

Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*

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Bird song is generally regarded as a sexually selected trait, and may represent a reliable handicap signal under at least certain conditions. Females may use the degree of male song production as a reliable cue to male condition or territory quality. We investigated the effect of supplementary feeding on song output in the migratory Australian reed warbler *Acrocephalus australis*. We experimentally increased the food availability on alternate days, and recorded several weather variables. We measured song rate and song length independently. Supplementary fed birds sang more on feeding days than on non-feeding days, while control birds did not show this effect. Song output was not significantly associated with any of the weather variables examined. Our results indicate that singing has the potential to serve as a reliable handicap signal to territorial food availability irrespective of the prevailing weather conditions. We discuss the role of energetic constraints and behavioural flexibility on the signaling function of song.

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The handicap principle (Zahavi 1975, 1977) proposes that male traits that impose a cost on the signaller may reliably advertise male 'condition' (e.g. energetic or nutritional state; Nur and Hasson 1984). Males that display a larger handicap should be in better condition, which may in turn reflect territory quality (food availability) or genetic qualities of the male (Greig-Smith 1982, Tamm 1985, Reid 1987). The handicap principle further requires that the optimal expression of a costly trait depends on the current condition of the bearer of the trait, and as such, plasticity in the expression of male phenotypic traits is essential to the handicap principle

(Zahavi 1977, Nur and Hasson 1984). Such flexibility will be advantageous to individuals bearing costly traits when there is temporal or spatial variation in the costs of a trait, by allowing the trait to be maintained at the optimum level of expression (Brooke et al. 1998). Indeed, phenotypic plasticity may be more important to fitness than the actual value for a particular trait (Jordan and Snell 2002), although few studies have addressed this point for commonly observed signaling systems.

Singing by male songbirds may represent one such male handicap trait. Singing is used by male songbirds to compete with other males in establishing and defending

territories and to attract both social and extra-pair mates (Searcy and Andersson 1986, Catchpole and Slater 1995). Singing is thought to be costly because of the energetic demands of song production (Lambrechts and Dhondt 1988, Eberhardt 1994, Chappel et al. 1995, Oberweger and Goller 2001), the temporal constraints imposed on other activities such as foraging (Reid 1987, Galeotti et al. 1997, Saino et al. 1997, Lucas et al. 1999) and the increased risk of depredation (Krams 2001). Such costliness should prevent cheating (Grafen 1990), so singing may represent a reliable cue to male health and energetic state (Reid 1987, Catchpole and Slater 1995, Lucas et al. 1999, Oberweger and Goller 2001). Accordingly, males that have a higher song output (more and/or longer songs) may be more attractive to females because they are likely to occupy better territories (Yasukawa 1981), or be in better condition (Hutchinson et al. 1993, Beani and Dessi-Fulgheri 1995).

So far, most studies have assessed male song output by measuring song rate. A positive association between male song rate and pairing or mating success has been reported in studies on sedge warblers *Acrocephalus schoenobaenus* (Buchanan and Catchpole 1997), willow warblers *Phylloscopus trochilus* (Radesäter et al. 1987, Nyström 1997) and pied flycatchers *Ficedula hypoleuca* (Alatalo et al. 1990), but not in others e.g. stonechats *Saxicola torquata* (Greig-Smith 1982) and dunnocks *Prunella modularis* (Davies and Lundberg 1984). It is therefore important to understand under which environmental conditions singing has the potential to act as a reliable handicap signal, because these may have implications for the sexual selection of song. Climate, for instance, may have a crucial but often overlooked influence on the value of energetically costly handicap signals such as singing, because variables such as ambient temperature may affect the energetic demands of signal production and thus the reliability of the signal (Gottlander 1987, Reid 1987).

In this study, we examine the proximate causes of variation in song output, taking into account both song rate and song length, in male Australian reed warblers *Acrocephalus australis*. We report the results of a long-term supplementary feeding experiment and examine several weather variables to investigate: 1) whether song output may act as a reliable, behaviorally flexible handicap signal to territorial food availability, and 2) to what extent other external factors (weather conditions, date) influence song rate independently of food availability. Although song output has been well studied in several closely related European *Acrocephalus* species (Catchpole 1973, 1983, Hasselquist and Bensch 1991, Hasselquist et al. 1996, Buchanan and Catchpole 1997, FeBl and Hoi 2000, Čapek and Kloubec 2002), this is the first detailed study on singing behavior in the Australian reed warbler.

