas entre cada una de ellas, cambiando posteriormente a otro tipo de canto. En el Carbonero común *Parus major* se describió por primera vez que cuando un macho canta un tipo particular de canción, el volumen del canto va disminuyendo de forma progresiva. Este fenómeno se denomina «decaimiento» y está principalmente causado por la duración de las pausas entre estrofas. Este decaimiento puede deberse a la fatiga neuro-muscular o a una disminución de la motivación para cantar. En el presente estudio se analiza la aparición del decaimiento vocal durante un periodo de alto volumen de canto (el coro del alba) en el Herrerillo común *Parus caeruleus*. El decaimiento apareció en el 31% de las 104 sesiones de canto gravadas. La mayoría de los machos aumentaron el volumen de su canto al cambiar a otro tipo de canción. Varias evidencias sugieren que el decaimiento en el volumen de canto en el Carbonero común y el Herrerillo común puede ser utilizado por las hembras como una pista que refleja la calidad del macho o de su territorio. La hipótesis de la anti-fatiga predice que los machos que tienen mayor repertorio vocal deberían mostrar menor decaimiento, debido a que pueden cambiar más a menudo a otros tipos de canto, evitando así la fatiga neuro-muscular. Nuestros datos basados en 20 machos de Herrerillo común sólo proporcionan una débil evidencia a favor de esta hipótesis. Sin embargo, esta predicción puede también analizarse a nivel interespecífico, aunque por el momento se precisa información de más especies. De las tres especies de Páridos analizadas, los Carboneros comunes muestran los repertorios menores y los mayores niveles de decaimiento, mientras que los Carboneros garrapinos *P. ater* poseen los mayores repertorios vocales y la caída aparece raramente.

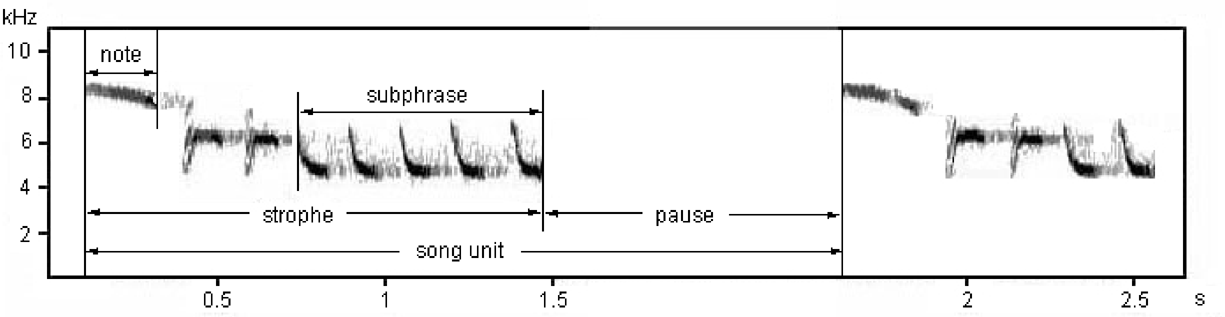

Figure 1.- Sound spectrogram of a strophe of a three-note song type (ST1) of a blue tit *Parus caeruleus* male.

Introduction

Most passerine birds sing multiple versions of the species-specific song. The total number of such song types an individual uses is referred to as its repertoire size. Among species, repertoire sizes can vary from one to several thousand (see Table 8.1 in Catchpole & Slater, 1995). In general, one can distinguish between two groups of species. Continuous singers are those that sing without breaks for a longer period of time by switching continuously from one song type to the next (e.g. the nightingale *Luscinia megarhynchos*). These species usually have large repertoires. Discontinuous singers repeat each song type a variable number of times in a song bout with longer pauses between each strophe (e.g. the great tit *Parus major*). Discontinuous singers usually have relatively small repertoires (Hartshorne, 1956). There is also variation in repertoire size within species: individuals differ in the number of song types they can sing and in the frequency with which they switch between these types. Both song complexity (e.g. repertoire size) and song output (the amount of time spent singing) might reflect a male's singing capacity and might therefore have evolved under sexual selection. Indeed, several studies have shown that females preferentially mate with males with more elaborate repertoires or with the highest song rate (reviews in Andersson 1994, Catchpole & Slater, 1995). Song complexity and/or output might be an indicator of territory quality (e.g. McGregor et al., 1981; Hoi-Leitner et al., 1995), quality of parental care (e.g. Greig-Smith, 1982) or male genetic quality (e.g. Hasselquist et al., 1996).

