Singing and mating success in water pipits: one specific song element makes all the difference

UELI REHSTEINER, HANNES GEISSER & HEINZ-ULRICH REYER

Zoological Institute, University of Zürich

Abstract. Positive correlations between male vocalization and reproductive success have been documented for many animal species. They are usually based on differences between males in vocalization rate, duration or repertoire size. Here, we present probably the first field study linking differences in territorial overlap and mating status to differences in a single, clearly definable song element, the 'Snarr'. Male water pipits, *Anthus spinoletta*, with high Snarr scores were mated more often than males with low scores, and their territories overlapped less with those of neighbours. Although correlating positively with male body condition, the frequency of the Snarr did not reflect male age, territory size, territory quality in terms of food and paternal performance. Therefore, it seems unlikely that the higher mating success of males with high Snarr scores results from active female choice of high-quality males; rather, high Snarr scores seem to signal dominance in males. Likely mechanisms that produce the link between vocalization and mating success, and potential costs that prevent some males from producing the Snarr at a higher rate, are discussed.
© 1998 The Association for the Study of Animal Behaviour

In recent years, several experimental and comparative studies have demonstrated that males singing or calling for longer, more frequently or with more complex repertoires have higher reproductive success than males with less elaborate vocal performance. Andersson (1994, pp. 132–142) listed more than 60 species with such a relationship, most of them birds and anurans, followed by insects and at least one mammal. The evolution and functioning of vocalizations as secondary sexual characteristics are usually explained by assuming that more elaborate acoustic signals are beneficial in male–male competition and/or female choice, thus providing their bearer with a reproductive advantage over other individuals of the same sex (Catchpole 1982, 1987; Searcy & Andersson 1986). As a necessary, although not sufficient, precondition for achieving such benefits, the trait must contain reliable information about the owner's quality.

For bird songs, several studies have shown that this is true. Song length and repertoire size can be indicators of a male's age, experience and parental abilities in terms of nest defence and chick feeding (Greig-Smith 1982; Searcy 1984; Eens et al. 1991; Lampe & Espmark 1994) and can reflect the signaller's dominance status, body condition, energetic scope and access to food resources (Searcy 1979; Davies & Lundberg 1984; Gottlander 1987; Lambrechts & Dhondt 1988; Ryan 1988; Vehrencamp et al. 1989; Otter et al. 1997). Low singing rates may also betray physiological deficiencies, such as reduced oxygen transport owing to haematophagous mites or insufficient gonadal development and low sperm numbers (Møller 1991).

Thus, using status and other information about quality encoded in a song has obvious benefits for both sexes: a male can avoid unnecessary skirmishes with superior competitors and/or familiar neighbours; a female can reduce her costs of searching for mates and select those individuals as social and/or extra-pair copulation partners that improve her fitness, either directly by enhancing her immediate reproductive success ('phenotypic benefits'), or indirectly by producing offspring that inherit their father's superior condition and, thus, survive and reproduce better ('genetic benefits'; Andersson 1994).

In this paper we investigate the relationship between song and mating success in the water

Correspondence: H.-U. Reyer, Zoological Institute, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland (email: ulireyer@zool.unizh.ch).

pipit, *Anthus spinoletta*, a small, insectivorous, ground-nesting passerine, which breeds in the Alps above the timberline. Given its monogamous social mating system, occasional polygyny and a slightly male-biased sex ratio, some territorial males remain unmated ('bachelors') in any one season (Bollmann 1995; A. R. Schläpfer, unpublished data). With an annual mortality rate of 44% this will result in drastic negative consequences for lifetime fitness. We therefore expected strong selection on traits that improve chances in male–male competition and female attraction, and, since males spend much time in elaborate song-flights, which vary between individuals in repertoire and length, that song would have an effect on mating success.

METHODS

Study Site and Species

We performed the study in the Dischma valley (46°46′N, 9°53′E) near Davos, Switzerland. The valley runs from south-southeast to north-northwest and has a continental or moderate central-alpine climate with average temperatures of −6.1°C in January and +8.9°C in July. Snowfall is possible during every month of the year, even in the lowest parts of the valley. The 200-ha study area lay above the timberline and extended from 1830 to 2300 m elevation. It included the valley floor, mainly covered with pastures, and both slopes where dwarf shrubs, *Juniper*, *Rhododendron*, *Calluna*, and alpine meadows are the dominating vegetation types.

This treeless habitat is the typical breeding ground of the water pipit. The bird is common and widespread above the alpine timberline up to 3000 m elevation (Glutz von Blotzheim & Bauer 1985) with densities between 5.5 and 6.2 territorial males/10 ha during the period of our study (1990–1992). Males return from the wintering areas in April and perform conspicuous songflights which serve to establish territories and attract the females, which arrive a few days later.