Methods

Study site and species

Migratory Australian reed warblers arrive in south-eastern Australia over the course of several weeks and establish small breeding territories, which are vigorously defended against conspecific males and persist throughout the breeding season. Foraging takes place both on the breeding territory and on communal, non-defended feeding areas outside the reed beds (no singing occurs here). All males sing on their territories frequently throughout the breeding season, even after acquiring a mate (Cramp 1992), and extra-pair fertilizations are common (affecting approximately 50% of clutches; Berg 1998, M. Bleeker, M. Berg and J. Welbergen unpubl. data). The social mating system is generally monogamous, although polygyny may occur (Brown and Brown 1986, M. Berg and J. Welbergen unpubl. data).

The study was conducted at Edithvale-Seaford Wetlands, Australia (38°02'S, 145°07'E) in 10 ha of Australian reed *Phragmites australis* bordering a lake. We selected two equally sized 'blocks' of reed, each ca 300 m × 50 m and situated on opposite sides of a lake (ca 500 m apart), on the basis of their subjective homogeneity, comparability in reed structure, and proximity to water (in order to minimize natural differences in food availability and nesting sites between the treatments). Data were gathered from 7 October to 7 December 2000, the main breeding season of the Australian reed warbler. Birds were color-ringed for individual identification. Comprehensive weather data (ambient temperature, relative humidity, dew point temperature, atmospheric pressure and wind speed) were obtained from the Bureau of Meteorology (Melbourne), and were recorded in an open area adjacent to the study site. Weather variables were recorded on a 3 hourly basis and averaged for each night time (21.00 to 06.00 hours) and day time period (09.00 to 18.00 hours).

Supplementary feeding experiment

We experimentally manipulated habitat quality by providing an artificial supplementary food source. Each of the two blocks of reed forming the study site was divided into two equally sized treatment 'areas' which were randomly assigned to either receive supplementary feeding or to serve as a control for disturbance arising from the supplementary feeding treatment. We provided supplementary feeding in only two areas, comprising several adjacent territories each, rather than more smaller areas or individual territories, in order to reduce the potential for intrusions between treatment areas to affect song rate (see Discussion). In each block, we made parallel transects spaced 20 m apart and running perpendicular to the lake edge. Plastic trays (20 cm

diameter, 3 cm deep, supported ca 1 m high on a pole) were placed every 20 m along the transects in the supplementary feeding areas (breeding territory size is typically at least 20 m in diameter (J. Welbergen and M. Berg unpubl. data). Each tray was filled with ca 30 g of live blowfly maggots (*Calliphora* sp. larvae; Ritebait) in processed bran or rice husks every other morning at approximately 11.00 hours. Feeding on alternate days allowed us to make a powerful within area comparison between supplementary feeding days and control days to examine the effects of the experimental treatment on song rate. The estimated field metabolic rate for a breeding Australian reed warbler is 80 kJ per day (Williams 1996), so 30 grams of maggots at approximately 4.5 kJ/g (Inaoka et al. 1999) represents more than 1.25 times the daily energy requirements of one individual during reproduction assuming an assimilation efficiency of 75% (Castro et al. 1989). Maggots were unable to escape from the trays. Supplementary feeding was carried out from 7 October to 7 December. When feeding, we also walked along the transects in the control areas to generate equal disturbance. Remote video observations at random feeding trays ($2.75 \text{ h} \pm 0.90 \text{ SD}$ each, $n=7$) revealed that Australian reed warblers routinely consumed the supplementary food and that no other bird species fed on the maggots. The maggots were usually largely depleted within several hours and were always gone by the following day. In other studies on this species, this supplementary feeding method increased female incubation attendance (males do not incubate; Eikenaar et al. 2003) and nestling food provisioning by both sexes, but had no detectable effect on nest predation rates (J. Welbergen and M. Berg unpubl. data).

Singing observations

We made singing observations of the colour-banded population from a 3.5 m high step-ladder ladder on 16 random days from 4 November to 7 December. Most males were paired and breeding during this period. By using both visual and auditory cues we could assign territories to all males (supplementary fed areas: 28, control areas: 22). We made observations from the ends of each transect, and moved to the next transect every 15 minutes. From each position we observed males in the reed as far as the next transect on each side, thus each area of reed was observed during two consecutive 15 minute periods per day. Observations were made once from each end of each transect. To avoid effects from observation order, each of the areas was observed both from left to right and from right to left. Each area was observed as described on four different days, yielding a total observation time of two hours. Time constraints precluded us from observing more than one area per day.