Despite many studies, the significance of repertoire size and song output in discontinuous singers is far from clear. A detailed study on song type switching in the great tit suggested an interesting link between repertoire size and song output. Lambrechts & Dhondt (1987) noticed that in many individuals the length of the pauses between strophes increased as the bout of one song type continued and that in some cases the strophes also became shorter. Thus, singing the same song type for an extended period of time often led to a decline in the percentage of actual time spent singing (referred to as performance). Lambrechts & Dhondt (1987) termed this decline in performance 'drift'. Lambrechts & Dhondt (1988) proposed a new hypothesis to explain the function of repertoires. The 'anti-exhaustion hypothesis' suggests that singing a long series of strophes of the same song type leads to fatigue in particular syringeal muscles of the singer and therefore to a decline in performance. Switching to another song type involves a different pattern of contractions of syringeal muscles and thus allows the bird to sing at a higher song rate again. Indeed, Lambrechts & Dhondt (1988) showed that great tits increased their performance again after switching to another song type. Thus, a song repertoire might be an adaptation to guarantee a continuous high song output. Although this hypothesis is intuitively attractive, it has been criticised because evidence that singing exhausts the syringeal muscles is lacking. Weary et al. (1988) proposed the alternative explanation that the decline in singing performance reflects a decrease in motivation to sing rather than exhaustion. If drift is caused by a decline in motivation, then a bird should be able to increase its song output after a motivational stimulus has been presented (e.g. a rival song). If drift were caused by neuromuscular exhaustion, birds should not be able to increase song output without switching song types. Weary et al. (1988) tested this prediction by playing song to great tits during the day. They found that males increased song output following each playback presentation but not after a switch to another song type. Lambrechts (1988) suggested that the test performed by Weary et al. was inappropriate, because exhaustion is less likely to happen during the day, when song output is lower. In an attempt to solve the issue, both teams joined forces and compared the response to playback during the dawn chorus (high song output) and during the day (low song output). This study (Weary et al., 1991) showed that drift was more common during the period of high song output (supporting the exhaustion hypothesis), but that the increase in song output after playback was similar during the high and low song output periods (supporting the motivation hypothesis). It was concluded that the two hypotheses are not mutually exclusive.

The phenomenon of drift has not received much further attention: it has been studied in the coal tit *Parus ater* (Adhikerana, 1992) and recently a similar

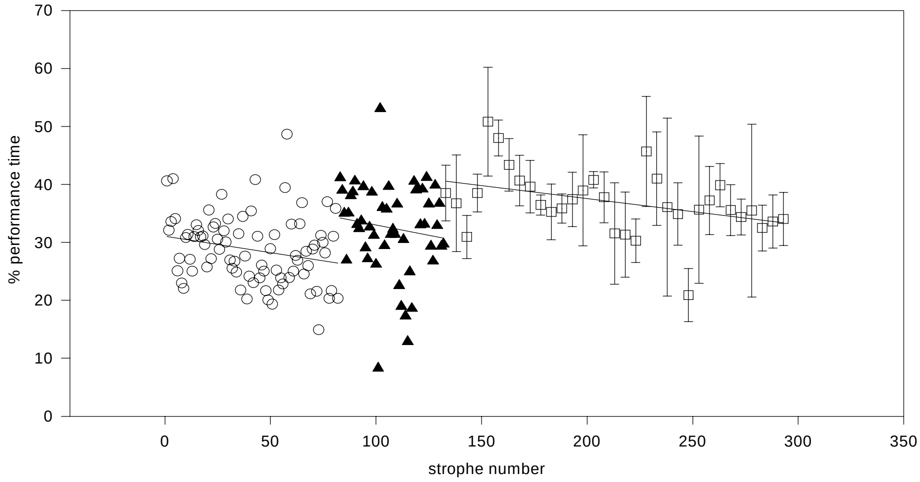

Figure 2.- Decline in percentage performance time in three successive song bouts of male blue tits (circles: ST7, triangles: ST1, squares: ST2); the decline in performance is significant in the first and last bout. Each point in song bout three represents the mean of five song units±s.d. Notice that the performance increases after each switch to a new song type.

phenomenon has been shown in the collared dove *Streptopelia decaocto* (Ballintijn & Ten Cate, 1999). Interestingly, the hypothesis that repertoires are adaptive because they allow individuals to continue to sing with a high song output, has not been tested.