Songs and their Analysis

We recorded the songs of 75 males from April to the end of June in 1990, 1991 and 1992. For 71 of them we knew the social mating status, that is,

whether they were monogamous, polygynous or unmated. For several males and females (all of them colour-banded) we also had information about their age ($N=53$), body measurements ($N=43$), territory size ($N=44$), territory-specific food supply ($N=31$) and/or reproductive success ($N=34$). Body measurements were also available for 22 of their females.

Most sound recordings were made between 0530 and 1230 hours, and a few between 1800 and 2100 hours. We used a Sony TC 5-DM tape-recorder, Sony metaltapes and a Technics RP-VK 10 microphone fixed into a 60 cm parabolic reflector. Sonagrams were produced and analysed on a MEDAV colour spectrograph (Digitale Signalverarbeitung GmbH, Uttenreuth, Germany).

Songs produced during flights can be divided into several distinct element types and phrases according to acoustic, sonagraphic and temporal factors (see also Fig. 1a, b).

(1) A-element and -phrase. The first element of a song was termed A. Therefore, by definition, it occurred in every bird's repertoire. Its structure varied considerably between males, but was specific for a particular individual. All A-elements produced in a sequence are called an A-phrase.

(2) B-element and -phrase. The B-element followed the A-phrase and preceded elements C and Snarr. It also varied considerably between birds, resembling the A-element in some birds but not in others, and was totally lacking in the repertoire of about 60% of the males. All B-elements together are termed a B-phrase.

(3) C-element and -phrase. The C-element and -phrase, which occurred after the A- or B-phrase, showed a characteristic sonagraphic picture that hardly differed betwen males.

(4) Snarr-element and -phrase. The Snarr, a strange sounding, rasping or grating element and phrase with a broad frequency band, was always sung after the A- or B-phrase and could follow or precede the C-phrase.

In contrast to the A- and B-phrases which were identified only by their temporal position within a songflight, C- and Snarr-phrases could be recognized by their unique acoustic and sonagraphic patterns. Two further elements (D and E), one occurring in the repertoire of six of the recorded males, the other in the song of only one male, were not included in the analysis.
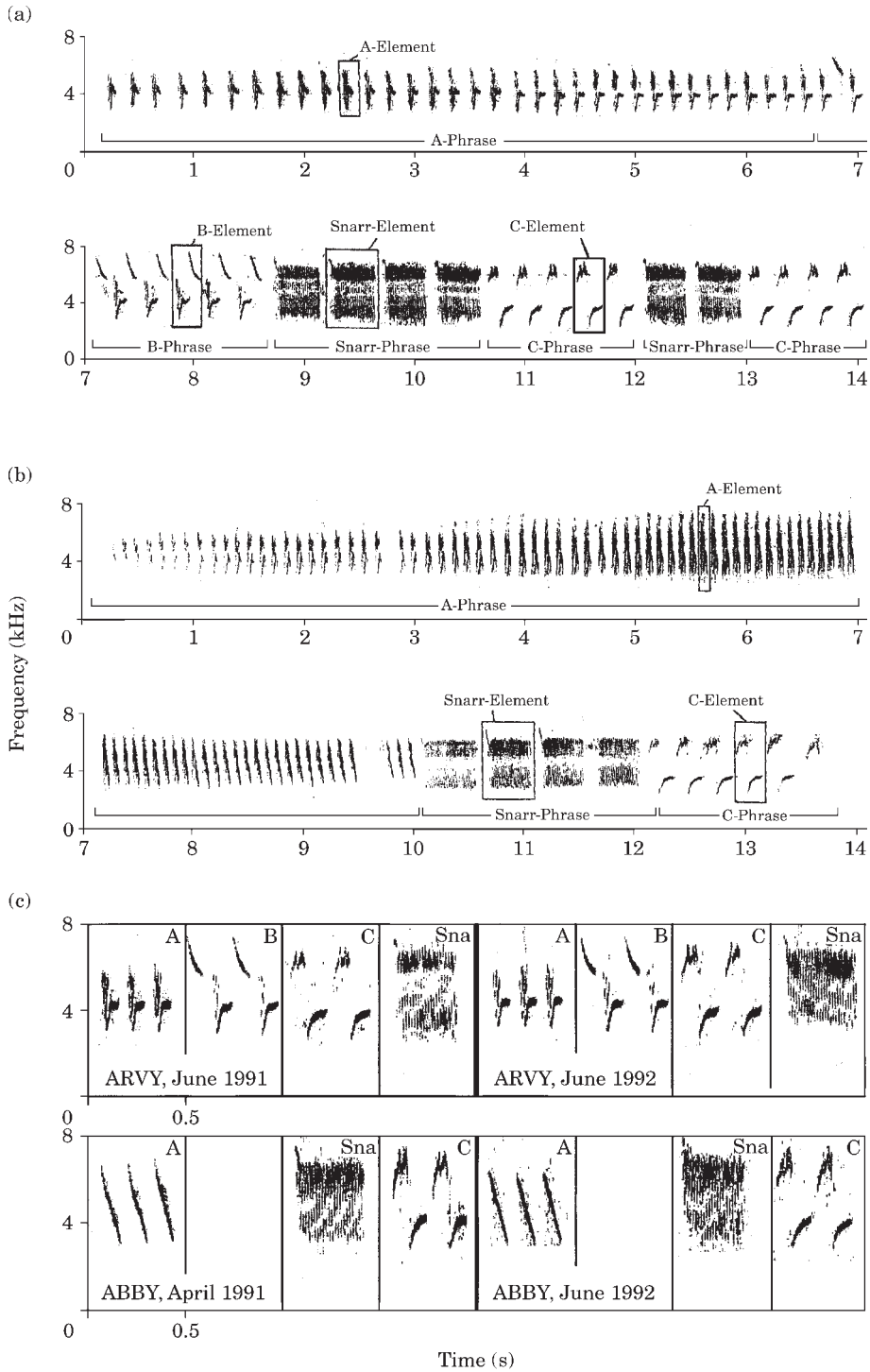
Figure 1. (a, b) Full sonagrams of two unrelated male water pipits and (c) elements of two individuals, each recorded in 2 successive years.