Australian reed warblers sing throughout the day and occasionally at night, but they have two diurnal peaks of song activity at morning and at evening, like most song birds (Møller 1991a, Staicer 1996). Singing during dusk is most likely to be affected by previous foraging success (Thomas 1999). We observed one area per day, alternating between experimental and control areas, during the evening singing peak (16.00 to 19.00 hours). We avoided making observations on the four days with some rain (20.2 mm) because birds stop singing. For each singing observation we plotted the location of males on a map and recorded the number of separate songs (at least 5 seconds in between vocalisations) sung by each male during the 15 minutes. Due to the length of the observation period and the fact that males continue to sing frequently throughout the breeding season, all males were located during singing observations. Territories remained stable throughout the period of singing observations. In order to compare song length variation between treatments, the lengths (to nearest second) of up to 20 ($17.7 \pm 5.6 \text{ SD}$) separate consecutive songs were timed using a stop watch from a random sub-sample of 11 control and 8 supplementary fed non-neighbouring males after pairing.

Data analyses

All statistical tests were performed using SPSS 11 for Windows (SPSS Inc. 2001) and followed Quinn and Keough (2002). Individual song rates were log transformed prior to analysis to improve normality and equalize variance between groups. Non-parametric tests were used when data were non-normally distributed. All P-values reported are two-tailed and considered significant when $P < 0.05$.

To examine the relationship between date, climate and song rate, we conducted a principal component analysis on date and the five weather variables (ambient temperature, relative humidity, dew point temperature, atmospheric pressure and wind speed) for the night time and day time periods immediately preceding each singing observation. Collinearity between several of these variables made their use together in a model inappropriate (tolerance values < 0.1). Varimax rotation had little effect on the variance explained by each component but was used to improve the biological interpretability of the components. We used analysis of covariance to compare mean song rate for each day to the principal components derived from date and the weather variables while controlling for the experimental treatment (fixed factor).

Males within each treatment area (two supplementary fed and two control) may not be independent (e.g. if individual song rates are influenced by unforeseen similarities between the two areas in each experimental

group or neighbouring song rates), leading to pseudo-replication (Hurlbert 1984). Therefore, as there are only two independent treatment area replicates we have refrained from presenting statistical comparisons of song rates between the supplementary fed and control groups. To examine the effect of supplementary feeding on song rate more effectively, we carried out a randomized complete block design analysis of variance with paired comparisons (treatment day as a fixed factor and male as a random factor) to compare individual song rates between feeding days and control (non-feeding) days separately for both the supplementary fed and control areas. Song lengths were taken from a random sample of males from throughout the study site and the mean value for each male was used as the unit of comparison.

Results

The mean song length of supplementary fed males did not differ from control males. The mean song length was $1.74 \text{ s} \pm 0.34 \text{ SD}$ (range 1–5 s, $n=11$) for control males and $1.53 \text{ s} \pm 0.30 \text{ SD}$ (range 1–4 s, $n=8$) for supplementary fed males (Mann-Whitney U-test: $Z=1.274$, $P=0.211$).

We retained the first four components of a principal component analysis on the weather variables (day time and night time periods preceding each singing observation) and date, as they had eigenvalues greater than one and together explained more than 85% of the total variance. Furthermore, all components greater than four had no simple biological interpretation. Table 1 shows the factor loadings from the principal component analysis. In summary, PC1 (31.5% variance) had strongly positive loading from humidity and dew point temperature (day time and night time). PC2 (22.4% variance) had strongly positive loading from ambient temperature (day time and night time) and moderately positive loading from day time dew point temperature, and strongly negative loading from day time wind speed. PC3 (20.1% variance) had strongly positive loading from atmospheric pressure (day time and night time) and date. PC4 (11.6% variance) had strongly positive loading from

Table 1. Factor loadings for the first four principal components extracted from the weather variables and date.

