Original Article

Serins respond to anthropogenic noise by increasing vocal activity

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Increasing levels of anthropogenic noise interferes with the acoustic communication of birds. Adaptive shifts in song characteristics (frequency and amplitude) and in the spatial and temporal patterns of singing behavior in the face of noise pollution have been documented. We provide evidence for another response, increased time spent singing, in a successful suburban bird, the serin Serinus serinus. Serins increased the proportion of time spent singing at posts in relation to changes in noise levels both in space and in time up to a threshold at approximately 70 dBA, whereas time spent at singing posts was not related to noise levels. This response could be related to the characteristics of the serin's song (high pitch and presumably low metabolic and neuromuscular costs) that would reduce the relative effectiveness of song shifts. However, vocal activity decreased sharply above the 70 dBA threshold, suggesting that this strategy is costly. Because singing time may trade off with vigilance time, our data suggest that bird populations in noisy city environments may face an increased challenge for survival compared with quiet areas, even for species whose song characteristics reduce the interference of urban noise with acoustic communication. Key words: anthropogenic noise, noise threshold, Serin, Serinus serinus, vocal activity. [Behav Ecol 22:332-336 (2011)]

nthropogenic noise is increasing worldwide as a conse-A quence of widespread urbanization and the development of transport networks (Marzluff et al. 2001; Barber et al. 2010). Many animals rely on acoustic signals to communicate, and there is ample evidence for a series of behavioral strategies that maximize the active space of acoustic signals in noisy habitats (Brumm and Slabbekoorn 2005).

Songbirds' reproduction depends strongly on acoustic communication (Gil and Gahr 2002). Studies on the behavioral responses of birds to anthropogenic noise have been focused on shifts in the characteristics of songs to exploit frequency ranges or times where noise is lower. Most studies have documented shifts toward high-frequency notes that reduce acoustic interference from the low-frequency anthropogenic noise (Slabbekoorn and den Boer-Visser 2006; Bermúdez-Cuamatzin et al. 2009; see, however, Nemeth and Brumm 2009 for an alternative explanation). Amplitude shifts (i.e., singing louder songs) have also been demonstrated (Brumm 2004), as well as temporal shifts (i.e., singing during periods of low noise; Fuller et al. 2007). Spatial shifts are changes in bird abundance and community structure favoring species with high-frequency songs close to sources of noise (Francis et al. 2009). Spatial shifts could be direct, mediated by habitat selection, or indirect, mediated by negative effects of noise on breeding success, mate attraction, body condition, or vigilance rates (reviewed in

ference by increasing the amount of time spent singing and/or by increasing the redundancy of the song (Brumm and Slater 2006). Indeed, these responses have been demonstrated for birds faced with natural sources of noise (Brumm and Slater 2006), as well as in laboratory conditions (reviewed by Brumm

Francis et al. 2009). Apart from shifting songs, birds may reduce acoustic interrestrictions (Catchpole 1996; Brumm and Slater 2006), by metabolic costs of birdsong production (Ward and Slater 2005), or by trade-offs between singing time and feeding or vigilance time (Greig-Smith 1983; Campos et al. 2009). We tested whether serins Serinus respond to anthropogenic noise by increasing vocal activity in field conditions. This response can be expected due to the high-pitched song of serins (Mota and Cardoso 2001). However, costs associated to increased singing time would eventually produce threshold noise values over which such costs might outweigh benefits. Indeed, quadratic relationships between noise levels and call rates in chickens have been reported recently (Brumm et al. 2009), and Cynx et al. (1998) showed that zebra finches Taeniopygia guttata cease to sing at high levels of background noise (ca. 80 dB). Both studies were conducted, however, in

laboratory conditions. This will be the first demonstration of

a potentially effective response to anthropogenic noise, in-

et al. 2009). The effectiveness of this strategy would depend,

however, on the relation between the benefits obtained and its

costs. Low-frequency songs would be almost completely

masked by anthropogenic noise independently of singing

activity, thus favoring song shifts. High-frequency songs are

still masked by anthropogenic noise because energy in the

spectral region of an acoustic signal also contributes to masking

signals in other frequencies, albeit to a lesser extent (Parris and

Schneider 2008). Increasing singing time would then com-

pensate for this masking in the case of high-frequency songs.