We studied the decline in singing performance over time in the blue tit *Parus caeruleus*. Similarly to great and coal tits, blue tits are discontinuous singers with a relatively small repertoire and they produce a distinct dawn chorus during the fertile period of their mate (Mace, 1987). Poesel et al. (MS) showed that older males sang with a higher performance compared to yearling males and that females mated to males with a higher average performance during the dawn chorus started laying earlier. Thus, there is some evidence that song output is an indicator of male or territory quality in the blue tit. The latter study also found that females mated to males that showed less drift in their song bouts laid larger clutches. The aim of this study is (1) to describe the phenomenon of drift in blue tit song, (2) to compare the frequency of drift among several *Parus* species and (3) to discuss our results in relation to the anti-exhaustion and motivation hypothesis. The anti-exhaustion hypothesis provides an adaptive and mechanistic explanation for the occurrence of a repertoire. If larger repertoires allow individuals to sing continuously with a high song output, one can predict a negative relationship between repertoire size and the occurrence of drift during a period of high song output such as the dawn chorus. Another prediction is that there is a positive relationship between repertoire size and the average performance during the dawn chorus.We investigate these predictions at the intra- and interspecific level.

Methods

We studied a blue tit population in a mixed deciduous woodland at Kolbeterberg in Vienna (48°13’N, 16°20’E), Austria. The study plot of 35 hectares contains 226 nestboxes for blue tits. Most individuals were colour-banded and all breeding attempts were closely monitored as part of a long-term study. Between the 1st and the 21st of April 1998, we recorded 20 male blue tits at dawn using a Telinga Stereo-condenser microphone (Stero-Dat-Mic), mounted in the focus of a Telinga Pro 5 parabolic sound reflector (57 cm diameter), connected to a Sony WM-D6C cassette recorder. Each morning, between 4:29 and 5:34 MEST, we recorded the entire dawn chorus of a colour-ringed male blue tit in the vicinity of the nestbox in which his mate roosted. We stopped recording and considered the dawn chorus as finished when the male did not sing for a minimum of five minutes, while simultaneously engaging in an alternate activity, such as foraging. All males were recorded during the presumed fertile period of the female (between day –8 to 11, where day 0 is the day of the first egg). The recorded song was later analysed using the computer program Avisoft Sonagraph 3.0 for Windows (Specht, 1993). For each strophe, we determined to which song type it belonged (based on the classification by Bijnens 1988; see example Figure 1). We define repertoire size as the number of different song types sung by a male during a single dawn chorus. This is an underestimation of the true repertoire size (i.e. the total number of song types a male can produce), because it is unlikely that each male sung all song types during a single dawn chorus. We noted the number of switches between song types and multiplied this with the number of different song types to calculate versatility. We also measured the following song variables: (1) the duration of each strophe in seconds (strophe length), (2) the duration of the interval between two consecutive strophes in seconds (pause length), (3) the percentage performance time of a song unit (from here onwards simply referred to as performance), calculated as strophe length divided by the sum of strophe and pause length (= a song unit;

Table 1. Within-male comparisons of bout duration, average performance during the entire bout and average performance during the first ten song units of the bout for bouts with and without drift. Data shown are mean±s.e. (n=16 male blue tits).

	Drift			
	Yes	No	T_s^*	p
Bout length (seconds)	342±51	232±25	37	0.110
Performance (total bout)	37.3±1.6	34.3±1.7	28	0.039
Performance (first 10)	40.1±1.5	34.6±1.9	12	0.004
Performance (last 10)	32.2±1.5	33.4±1.8	43	0.200

*Wilcoxon's signed-ranks test (paired observations).

see Figure 1) and multiplied by 100 (%) and (4) the occurrence of drift. To determine the latter, the slope of a linear regression expressing performance as a function of strophe number was calculated for each song bout, i.e. for repetitions of strophes of the same song type. We only included song bouts that consisted of at least ten strophes to ensure that the calculation of drift was statistically meaningful. Following Lambrechts & Dhondt (1986) we concluded that drift occurs when performance declines significantly over time (see Figure 2 for an example). In addition, we considered the change of performance over the entire dawn chorus by calculating the slope of a linear regression expressing the mean performance of a song bout as a function of bout number.

Individuals sing in bouts, i.e. a variable number of phrases of the same song type, before they switch to another song type or stop singing. In total we recorded 104 complete bouts. For each bout we calculated an average strophe length, pause length and performance. We then used the averages of these values over the entire dawn chorus as a measure for individual males. Statistical analyses were performed with the software package SPSS 10.0 for Windows, based on Sokal & Rohlf (1995). All reported tests are two-tailed and based on a sample size of 20 individuals unless stated otherwise.