	PC1	PC2	PC3	PC4
Day temperature	-0.41	0.67	0.39	-0.33
Night temperature	0.00	0.88	-0.27	0.09
Day humidity	0.91	0.00	-0.28	0.15
Night humidity	0.83	-0.36	0.25	-0.20
Day dew point	0.77	0.61	-0.04	-0.07
Night dew point	0.89	0.21	0.08	-0.19
Day pressure	0.38	0.00	0.70	0.52
Night pressure	0.12	-0.12	0.94	-0.10
Day wind speed	-0.15	-0.79	-0.05	0.01
Night wind speed	-0.20	-0.01	-0.04	0.90
Date	-0.37	0.03	0.72	-0.04

night time wind speed and moderately positive loading from day time atmospheric pressure.

To examine the relationships between song rate and date and weather, we compared the mean song rate for each day with the four principal components derived from date and the weather variables (Fig. 1). We included feeding treatment as a fixed factor with four levels (control areas on control days, control areas on feeding days, feeding areas on control days, and feeding areas on feeding days) to control for the effect of experimental food availability. There were no significant relationships between mean daily song rate and any of the principal components (ANCOVA: PC1, $F_{1,15}=1.532$, partial $\text{Eta}^2=0.161$, $P=0.251$; PC2, $F_{1,15}=0.673$, partial $\text{Eta}^2=0.078$, $P=0.436$; PC3, $F_{1,15}=0.199$, partial $\text{Eta}^2=0.024$, $P=0.667$; PC4, $F_{1,15}=0.881$, partial $\text{Eta}^2=0.099$, $P=0.375$). The partial Eta^2 is the proportion of the total variability attributable to an individual variable. The conclusions of this analysis were robust to the exclusion of feeding treatment as a factor (PC1, $F_{1,15}=2.289$, partial $\text{Eta}^2=0.172$, $P=0.158$; PC2, $F_{1,15}=0.678$, partial $\text{Eta}^2=0.058$, $P=0.428$; PC3, $F_{1,15}=0.026$, partial $\text{Eta}^2=0.002$, $P=0.875$; PC4, $F_{1,15}=3.703$, partial $\text{Eta}^2=0.252$, $P=0.081$).

The mean song rates (songs per 15 minute observation) of supplementary fed males were $5.4 \pm 0.6 \text{ SE}$ on feeding days and 3.8 ± 0.5 on non-feeding days (mean 4.6 ± 0.4), and for control males they were 3.0 ± 0.6 on feeding days and 2.4 ± 0.7 on non-feeding days (mean 2.8 ± 0.4 ; Fig. 2). To examine the association between the supplementary feeding treatment and song rate, we made paired comparisons of individual song rates between control and supplementary feeding days separately for both the control and supplementary fed areas. There was no difference between feeding and non-feeding days in control areas (ANOVA: $F_{1,21}=0.030$, $P=0.865$), but males in supplementary fed areas sang at significantly higher rates on feeding days than non-feeding days ($F_{1,27}=13.180$, $P=0.001$; Fig. 2).

Discussion

Song as a handicap signal

If song is to be an effective handicap signal, it must be costly to the bearer and behaviorally flexible (Zahavi 1975, 1977, Nur and Hasson 1984, Grafen 1990), and our results on song rate support these notions. Supplementary fed males sang significantly more on feeding days than on non-feeding days while control males did not. Each feeding day alternated with a non-feeding day, and such flexibility should be beneficial to males by allowing them to maintain their song output at the optimum level under varying environmental conditions (Brooke et al. 1998). The increase in song rate observed on supplementary feeding days equated to 6.4 (42%)