Concerning costs, increasing singing time or song redun-

dancy may be constrained by informational or neuromuscular

MATERIAL AND METHODS

creased singing time, in wild birds.

Study area

The study area is a large (24 ha) suburban park surrounded by annual and perennial dry croplands and pastoral woodlands

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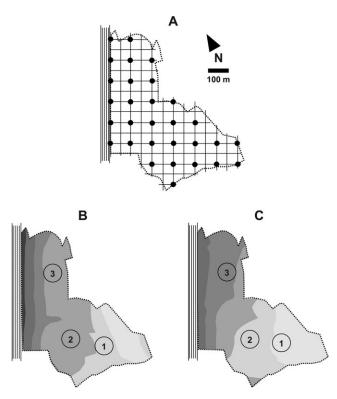


Figure 1 Map of the study area showing (A) the 50×50 m grid covering the whole park used to locate noise measurements. Dots indicate sampling points distributed regularly throughout the grid to generate isoline maps for working days (B) and weekend days (C) by means of linear interpolation that were further checked by measurements taken in the remaining intersection points of the grid. Isoline maps show noise zones from >80 dBA (darkest gray, only present during working days close to the highway) to <40 dBA (lighter gray, at the south eastern part). Gray grading indicates zones of 70–80, 60–70, 50–60, and 40–50 dBA. The highway that runs parallel to the western side of the study area in indicated by a striped band, and it is drawn to scale. Numbers within circles indicate the 3 areas where serins' vocal activity was measured both during working days and weekends.

(cereal, olive groves, and dehesas) except along its western border, which is delimited by a 600 m straight section of the Madrid–Toledo highway (Figure 1). Vegetation structure is fairly homogeneous as the park is a regularly spaced plantation of Aleppo pine *Pinus halepensis* and Arizona cypress *Cupressus arizonica* 10–15 m tall with 50–100% tree cover and almost no shrub cover on a surface that slopes up gently westwards. The access to the park is located in its northwestern corner and includes an 8 ha recreation area provided with seats, tables, and fire places. Fieldwork was carried out in May–June 2004.

Noise maps

We developed noise maps with a 50×50 -m resolution for both working days and weekends using a sound meter RION NL-05 provided with a UC-52 microphone. The sound meter was placed at the intersections of a 50×50 -m grid covering the whole park (109 sampling points; for details, see Figure 1 and Parra 2005). Noise was measured with the microphone oriented westwards (i.e., toward the highway) during 5 min in Leq mode ("Equivalent continuous sound pressure level," the instantaneous level of acoustic energy received averaged over the measuring period; Harris 1997). Measurements were made between 8:00 and 11:00 AM during both working days

(Monday–Thursday) and weekend days (Saturday and Sunday). In mid-May, we measured sound level at 30 sampling points distributed regularly throughout the grid to generate isoline maps for working days and weekend days by means of linear interpolation, rounded to the nearest 10 dBA (Figure 1). The accuracy of the isoline maps was evaluated by measuring noise at the remaining points (79) in mid-late June.