For each male we measured the following 13 time and structure variables (the first, Repsize, applies to the individual, all others refer to each songflight).

Repsize: repertoire size of an individual, that is the maximum number of different elements found in all analysed songs of a particular individual.

Duration: absolute duration (s) of a songflight.

Repused: average number of different element types sung per songflight. Since water pipit males often do not sing their whole repertoire during a songflight, Repused was usually smaller than Repsize.

Totelm: total number of elements in a song flight, irrespective of their type.

Number A (B, C, Snarr): the total number of all A-elements (respectively B-, C- and Snarr-), produced within a songflight.

% A (B, C, Snarr): percentage of A-elements (respectively B-, C- and Snarr-), in relation to Totelm.

Aper3: a rhythm unit, expressed as the number of A-elements within 3 s of the middle, most regular part of the A-phrase. This variable was not calculated for elements B, C and Snarr.

We further measured a total of 12 frequency- (or pitch-) related variables, three each for the elements A, B, C and Snarr.

Alow (B, C, Snarr): lowest frequency (kHz) of elements A (B, C, Snarr) in an individual's songs.

Aup (B, C, Snarr): highest frequency (kHz) of elements A (B, C, Snarr) in an individual's songs.

Adiff (B, C, Snarr): differences (kHz) between the highest and lowest frequency of each element.

Statistical Analysis

We analysed 835 songs from 75 males. We recorded 3–37 per bird with an average of 11. Analyses of variance (ANOVAs) showed that even with only three songs/male variance in variables was significantly smaller within than between individuals ($P<0.05$). We therefore felt justified to average variable values from all songs of the same male, independent of the sample size. As a result, each bird entered the subsequent analyses only once.

Since some of the measured song variables were likely to be correlated, we first performed two principal component analyses (PCA), one with the time/structure variables, the other with the frequency variables, to reduce dependent variables to a smaller number of independent factors (Sokal & Rohlf 1969). Following the recommendations of Aspey & Blankenship (1977) and Bauer (1986), we extracted only factors with eigenvalues ≥ 1 (Kaiser criterion), used factor loadings of ≥ 0.55 for interpreting (i.e. naming) the varimax-rotated factors and only considered loadings of ≥ 0.45 to be meaningful. To test for song differences between males, the individuals' scores on the resulting factors were then related to mating status by using multivariate and univariate analyses of variance (MANOVA, ANOVA). To test whether song differences reflect differences in male quality, we related the important song factor emerging from these analyses (Snarr) to the males' phenotype, territorial defence, territory quality and reproductive success by means of analyses of variance and regression analysis. Phenotype features included age, length of the eighth primary, tarsus length and body weight, the latter expressed as a residual to control for the effects of year and day during the season. Territorial defence was measured by size and percentage overlap with neighbouring territories, territory quality by insect biomass sampled with a sweep net. Reproductive success was represented by the absolute numbers of eggs, nestlings and fledglings per season as well as by hatching and fledging rates. Details on measuring these variables are given by Frey-Roos et al. (1995), Bollmann et al. (1997) and Brodmann et al. (1997). All statistical tests were done with SYSTAT 6.0.1.

Means are given with standard deviations.

RESULTS

Song Structure

Water pipit males perform a parabolic songflight that ascends from an elevated perch (e.g. a boulder), continues with a horizontal part and ends with a downward gliding phase. During the whole period they produce a rhythmical, fairly monotonous song by rapidly repeating a few element types which occur in phrases (Fig. 1a, b). The song duration of 75 males was 15.3 ± 2.3 s. The birds had a repertoire size of 3.2 ± 0.8 element types, but they used only 2.7 ± 0.8 element types per song. Among the six distinguishable

elements found in our population, element A was sung by every male, elements C and Snarr by about 90%, element B by 40% and elements D and E by less than 3%. In terms of proportion, element A was even more dominating: out of the 79.8 ± 22.3 total elements produced on average during a song, the vast majority ($80.1 \pm 15.7\%$) were of type A, followed by types B ($8.2 \pm 12.1\%$), C ($6.6 \pm 6.1\%$) and Snarr ($4.0 \pm 2.8\%$). Depending on the element type, frequencies ranged from a mean lowest value of 2917 to a mean highest value of 7367 Hz.