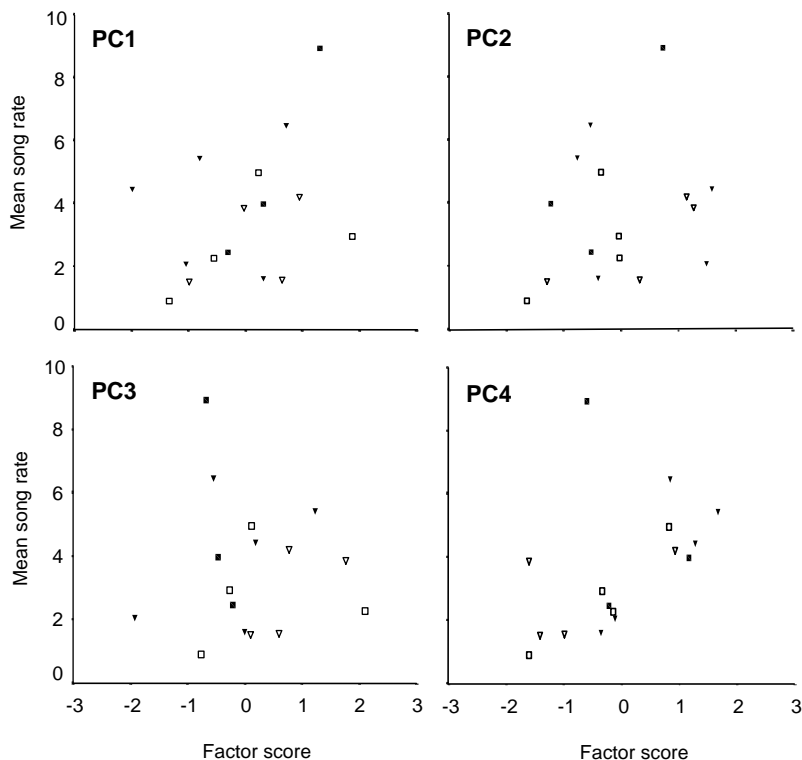


Fig. 1. Relationships of mean song rate for each day versus PC1 to 4 (principal components derived from date and ten weather variables; see Table 1). Filled symbols correspond to supplementary fed areas and open symbols to control areas; squares correspond to supplementary feeding days and triangles correspond to control days. No regression was significant (see text). Each area (two supplementary fed and two control) was observed four times on random days ($n = 16$ days).

extra songs per hour for supplementary fed males, and is thus likely to be important in mate attraction and/or territory tenure. By contrast, control males showed an

increase of 2.4 (25%) extra songs per hour. Song length did not differ significantly between treatments, indicating that males with reduced energetic constraints invest in more frequent singing rather than longer songs.

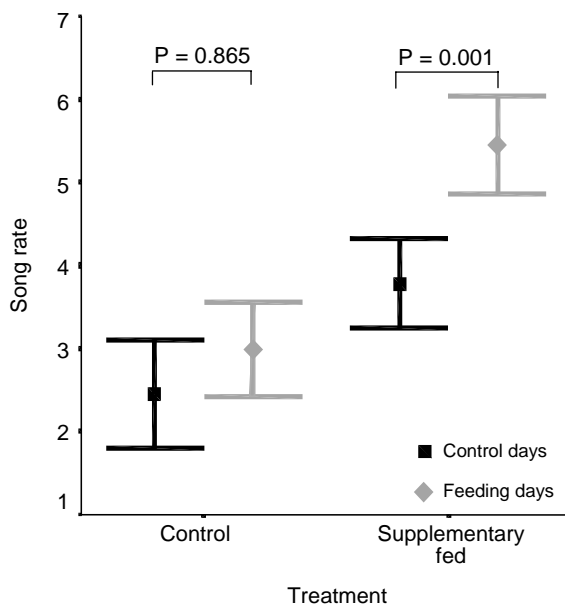


Fig. 2. Song rate (number of songs per 15 minutes) grouped by supplementary feeding treatment and separated into control days (black bars) and supplementary feeding days (gray bars). $n = 22$ control males and 28 supplementary fed males. Mean \pm SE.

These results suggest that song rate is directly constrained by energy reserves (Lambrechts and Dhondt 1988, Eberhardt 1994, Chappel et al. 1995, Oberweger and Goller 2001) and/or imposes temporal constraints on foraging (Reid 1987, Galeotti et al. 1997, Saino et al. 1997, Lucas et al. 1999). Of nine previous studies considering the effect of supplementary feeding on song output in free-living birds (Thomas 1999), seven reported a significant positive relationship between food supplementation and either overall time spent singing (Cuthill and MacDonald 1990, Cucco and Malacarne 1997, Thomas 1999), or song rate (Searcy 1979, Davies and Lundberg 1984, Gottlander 1987, Strain and Mumme 1988). Laboratory studies have indicated that singing increases metabolic rates considerably over basal metabolic rates (Ward et al. 2003). However, these energetic costs may represent only a slight increase in metabolic rate relative to other common daytime activities such as perching (Ward et al. 2003). Thus, temporal constraints on foraging rather than direct energetic costs may be the main energetic constraint on song output.