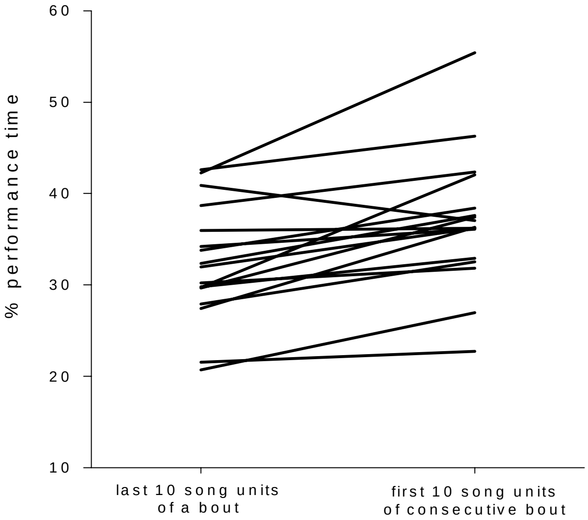

Figure 3.- Change in percentage performance time after a switch to another song type. Data points represent mean values for each male (based on 2-8 consecutive bouts per male; mean: 3.2). The increase in performance after song type switching was highly significant (paired t-test: t=-4.51, d.f.=16, p<0.001).

Results

Variation in song output among individuals

Overall, the recorded song could be assigned to seven song types and individual males had a repertoire of two to five different types. Males sang strophes of a particular song type for a period of time varying between 38 seconds and 23 minutes (bout length). Individual males differed in mean strophe length (range: 1.15-1.72 seconds; Kruskal-Wallis analysis of variance: H=38.6, d.f.=19, p=0.005) as well as in performance (range: 25.0-45.6%; H=55.4, d.f.=19, p<0.001). Average strophe length and performance also differ depending on the song type. Thus differences among individuals might reflect the use of different song types. However, when average measures for each song type are considered as repeated measures for each individual, both strophe length and performance show a significant repeatability (Poesel et al., unpubl.), suggesting that individuals differ in singing performance.

Changes in performance within song bouts

Within a song bout performance increased in 19 (18.3%) but declined in 85 (81.7%) of 104 bouts. The decline was significant, i.e. drift occurred in 32 song bouts

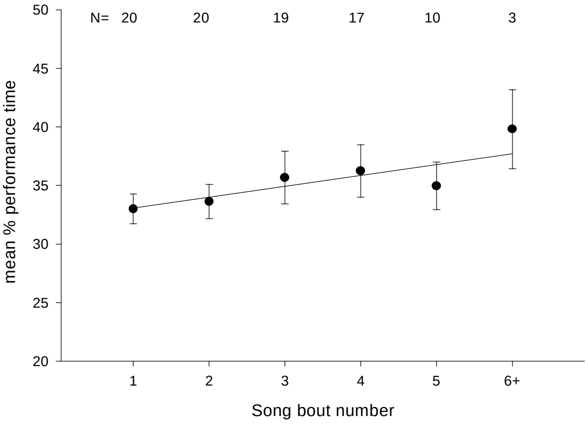

Figure 4.- Mean percentage performance time (±s.e.) of bouts according to their order in the dawn chorus. Numbers at the top of the graph represent sample size (number of males). The regression line is significant (r=0.86, n=6, p=0.03).

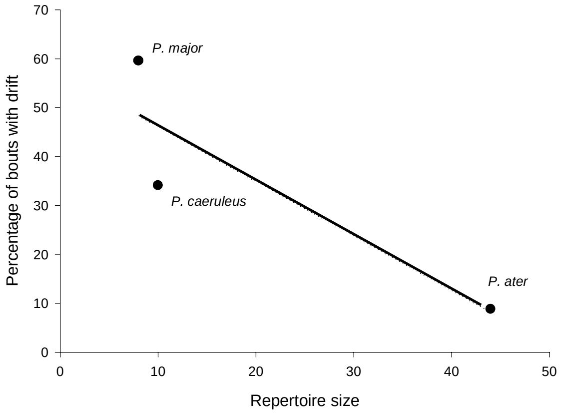

Figure 5.- Inter-specific relationship between the occurrence of drift and repertoire size. Data on repertoire size stem from the following studies: great tit (McGregor et al., 1981), blue tit (Bijnens & Dhondt, 1984), coal tit (Haftorn 1990). Data on the frequency of drift are from the following studies: great tit (Lambrechts & Dhondt, 1988), blue tit (this study), coal tit (Adhikerana, 1992).