Figure 1a, b provides two examples of typical songs, which illustrate the inter-individual variability in the elements of the first song phrase (A and B), the lack of individual differences towards the end of the song (Snarr and C) and the typical succession of element types. The sequences ABSnarrC (Fig. 1a), ASnarrC (Fig. 1b) and ACSnarr combined were typical for 73.4% of all males. Any of the other 12 combinations (e.g. AC, ABD, ABSnarr) characterized less than 5% of the individuals. Only three males had songs with more than one sequence.

The sequence of the elements and other specific features of a male's song were determined during his first year of life and did not change thereafter (cf. Fig. 1c). A multivariate analysis of variance, based on seven males, each recorded in 2 consecutive years, yielded significant individual differences in repertoire size ($P=0.007$), rhythm ($P<0.001$) and proportion of the Snarr ($P=0.029$; Wilks' λ: $F_{18,11}=15.437$, $P<0.001$), but no annual differences in any of the three variables (Wilks' λ: $F_{3,4}=0.785$, NS).

Correlations Between Song Variables

A principal components analysis (PCA), performed on data from 835 songs of the 75 individuals, reduced the original 13 time/structure variables to five independent factors (Table I). Factors 1 and 2 were related to 'repertoire size' and the 'rhythm' of the song, respectively. Factors 3 and 4 characterized the amount of elements Snarr and C which were typically found at the end of a songflight. Factor 5 described 'song duration'. From the loadings it is obvious that longer songs typically contained more elements, especially of type A, but did not necessarily result in a larger repertoire. Together all five factors

Table I. Results of two principal component analyses (PCA), one based on time/structure variables (factors 1–5), the other on frequency variables (factors 6–8)

Variable	Loading
Factor 1 Repertoire size 30.8%	
Number B	0.94
% B	0.94
% A	-0.91
Repused	0.80
Repsize	0.75
Factor 2 Rhythm 15.1%	
Aper3	0.98
Totelm	0.71
Number A	0.65
Factor 3 Amount of Snarr 17.0%	
Number Snarr	0.95
% Snarr	0.93
Factor 4 Amount of C-elements 16.3%	
Number C	0.98
% C	0.97
Factor 5 Song duration 14.1%	
Duration	0.99
Totelm	0.67
Number A	0.57
Factor 6 Snarr frequencies 22.7%	
SnarrLow	0.64
SnarrUp	-0.68
SnarrDiff	0.91
Factor 7 A frequencies 26.3%	
ALow	-0.75
AUp	0.79
ADiff	0.97
Factor 8 C frequencies 21.5%	
CLow	-0.52
CUp	0.89
CDiff	0.88

Despite having two separate PCA, the extracted factors are numbered consecutively (1–8) to ease comparisions with subsequent analyses. Loadings, that is, correlations between original variables and the extracted factors are shown only when $\geqslant 0.45$. Percentage values indicate the proportion of variance explained by the respective factor. For variable abbreviations and further explanations, see Methods.

explained 93.3% of the total variance in the time/structure variables.

Table I also shows results of the PCA based on frequency (i.e. pitch) variables. The analysis is based on only those elements that occurred in at least 90% of the males (A, C, Snarr). However, inclusion of the rarer element B, and thus a reduction of the data set, does not seem to affect the grouping. In both cases, the PCA resulted in as many factors as element types were considered,

**Table II.** Song in relation to mating status

Factor	Song characteristics	F	P
	Univariate F tests		
1	Repertoire size	0.659	0.583
2	Rhythm	0.524	0.669
3	**Amount of Snarr**	**5.678**	**0.003**
4	Amount of C-elements	1.991	0.134
5	Song duration	0.715	0.550
6	Snarr frequencies (kHz)	0.105	0.957
7	A frequencies (kHz)	1.107	0.360
8	C frequencies (kHz)	0.726	0.544
	Multivariate test		
	Wilks' λ (df=24, 74)	1.803	**0.029**

The results are shown of a MANOVA relating the factor scores of the song characteristics extracted by the PCA of Table I to three categories of male reproductive status: unmated; mated, but no fledglings reared; mated and fledglings reared. Significant results are printed in bold.

and the three frequency measures of each element type correlated strongly with the same factor.