All previous studies examining the effect of supplementary feeding on song output were conducted in climates considerably cooler than that of our study (average hourly temperature during our study period

17.4°C, range 7.8–33.4°C). Moreover, Strain and Mumme (1988), and Thomas (1999) undertook experimental observations primarily during the winter, non-breeding period, while Gottlander (1987) only found a significant effect during the coldest periods (4–11°C) of the study. Energetically costly signals such as singing may be less reliable under less physiologically stressful environmental conditions, such as warm temperatures and at dusk rather than dawn (Reid 1987). Reid (1987), studying Ipswich sparrows *Passerculus sandwichensis princeps* in Nova Scotia, Canada, observed that song rates were less sensitive to ambient temperature in a mild year, in June (the warmest month of the study) and in the afternoon.

Climate and seasonal variation

In addition to variation in food availability or foraging success, date and climate variation may be an important source of variation in song rates (Gottlander 1987). Breeding status may have a large impact on song rates (Møller 1991b), so one might expect a population wide relationship between date and song rate if birds breed reasonably synchronously. Ambient temperature has been linked to variation in song output in a number of species due to the higher energetic costs of maintaining body temperature at low ambient temperatures (Gottlander 1987, Reid 1987, Thomas 1999). Such relationships are often difficult to interpret because there are frequently strong inter-relationships between such variables (e.g. date, temperature and relative humidity), but this can be overcome with factor analysis. We found no significant relationships between song rate and the first four principal components derived from date and ten weather variables (Table 1). Thus date and the prevailing weather conditions did not seem to strongly influence song output in our study. High nest depredation rates and rapid re-nesting mean that breeding synchrony is low in our study population, and extra-pair fertilizations commonly occur throughout the breeding season (Berg 1998, M. Bleeker, M. Berg and J. Welbergen unpubl. data), which may explain the lack of a relationship between song rate and PC3 (date and atmospheric pressure). Temperature may be less influential on singing in warm conditions and at dusk (when the birds have foraged throughout the day, Reid 1987, Thomas 1999), as in our study.

Experiments where supplementary food is provided over relatively long time periods, as in this study and a number of others (Thomas 1999, Table 2), may introduce a number of problems. Territory size and density may be affected (Davies and Lundberg 1984, 1985), and this could have a large effect on song rate (McShea and Rappole 1997). Male density did not appear to differ significantly between the equally sized supplementary

fed (28 males) and control areas (22 males; $\chi^2 = 0.641$, $P = 0.423$).

Territories with high food availability may suffer from more conspecific intrusions, particularly from territories with lower food availability (Tobias 1997). This may lead to increased song rate in supplementary fed territories (Wolf 1975, Møller 1991a), although studies of calliope hummingbirds *Stellula calliope* (Tamm 1985) and red-winged blackbirds *Agelaius phoeniceus* (Searcy 1979) found that supplementary feeding had no effect on intruder pressure. Furthermore, we do not believe that control individuals intruding onto supplementary fed territories led to the observed increase in song rates for the following reasons: 1) no individuals from control areas were observed feeding at supplementary feeding trays ($n = 7$ random trays observed for $2.75 \text{ h} \pm 0.90 \text{ SD}$ each, and all observations were performed immediately after feeding), 2) extensive catching in all areas during color-banding revealed only one case of an inter-area intrusion, and 3) since our supplementary feeding was conducted in two areas of several contiguous territories most fed territories did not have non-fed neighbors nearby. All previous studies reviewed in Thomas (1999) that examined the effect of supplementary feeding on song output except one directed supplementary feeding to single, non-adjacent territories. The exception (Enoksson 1990) provided food to a block of contiguous territories but failed to find an effect of supplementary feeding on song output. It is possible that single male feeding, even when relatively short-term, is more likely to lead to a substantial increase in the intrusion pressure from non-fed conspecifics in adjoining territories. Short-term supplementary feeding experiments are an alternative to long-term supplementary feeding. However, some individuals may not become fully accustomed to the experimental feeding, intruder pressure may still increase and effects of food availability arising from more long-term changes in individual condition will not be detected.

Conclusions

It appears that the benefits to females of choosing a male with a high song rate would include non-genetic (direct) benefits, such as a better territory. To date, most studies on the signaling function of song have been conducted in relatively cool climates, and until more studies from other climates are published it may be difficult to know if the results are general or specific to certain environments. Future research should also focus on identifying potential female preferences for high male song output and on quantifying the potential fitness outcomes of female choice for male song production. Finally, if song rate is to be a proper 'strategic choice' handicap signal, the costs of singing must also increase differentially for

individuals of different quality (Grafen 1990), and this point remains to be adequately tested.

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