Vocal activity of serins

Serins S. serinus were the commonest singing birds in the study area (Parra A, personal observation). Vocal activity was measured in each of the <40, 40-50, 50-60, 60-70, and <math>>70dBA bands of the working days noise map as the >80 dBA band was too narrow to hold a minimum number of bird territories (Figure 1). Serins forage on the ground and in low vegetation and nest on tall shrubs and trees. Males sing from high singing posts in trees and, occasionally, during short flights between posts (Cramp and Perrins 1994). As it was logistically unfeasible to follow individual birds continuously to measure time budgets (i.e., the absolute amount of time spent singing), we estimate the vocal activity of individual birds by means of focal observations at singing posts (Altmann 1974). We looked carefully for male serins within each noise band. When a bird perched nearby, we started a stopwatch, verified noise levels with the sound meter, measured the time spent singing with a second stopwatch, stopped the first stopwatch when the bird flew away, and verified again noise levels. Total observation time and the amount of time spent singing were obtained from the stopwatches' records. A few first observations lasting less than 60 s were not considered (Altmann 1974); instead, we followed individual males until we were able to measure its singing behavior during longer periods. This procedure was followed until we obtained data for 5 birds per band, thus providing a balanced data set (Underwood 1997). High abundance (density for similar habitats in Spain is 1.6-1.7 birds/ha; Carrascal and Palomino 2008) and high fidelity to particular singing posts (Mota 1999) reduced the likelihood of sampling the same individual twice. Besides, we kept a minimum distance between sampling sites of 50 m. Minimum distances, the size of the smallest noise band (Figure 1), and balanced designs were the reasons for the sample sizes established. The whole procedure was repeated during weekends in 3 areas of the park in which noise levels changed from working to weekend days (Figure 1). Relationships between noise level and relative vocal activity (proportion of observation time that birds spent singing) were analyzed with generalized linear models (GLMs) on arcsintransformed data and potential confounding effects of observation time at singing post on relative vocal activity by means of GLMs on log-transformed data.

The vocal activity of birds varies both with time of day and with the season (Catchpole and Slater 2008). To avoid confounding effects, noise bands were sampled on consecutive days following a random order which was: 31 May, >70 dBA band; 1 June, 50–60 dBA band; 2 June, <40 dBA; 3 June, 40–50 dBA; 7 June, 60–70 dBA for working days; and 30 May, zone 2; 5 June, zone 1; 6 June, zone 3 for weekends days (see Figure 1). We sampled each band thoroughly from 8:00 and 11:00 AM to avoid both the dawn chorus and the silent midday period, recording the order in which measurements were made to test whether vocal activity within each noise band changed significantly during sampling.

RESULTS

Measured noise levels in the 79 grid points sampled in mid-July fitted closely to interpolated values based on the 30 points 334 Behavioral Ecology

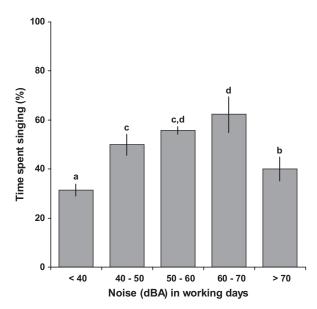


Figure 2 Proportion of time spent singing by serins *Serinus serinus* (means and 95% confidence interval, back-transformed; n=5) according to levels of anthropogenic noise during working days. Means sharing the same letters did not differ significantly at the 0.05 level (Tukey test).

sampled in mid-May ($R^2 = 87.37\%$ and 79.46%, P << 0.0001, for working days and weekends, respectively; v-intercepts did not differ from 0, P = 0.272 and 0.461, respectively, and slopes did not differ from 1, P = 0.464 and 0.892, respectively). Noise levels varied between >80 dBA (83.2) close to the highway during working days and <40 dBA (35.4) during both working and weekend days in the eastern side of the park (Figure 1). Noise isolines were fairly parallel to the highway, as expected from the homogeneous slope and vegetation structure of the park, which would produce a homogeneous attenuation of traffic noise (Brumm and Slabbekoorn 2005). Noise levels decreased during weekends both close to the highway (from >80 to 70–80 dBA) and in the eastern side of the park (from 40-50 to <40 dBA) and increased in the recreation area from 50-60 to 60-70 dBA (Figure 1), in relation with decreasing traffic intensity and increasing recreational activities during weekends, respectively (details in Parra 2005).