Mating Status in Relation to Song

Next, we performed an analysis of variance (MANOVA) in which scores of the five time/ structure and the three frequency factors from Table I were simultaneously related to three classes of male mating status: (1) unmated, (2) mated without successful reproduction during the season, (3) mated and fledging one or two broods. The result shows a significant overall difference between the classes ($P<0.05$) which, according to the univariate analyses, can be attributed to a single factor, namely factor 3 representing the absolute and relative number of Snarr elements ($P=0.003$; Table II). Neither the other four time/ structure, nor any of the three frequency, factors contributed significantly to the discrimination. Pair-wise comparisons show that all Snarr measures (absolute and relative numbers as well as scores of factor 3) were significantly lower for unmated than for mated males, but did not differ between mated males that did or did not reproduce successfully (Fig. 2). Also, among those successful breeders for which we know the precise number of fledglings, there was no correlation between Snarr scores and reproductive success ($r=0.066$, $N=21$, NS).
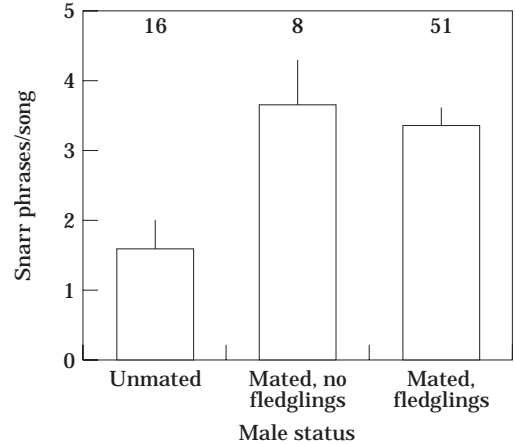
Figure 2. Number of Snarr phrases in songflights of 75 water pipits, broken down into three categories: unmated males, males rearing no fledglings and mated males with fledglings. Least square means (+SE) from an ANOVA are shown. Numbers above the bars indicate sample sizes. Pair-wise comparisons with Scheffé's multiple range test show significant differences between unmated and both categories of mated males (both $P \leq 0.032$), but not between successful and unsuccessful mated males ($P=0.913$).

## The Snarr, Territoriality and Breeding Performance

The clear-cut song difference between mated and unmated males and the lack of a similar difference within the mated category suggest that producing the Snarr might have affected territory establishment and pair formation but did not influence breeding performance once a male was mated. To test this hypothesis further we performed three MANOVAs after grouping individuals into two distinct categories: the 'low Snarr' males with an average time spent singing the Snarr phrases of 1.8% (range 0–4.4) and 'high Snarr' males with an average of 12.6% (range 6.2–29.5). The first two MANOVAs included all males, and related their mating status and membership in the 'low' or 'high Snarr' group to two correlates of territorial defence (territory size and overlap) and one measure of territory quality (prey density). The third analysis, considering mated males only, searched for differences between 'low' and 'high Snarr' males in terms of parental performance (absolute numbers of eggs, nestlings and fledglings per season and hatching and fledging rates).

Table III. Song and territory characteristics

Source of variation	Wilks' λ		Territory size		Territory overlap		Prey density		
	$F_{2,31}$	P	$F_{3,30}$	P	$F_{3,30}$	P	MS	$F_{3,30}$	P
Matedness	14.772	**<0.0001**	0.277	0.602	29.768	**<0.0001**	0.830	0.007	0.932
Snarr amount	20.423	**<0.0001**	0.057	0.812	40.265	**<0.0001**	8.602	0.773	0.387
Snarr*matedness	11.358	**<0.0001**	0.015	0.905	21.712	**<0.0001**	0.083	0.007	0.932

Summary statistics of relationships between territory size and overlap, prey density within the territory, and matedness and amount of Snarr (low, high) in the songs of the territory owner. Significant results are printed in bold.
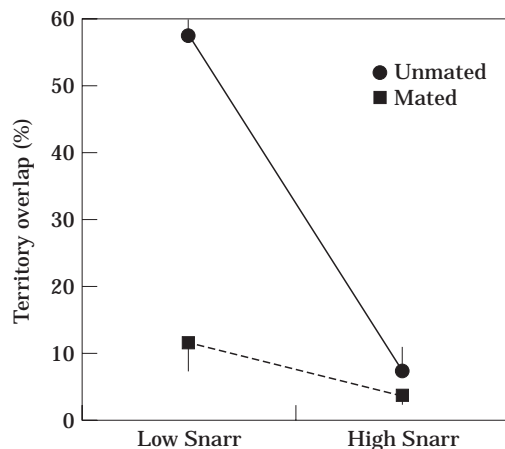
Figure 3. Percentage of territory overlapped by neighbours in relation to matedness and amount of Snarr (low versus high) in the songs of males. Least square means from an ANOVA ± SE are shown.

Territory quality and size were not related to mating status and Snarr scores, but territory overlap was. Overlap was lower in mated males and in those with high Snarr scores than in unmated males and those with low scores. A significant Snarr* status interaction indicates that an increase in Snarr score reduced overlap more in unmated than in mated males (Table III, Fig. 3).

In terms of parental performance, the respective MANOVA yielded no significant result (Wilks' λ: $F_{5,19} = 0.530$, NS). 'Low' and 'high Snarr' males did not differ in any of the five measures for reproductive success (all $P > 0.222$; univariate ANOVAs). Thus, males with high Snarr scores seemed to be superior in defending territories, but not in rearing offspring.