(30.8%). Drift was mainly caused by an increase in pause length between the strophes over time, not by a shortening of the strophes. Average performance was negatively correlated with average pause length ($r=-0.69$, $n=20$, $p<0.001$), but not with mean strophe length ($r=0.36$, $p=0.12$).

Bouts with drift were not significantly longer but showed a significantly higher average performance than those without drift (Table 1). The performance at the start of the bout was much higher in bouts with drift compared to those without, but both bout types ended with a similar performance (Table 1).

We compared the performance of the last 10 song units of each bout with the first 10 song units of the consecutive bout. We only used pairs of bouts that followed each other immediately (without a longer than normal inter-strophe pause). In total 55 song switches in 17 individuals could be used. When individuals switched song types the performance increased (e.g. Figure 2) and this increase was highly significant (Figure 3). Only one individual showed a decrease in performance after song type switching. This male sang with a high average performance and did not show drift in any of his bouts.

Changes in song output over the entire dawn chorus

The change in song output over the dawn chorus was calculated as a linear regression of average performance per bout in function of bout number. Eleven males (55%) increased their performance as the dawn chorus proceeded, while nine males (45%) decreased their performance. However, overall, the average performance of bouts increased significantly over the dawn chorus (Figure 4). The change over the entire dawn chorus did not depend on the proportion of bouts with drift (increase: 25% of bouts with drift, range: 0-75%; decrease: 34%, range 0-80%; Mann-Whitney U-test, $U=37$, $p>0.3$).

Repertoire size, versatility and song output

The average performance of a male over the entire dawn chorus showed only a very weak positive correlation with repertoire size (Spearman rank: $r_s=0.15$, $p>0.5$) and versatility ($r_s=0.12$, $p>0.5$). The proportion of bouts with drift was weakly negatively correlated with repertoire size ($r_s=-0.17$, $p=0.49$) and with versatility ($r_s=-0.19$, $p=0.42$).
The frequency with which males switched song types during the entire dawn chorus was only weakly correlated with the total duration of the dawn chorus ($r_s=0.19$, $p=0.41$), but was strongly correlated with repertoire size ($r_s=0.60$, $p=0.005$).

Discussion

Our data show that in the blue tit song output (performance) often declines as males continue to sing the same song type, which was mainly due to an increase of the pauses between successive strophes. Despite the decline of performance within bouts, more than half of the males increased their song output over the entire dawn chorus.

Tired of singing or tired from singing?

Lambrechts & Dhondt (1988) found that two factors influenced the extent of decline in performance throughout a bout: (1) the initial level of song output (the greater the initial output, the greater the subsequent drift) and (2) the number of switches between song types (after each song type switch performance increased again). Our analysis of blue tit song during the dawn chorus confirms both findings: bouts with drift started with a significantly higher performance than bouts without drift and after song type switching performance increased in all but one male. Thus one could conclude that a high output of a stereotyped song is hard to sustain over a longer period, supporting the anti-exhaustion hypothesis. The motivation hypothesis (Weary et al., 1988) would be supported if every change in song type would be the result of an increase in motivation to sing, e.g. via an external stimulus such as a neighbouring male’s song. Although we did not study this, male great tits often respond to a singing neighbour by singing the same song type (a phenomenon called ‘matched countersinging’; e.g. Krebs et al., 1981). A male might experience a song type switch by the neighbour as an escalation of the contest and thus as a motivational stimulus leading to a change in song type and an increased output.

Lambrechts & Dhondt (1988) found a decline in song output of great tits over the entire dawn chorus. They showed that after a switch from one song type to another the initial output level was not reached again. Blue tits, however, tended to increase their song output over the dawn chorus. These changes in song output were not related to the occurrence of drift, i.e. males that showed drift were equally likely to increase their performance than males that did not show drift.

Singing is assumed to be costly either in terms of time or energy. Questions about the energetic expenses of singing remain largely unanswered because direct measurements of energy expenditure during singing are difficult to make (Eberhardt, 1994). Lambrechts & Dhondt (1988) suggested that drift in the song of male great tits might be a result of neuromuscular exhaustion. They argued that this is more likely to occur in the group of discontinuous singers, such as the Paridae, because the repetition of the same song type over and over again uses the same coordination system of muscles and nerves in an extremely stereotyped way. Their idea that switching to another song type overcomes such muscular or neural constraints is based on the assumption that different song types use the coordination system in different ways. A recovery or even an increase in performance over the dawn chorus, as we found in the blue tit, suggests that song type switching is an effective method to overcome exhaustion.