Mean observation time was 105.5 s (95% confidence interval = 93.9-117.4, n = 40). The proportion of time spent singing by serins during working days differed significantly among areas with different levels of anthropogenic noise $(F_{4,20} = 54.15, P << 0.0001;$ one-way analysis of variance; Figure 2), whereas observation time did not $(F_{4,20} = 0.53, P =$ 0.804). Proportions of time spent singing and noise levels (mid-class values) fitted to a quadratic relationship ($F_{2,22}$ = 56.57, $P \ll 0.0001$, $R^2 = 82.24\%$) but not to a linear one $(F_{1.23} = 3.60, P = 0.070, R^2 = 9.78\%; least-squares regressions).$ Proportion of time spent singing was uncorrelated to observation time (r = -0.06, P = 0.702, n = 40) and did not vary significantly along each sampling morning ($r_s = -0.70 - 0.80$, P = 0.104 - 0.873; n = 8 test). The last result could be attributed to low power of each test as it was based on 5 birds only; nevertheless, a combination of the results of the 8 tests through z-transformations (Rosenthal 1991) gave the same result (combined $r_S = 0.075$, P = 0.644, n = 40).

Serins spent less time singing during weekends than during working days in the 2 areas where noise levels decreased ($t_8 = 4.71$, P = 0.001 and $t_8 = 2.46$, P = 0.039, respectively; Figure 3)

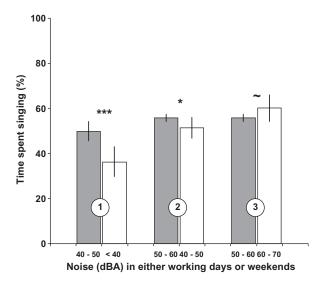


Figure 3 Proportion of time spent singing by serins *Serinus serinus* (means and 95% confidence interval, back-transformed; n=5) according to levels of anthropogenic noise in 3 areas (numbers within circles, which refer to Figure 1) where noise changed between working days (shaded bars) and weekends (open bars). ***P < 0.001; *P < 0.01;

and marginally more time in the area where noise increased ($t_8 = 2.00$, P = 0.081; Figure 3). Proportion of time spent singing depended on noise levels only, with no significant pure or interactive effects of week time (Table 1).

DISCUSSION

The homogeneity of the study area in slope, vegetation structure, and spatial location of the sources of anthropogenic noise produced noise maps that changed smoothly in relation to distance to noise sources. Changes from working days to weekends were also predictable in relation to changes in the intensity of human disturbance (traffic intensity and use of recreation areas). We took advantage of this "natural experiment" to measure the vocal behavior of serins in wild conditions, following a sampling design aimed at avoiding biases derived form potential confounding effects of temporal patterns of singing activity (e.g., Catchpole and Slater 2008). We were unable to measure the absolute amount of time that each individual bird spent singing because this is logistically unfeasible in field conditions, at least for small birds (Altmann 1974). Instead, we relied on samples based on focal

Table 1
Results of a 2-way analysis of variance testing for the effects of noise levels (<40, 40-50, and 60-70 dBA), time within the week (working days vs. weekends), and their interaction on the proportion of time spent singing by serins (arcsin-transformed)

Source	df	F	P
Week time (working days vs. weekends)	1, 24	0.82	0.374
Noise level	1, 24	96.07	<< 0.0001
Noise × week time	2, 24	1.63	0.216

Noise levels, week time, and their interaction had no effects on log-transformed observation times (F = 0.08–0.65, P = 0.919–0.426). df, degrees of freedom

observations of singing time relative to observation time, focusing on the real situations where male serins sing in field conditions (i.e., at singing posts). No systematic effects of sampling date, time, or duration of observations on singing activity were detected so that our relative estimate of vocal activity can be considered as an unbiased estimate of the absolute amount of time spent singing by male serins.