Phenotypic Correlates (Males and Females)

To test for potential relationships between song performance and other male qualities, we performed a multivariate analysis of covariance, which related Snarr scores to age (1 year or older) and three body measures (length of the 8th primary, tarsus length and body weight). Snarr scores were not related to age, feather or tarsus length, but increased significantly with body weight (Table IV, Fig. 4). When, for females, the same three body measurements were related to (1) the Snarr scores and (2) the body measurements of their mates, no significant relationships

Table IV. Song and male phenotypic traits

Source of variation	df	MS	F	P
Age	1	0.008	0.006	0.939
Feather length	1	0.181	0.142	0.712
Tarsus length	1	0.001	0.001	0.979
Body weight	**1**	**7.048**	**5.536**	**0.034**
Error	14	1.273		

Results of an ANCOVA testing for relationships between amount of Snarrs in songs (scores of factor 3) and male phenotype. The sample size ($N = 19$) of the analysed dataset is smaller than for the individual variables given in the Methods because phenotype data were incomplete for some males. Significant results are printed in bold.
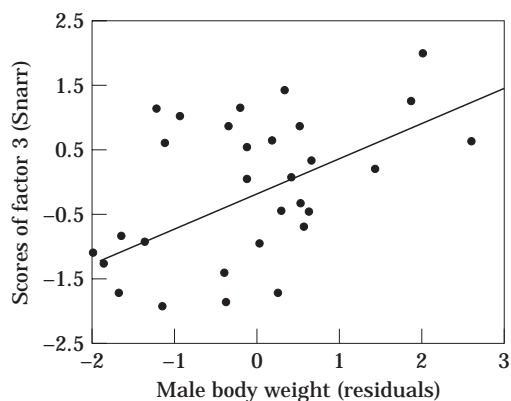
Figure 4. Amount of Snarr in the songs of males in relation to body weight. Amount of Snarr is expressed by the scores of factor 3 from Table I, body weight as the residual from an ANOVA, correcting for the effects of year and day during the season. The sample size is higher than that in Table IV because the plot includes 11 additional males of unknown age. The line is given by the equation $Y = -0.032 + 0.466X$, $N = 30$, $P = 0.007$.

were found (multiple regression: Snarr scores: $F_{3,15} = 1.576$, NS; MANOVA: measurements: $F_{3,13} \leq 2.423$, NS). Thus, there is no indication of assortative mating. The Snarr, which was related to male quality, seemed to affect territory defence but not to attract better females.

DISCUSSION

In most bird species, the acoustic parameters responsible for reproductive success are repertoire size and song rate or duration. Where specific

song elements have been identified as the relevant cues, these were related to song dialects differing between populations and/or males of different ages (e.g. O'Loghlen & Rothstein 1995). To our knowledge, this study on water pipits presents the first example of a significant link between mating success and a specific song element not reflecting age or population membership.

Among the 75 males we recorded, 12% were never heard to produce the Snarr and may not have possessed it in their repertoires. The vast majority of the birds differed only in the absolute and relative number of this element, suggesting some quantitative difference between males. Since water pipit songs do not change after the first year (Fig. 1c) and performance of the Snarr was not related to age (Table IV), song differences between males did not communicate differences in experience and/or survival abilities. The same age-independency exists in the closely related rock pipit, *Anthus littoralis*, and the meadow pipit, *A. pratensis* (Hötker 1989; Elfström 1990a, b). In contrast to some other studies (Radesäter et al. 1987; Reid 1987; Alatalo et al. 1990; Otter et al. 1997), we also found no relationship between a male's Snarr scores and prey density in his territory, nor with annual reproductive success of mated males. Given that about 50% of all foraging trips go to communal feeding sites outside the territory boundaries (Frey-Roos et al. 1995) and that reproductive failure is mainly due to snow and predation by adders, *Vipera berus* (Bollmann et al. 1997), these results are not too surprising. Yet, they illustrate that the Snarr cannot provide females with reliable information about a male's experience, food resources and paternal qualities. This makes the element an unlikely candidate for female choice and may also explain why, among those males that did get a mate, female quality (i.e. body weight, feather and tarsus length) was not related to amount of Snarr.

The Snarr is more likely to increase reproductive success through improved chances in male–male competition. The significant effect of the matedness∗Snarr interaction (Table III, Fig. 3) suggests that two birds (i.e. mated males and their females) can successfully defend their territory even without Snarrs, whereas single (i.e. unmated) males can better keep intruders out if their song contains this harsh element. Since only males establish territories early in the season (Bollmann

et al. 1997), low Snarr proportions in a song probably impair territorial exclusiveness against other males.