The motivation hypothesis is based on the assumption that variability in song output reflects motivational changes rather than neuro-muscular exhaustion. It predicts that an increase of internal or external motivational factors can lead to a recovery of high song output without a change of song types. Weary *et al.* (1991) tested this prediction experimentally by playing song to male great tits, and found a recovery in song output after each playback. Our observational data show that in some of the bouts with drift performance decreased during the first few strophes, then suddenly increased to a higher output and finally decreased again (see Figure 2). The reason for such a sudden increase of song output within a bout might be a motivational change. Although in this study external influences were not recorded, this confirms that an increase in percentage performance time without a switch to another song type is possible. However, an increase in song output after a motivational stimulus does not exclude the possibility that exhaustion occurs. If you have been running for a long time, your running speed probably declines, especially if you started running fast. In the end you might be really exhausted, but if a dangerous looking dog would cross your path, you might surprise yourself how fast you can run again. Obviously, both exhaustion and motivation are likely to influence performance.

The effects of neuro-muscular exhaustion can also be studied by considering single strophes. In the blue tit, the most common song types consist of three different elements, of which the last one is repeated rapidly in a trill. In some strophes, the notes that make up the trill are repeated more than 30 times. The small pauses between the notes that make up the trill often increase significantly over time, even though an entire strophe lasts only a second or two (our unpublished data). Moreover, in the longest trills, one sometimes observes that the notes at the end become less stereotyped. This strongly suggests that neuro-muscular exhaustion occurs, as it seems very unlikely that within this time period changes in motivation play a role.

Drift and repertoire size

The anti-exhaustion hypothesis predicts that individuals with larger repertoires should be better able to sustain a high song output, because they can change frequently to another song type. However, we only found very weak positive correlations between repertoire size or versatility and performance and very weak negative correlations between repertoire size or versatility and the occurrence of drift. Our sample size (20 males) might be too small to detect a significant effect, especially since repertoire size did not vary much among males (2-5).

The above prediction can also be tested at the inter-specific level. So far, drift has been studied in three species of the family Paridae, the great tit (Lambrechts & Dhondt, 1986, 1987, 1988), the blue tit (Bijnens, 1988; this study) and the coal tit *Parus ater* (Adhikerana & Slater, 1993). Recently Ballintijn & Ten Cate (1999) observed the same phenomenon in the vocalisations of a non-passerine bird, the collared dove *Streptopelia decaocto*. A prerequisite for the occurrence of drift is that birds sing or call discontinuously, i.e. repeat strophes of the same type several times before they switch to another type. For the three *Parus* species, the relationship between the occurrence of drift and repertoire size is as expected under the anti-exhaustion hypothesis (Figure 5). The great tit has the smallest repertoire and the highest proportion of bouts with drift: Lambrechts and Dhondt (1988) observed drift in 31 of 52 bouts. The blue tit has a slightly larger repertoire, and we found drift in 32 of 104 bouts (30.8%) that consisted of at least ten strophes. When including only bouts of at least 20 strophes (as Lambrechts & Dhondt, 1988 did), this figure changed to 34.1% of bouts. Coal tits have much larger repertoires of up to 44 different song types (Haftorn, 1990) and showed drift in only six of 68 (8.8%) of song bouts (Adhikerana, 1992, cited in Catchpole & Slater, 1995). One interesting prediction can be made: the subspecies of blue tits occurring on the Canary Islands (e.g. *P. caeruleus teneriffae*) should show much less drift, because they have much larger repertoire sizes compared to the nominate form (M. Eens et al., unpublished data). Obviously data from many more species or sub-species are needed to provide a solid test of the hypothesis.

The relevance of drift for mate choice

Lambrechts & Dhondt (1986) observed that in the great tit the amount of drift was negatively correlated with the dominance position at a winter feeder, and with survival and lifetime reproductive success. They suggested that drift as well as strophe length gave information about male quality. In blue tits, song strophe length has been shown to correlate with male survival (Bijnens, 1988) and success in gaining paternity (Kempenaers *et al.*, 1997), while Poesel et al. (unpubl.) found that females paired to males which showed drift during the dawn chorus laid smaller clutches. Thus, the occurrence of drift during the dawn chorus might be used by females as a cue to measure singing ability and thus male or territory quality.

Acknowledgements. We thank Kathi Foerster for help in the field, Hans Winkler for support and discussion and Ronald Smetacek for technical assistance.

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