Serins responded to changing levels of anthropogenic noise by adjusting their levels of vocal activity (proportion of time spent singing) to noise levels during working days. Birds even adjusted singing activity to short-term changes in noise between working days and weekends. Although we do not have data to discard the possibility that differences in individual quality in relation to habitat occupancy may have biased the results, we find it unlikely for 2 reasons. First, we would expect noisy habitats to attract low-quality birds, and these should have lower singing rates, which is contrary to what we have found. Second, the comparison between working days and weekends in the same sites controls for a possibly heterogeneity in birds' quality between different areas. To our knowledge, this is the first demonstration of this kind of response to anthropogenic noise in wild birds, alternative or complementary to the frequency, amplitude, temporal, and spatial shifts in bird's singing behavior already documented (Brumm and Slabbekoorn 2005; Bermúdez-Cuamatzin et al. 2009).

Serins sing in the 2–10 kHz frequency range with maximum intensities at around 6 kHz (Mota and Cardoso 2001; Hu and Cardoso 2009), well above the low-frequency bands (<2 kHz; Warren et al. 2006) where most anthropogenic noise occurs. These characteristics of the serin's song would reduce the effectiveness of frequency or amplitude shifts to deal with noise pollution. We did not record or analyze the sonograms of birds in our study area as studies on the variability of the serin's song suggest little variation in its spectral properties (Mota and Cardoso 2001) and our study setting only consider anthopogenic sources of noise of decreasing intensity. Spatial and temporal shifts in singing behavior would also been precluded by the dissimilarity between the characteristics of the serin's song and anthropogenic noise. Having songs with maximum intensities at frequencies well above those mostly occupied by traffic noise seems to make birds less susceptible to acoustic masking due to noise pollution (Francis et al. 2009). Maybe this would be a factor in explaining the recent expansion of the species throughout man-modified habitats all over Europe, together with changes in climate (Huntley et al. 2007).

High-frequency songs are still masked by low-frequency noise, albeit to a lesser extent than low-frequency songs (Parris and Schneider 2008). Responses to compensate for this interference are expected to be costly, and these costs would shape such responses. Vocal responses of serins to noise were highly nonlinear. Proportion of time spent singing increased at a decelerating rate in relation to the logarithmic (dBA) measure of noise. This relationship held up to a threshold of approximately 70 dBA, followed by a decrease in singing activity. Singing increases metabolic costs only slightly in canaries S. canaria, a close relative to serins (Ward et al. 2003), and sustained singing is not constrained by respiratory needs (Calder 1970). Therefore, metabolic or neuromuscular constraints do not seem to be the basis of the decrease in vocal activity of serins at high noise levels. Instead, it may be hypothesized that singing during more than 60% of the time would not be compatible with conflicting demands such as foraging, predator surveillance, or detection of conspecific signals (Greig-Smith 1983; Campos et al. 2009). Trade-offs with foraging activities may be excluded as serins forage mostly on the ground, singing activity was measured during displays at singing posts, and duration of displays did not differ in relation to noise levels either in space or in time. Increasing needs for time during song displays under high levels of noise to scan for approaching predators (Barber et al. 2010) or to listen effectively to conespecific signals (Brumm et al. 2009) could account for decreasing rather than sustaining song activity levels in wild serins faced with high levels of noise pollution.

Summarizing, we document a clear-cut nonlinear response of serins to anthropogenic noise not reported to date. This pattern of response suggests that compensating for increasing noise levels by increasing the proportion of time spent singing involved costs to singing individuals, even in species whose song characteristics are somewhat preadapted for effective communication under noise pollution (Hu and Cardoso 2009). Because singing time may trade off with conflicting demands while displaying such as predator surveillance or detection of conespecific signals, our data suggest that bird populations in noisy city environments may face an increased challenge for survival and reproduction with respect to quiet areas. Whether this response was due to one or several of the specific characteristics of the serin's song or can be generalized to other bird species deserves further study. Understanding the effectiveness of the different responses of birds to anthropogenic increases in noise levels would help predicting future species distributions in the face of global change, as well as to prevent distribution changes using noise management.

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