The proximate cause for this relationship presumably originates from the specific physical properties of the Snarr. As a mainly amplitude- (i.e. intensity-) modulated element with a broad frequency band and rapid onsets and offsets, it is easier to localize than clear notes, such as A–C, with one or two dominating frequencies (Becker 1982; Dooling 1982; Wiley & Richards 1982). Moreover, at least A and B predominate during the ascending and horizontal flight phase and, thus, are spatially decoupled from the actual territory location, whereas the Snarr is always produced during the final phase of the songflight when the male descends into his territory. This suggests to us that the element allows a male and his territory boundaries to be precisely located.

Similar to call intensity in some anurans (Arak 1983, 1988; Halliday 1983), better localization increases the 'domain of repulsion' against neighbouring males and, perhaps, the 'domain of attraction' (Parker 1983) towards females searching for a mate. As a consequence, the Snarr would lead to higher chances of getting mated, even if males and females were repulsed, or attracted randomly to male songs. However, the positive correlation with male body weight (Fig. 4) indicates that Snarr differences convey additional information about male phenotypic conditions. Possibly, lighter (i.e. weaker?) birds cannot bear the costs associated with the regular production of this element, but the nature of these costs remains obscure.

In contrast to the direct costs associated with developing status badges in plumage (e.g. Møller et al. 1996; Veiga & Puerta 1996), Snarr phrases themselves are unlikely to be costly to produce. In terms of time, the element, on average, amounted to only 9% (range 0–29.5%) of songflight length and was not correlated with song duration (Table I). In terms of energy, expenditure for an audible signal is a function of power output (dB) which in turn depends on the element's frequency (kHz) (Dooling 1982). The Snarr neither differs markedly from the other elements in its frequency range, nor seems louder. Therefore, producing it is unlikely to be metabolically more expensive than producing other kinds of elements. It may even be cheaper because rapid repetition of notes can make use of the syringeal membranes' elastic

properties (Brackenbury 1982; see also Ryan 1985, page 147 for a similar argument for anurans).

Indirect costs, resulting from the response of predators and/or conspecifics, are also not immediately obvious. In terms of survival, adult water pipits do not seem to be very prone to predation. We never saw an aerial predator attacking a male during its songflight, and terrestrial predators, especially adders frequently take nestlings, but not adults (Luiselli & Anibaldi 1990; Bollmann 1995). With this low overall predation rate, significant mortality differences between 'low' and 'high Snarr' males are unlikely. In terms of conspecifics, frequent territorial advertisement through the Snarr might increase aggressive male–male interactions which only males in better condition can afford. This could lead to the observed positive correlation between amount of Snarr and body weight (Fig. 4). However, social control alone seems to be an insufficient safeguard against the invasion of status cheats (Johnstone & Norris 1993) and apparently occurs less often than previously assumed (Slotow et al. 1993; see also Veiga 1993 and literature therein).

In conclusion, this study clearly demonstrates a link between a specific song element, the Snarr, and male condition and mating success; but the precise proximate and ultimate causes for this link remain unknown. They can be analysed only through playback and other experiments.

REFERENCES

Alatalo, R. V. C., Glynn, C. & Lundberg, A. 1990. Singing rate and female attraction in the pied flycatcher: an experiment. *Anim. Behav.*, **39,** 601–603.

Andersson, M. 1994. *Sexual Selection.* Princeton: Princeton University Press.

Arak, A. 1983. Male–male competition and mate choice in anuran amphibians. In: *Mate Choice* (Ed. by P. Bateson), pp. 181–210. Cambridge: Cambridge University Press.

Arak, A. 1988. Female mate selection in the natterjack toad: active choice or passive attraction? *Behav. Ecol. Sociobiol.*, **22,** 317–327.

Aspey, W. P. & Blankenship, J. E. 1977. Spiders and snails and statistical tales: application of multivariate analysis to diverse ecological data. In: *Quantitative Methods in the Study of Animal Behaviour* (Ed. by B. A. Hazlett), pp. 75–120. London: Academic Press.

Bauer, F. 1986. *Datenanalyse mit SPSS.* Heidelberg: Springer Verlag.

Becker, P. H. 1982. The coding of species-specific characteristics in bird sound. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 213–252. London: Academic Press.

Bollmann, K. 1995. The mating system of the alpine water pipit *Anthus spinoletta* in a variable environment: ecological, demographic and fitness aspects. Ph.D. thesis, University of Zürich.

Bollmann, K., Reyer, H.-U. & Brodmann, P. A. 1997. Territory quality and reproductive success: can water pipits *Anthus spinoletta* assess the relationship reliably? *Ardea*, **85,** 83–98.

Brackenbury, J. H. 1982. The structural basis of voice production and its relationship to sound characteristics. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 53–71. London: Academic Press.

Brodmann, P. A., Reyer, H.-U., Bollmann, K., Schläpfer, A. R. & Rauter, C. 1997. The importance of food quantity and quality for reproductive performance in alpine water pipits (*Anthus spinoletta*). *Oecologia (Berl.)*, **109,** 200–208.

Catchpole, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 297–319. London: Academic Press.

Catchpole, C. K. 1987. Bird song, sexual selection and female choice. *Trends Ecol. Evol.*, **2,** 94–97.

Davies, N. B. & Lundberg, A. 1984. Food distribution and a variable mating system in the dunnock, *Prunella modularis. J. Anim. Ecol.*, **53,** 895–912.

Dooling, R. J. 1982. Auditory perception in birds. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 95–130. London: Academic Press.

Eens, M., Pinxten, R. & Verheyen, R. F. 1991. Male song as a cue for mate choice in the European starling. *Behaviour*, **116,** 210–238.

Elfström, S. T. 1990a. Responses of territorial meadow pipits to strange and familiar song phrases in play-back experiments. *Anim. Behav.*, **40,** 786–788.

Elfström, S. T. 1990b. Individual and species-specific song patterns of rock and meadow pipits: physical characters and experiments. *Bioacoustics*, **2,** 277–301.

Frey-Roos, F., Brodmann, P. A. & Reyer, H.-U. 1995. Relationships between food resources, foraging patterns and reproductive success in the water pipit, *Anthus spinoletta. Behav. Ecol.*, **6,** 287–295.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1985. *Handbuch der Vögel Mitteleuropas. Vol. 10/II.* Wiesbaden: Aula-Verlag.

Gottlander, K. 1987. Variation in the song rate of the male pied flycatcher (*Ficedula hypoleuca*): causes and consequences. *Anim. Behav.*, **35,** 1037–1043.

Greig-Smith, P. W. 1982. Song-rates and parental care by individual male stonechats (*Saxicola torquata*). *Anim. Behav.*, **30,** 245–252.

Halliday, T. 1983. The study of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 3–32. Cambridge: Cambridge University Press.

Hötker, H. 1989. *Der Wiesenpieper. Neue Brehbücherei.* Wittenberg-Lutterstadt: A. Ziemsen-Verlag.

Johnstone, R. A. & Norris, K. 1993. Badges of status and the cost of aggression. *Behav. Ecol. Sociobiol.*, **32,** 127–134.

Lambrechts, M. M. & Dhondt, A. A. 1988. The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.*, **36,** 327–334.

Lampe, H. M. & Espmark, Y. O. 1994. Song structure reflects male quality in pied flycatchers, *Ficedula hypoleuca. Anim. Behav.*, **47,** 869–876.

Luiselli, L. M. & Anibaldi, C. 1990. The diet of the adder (*Vipera berus*) in two alpine environments. *Amphib.-Reptil.*, **12,** 214–217.

Møller, A. P. 1991. Parasite load reduces song output in a passerine bird. *Anim. Behav.*, **41,** 723–730.

Møller, A. P., Kimball, R. T. & Erritzoe, J. 1996. Sexual ornamentation, condition, and immune defence in the house sparrow, *Passer domesticus. Behav. Ecol. Sociobiol.*, **39,** 317–322.

O'Loghlen, A. L. & Rothstein, S. I. 1995. Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behav. Ecol. Sociobiol.*, **36,** 251–259.

Otter, K., Chruszcz, B. & Ratcliff, L. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behav. Ecol.*, **8,** 167–173.

Parker, T. R. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–164. Cambridge: Cambridge University Press.

Radesäter, T., Jakobson, S., Andbjer, N., Bylin, A. & Nyström, K. 1987. Song rate and pair formation in the willow warbler, *Phylloscopus trochilus. Anim. Behav.*, **35,** 1645–1651.

Reid, M. L. 1987. Costliness and reliability in the singing vigour of Ipswich sparrows. *Anim. Behav.*, **35,** 1735–1743.

Ryan, M. J. 1985. *The Tungara Frog: a Study in Sexual Selection and Communication.* Chicago: The University of Chicago Press.

Ryan, M. J. 1988. Energy, calling, and selection. *Am. Zool*, **28,** 885–898.

Searcy, W. A. 1979. Male characteristics and pairing success in red-winged blackbirds. *Auk*, **96,** 353–363.

Searcy, W. A. 1984. Song repertoire size and female preference in song sparrows. *Behav. Ecol. Sociobiol.*, **14,** 281–286.

Searcy, W. A. & Andersson, M. 1986. Sexual selection and the evolution of song. *A. Rev. Ecol. Syst.*, **17,** 507–533.

Slotow, R., Alcock, J. & Rothstein, S. I. 1993. Social status signalling in white-crowned sparrows: an experimental test of the social control hypothesis. *Anim. Behav.*, **46,** 977–989.

Sokal, R. R. & Rohlf, F. J. 1969. *Biometry.* San Francisco: W. H. Freeman.

Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in male sage grouse. *Anim. Behav.*, **38,** 885–896.

Veiga, J. P. 1993. Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution*, **47,** 1161–1170.

Veiga, J. P. & Puerta, M. 1996. Nutritional constraints determine the expression of sexual traits in the house sparrow, *Passer domesticus. Proc. R. Soc. Lond. Ser. B*, **263,** 229–234.

Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds. Vol. 2* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 132–181. London: Academic Press.