# Tango to traffic : a field study into consequences of noisy urban conditions for acoustic courtship interactions in birds

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# Chapter 6

## Negative impact of traffic noise on avian reproductive success

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## ABSTRACT

Traffic affects large areas of natural habitat worldwide. As a result, the acoustic signals used by birds and other animals are increasingly masked by traffic noise. Masking of signals important to territory defense and mate attraction may have a negative impact on reproductive success. Depending on the overlap in space, time and frequency between noise and vocalizations, such impact may ultimately exclude species from suitable breeding habitat. However a direct impact of traffic noise on reproductive success has not previously been reported. We monitored traffic noise and avian vocal activity during the breeding season alongside a busy Dutch highway. We measured variation in space, time and spectrum of noise and tested for negative effects on avian reproductive success using long-term breeding data on great tits *Parus major*. Noise levels decreased with distance from the highway, but we also found substantial spatial variation independent of distance. Noise also varied temporally with March being noisier than April, and the day time being noisier than night time. Furthermore, weekdays were clearly noisier than weekends. Importantly, traffic noise overlapped in time as well as acoustic frequency with avian vocalization behavior over a large area. Traffic noise had a negative effect on reproductive success with females laying smaller clutches in noisier areas. Variation in traffic noise in the frequency band that overlaps most with the lower frequency part of great tit song best explained the observed variation. Additionally, noise levels recorded in April, when eggs are laid and incubated, had a negative effect on the number of fledglings, independent of clutch size, and explained the observed variation better than noise levels recorded in March. *Synthesis and applications*. We found that breeding under noisy conditions carries a cost, even for species common in urban areas. Such costs should be taken into account when protecting threatened species, and we argue that knowledge of the spatial, temporal and spectral overlap between noise and species-specific acoustic behavior will be important for effective noise management. We provide some cost-effective mitigation measures such as traffic speed reduction or closing of roads during the breeding season.

## INTRODUCTION

Anthropogenic noise currently affects large areas of natural habitat worldwide[1,2]. Masking by noise interferes with the use of the acoustic signals critical to many animal species[3,4]. As a consequence, animals living in areas exposed to anthropogenic noise may suffer reduced reproductive success, which may ultimately lead to the exclusion of species from otherwise suitable habitat[5].
The majority of areas affected by noise are situated along major transport links, such as highways and railways[1,2]. The impact of traffic noise has been explored in a diverse range of taxa (bats; [6,]frogs; [7]), but has been studied most intensively in birds (e.g.[8,9]). Many studies have shown a reduction in breeding numbers in the vicinity of highways (e.g.[10,11]), but no study to date has been able to exclude confounding factors associated with roads and thus identify traffic noise as the key threat to birds[12].

An impact of anthropogenic noise on breeding numbers[13] and species richness[14] without confounding factors has been demonstrated in the vicinity of noisy gas compressor stations. However, extrapolating these findings to highway noise is far from straightforward. For instance, noise at gas compressor stations is constant in amplitude throughout the day and year[14], whereas most anthropogenic noise levels show strong daily, weekday versus weekend, and seasonal variation[12,15].

The negative effect of traffic noise on birds depends on the temporal and spectral overlap with relevant acoustic sounds[4]. Birds use a variety of vocalizations throughout the day but many species restrict the use of song, which is important in both territorial defense and female attraction, to the period around dawn[16]. The overlap between dawn song and peaks in traffic activity (e.g. the rush hour) may be an important factor in determining negative effects, and depends primarily on the time of year in combination with longitude and latitude[12]. Assessing temporal variation in noise levels is therefore an important step in understanding when noise overlaps most with the vocal activity of birds[2,5].
Spectral overlap is most dramatic for birds vocalizing at low frequencies (e.g. cuckoos, owls, woodpeckers and grouse) as traffic noise is typically loudest at lower frequencies[17] and low sounds attenuate less with distance and vegetation density[18,19]. Furthermore, fluctuations in low frequency transmission can change dramatically with weather conditions[20] resulting in unpredictable overlap levels.
Even when there is clear temporal and spectral overlap between traffic noise and birdsong, assessing whether there is a negative impact

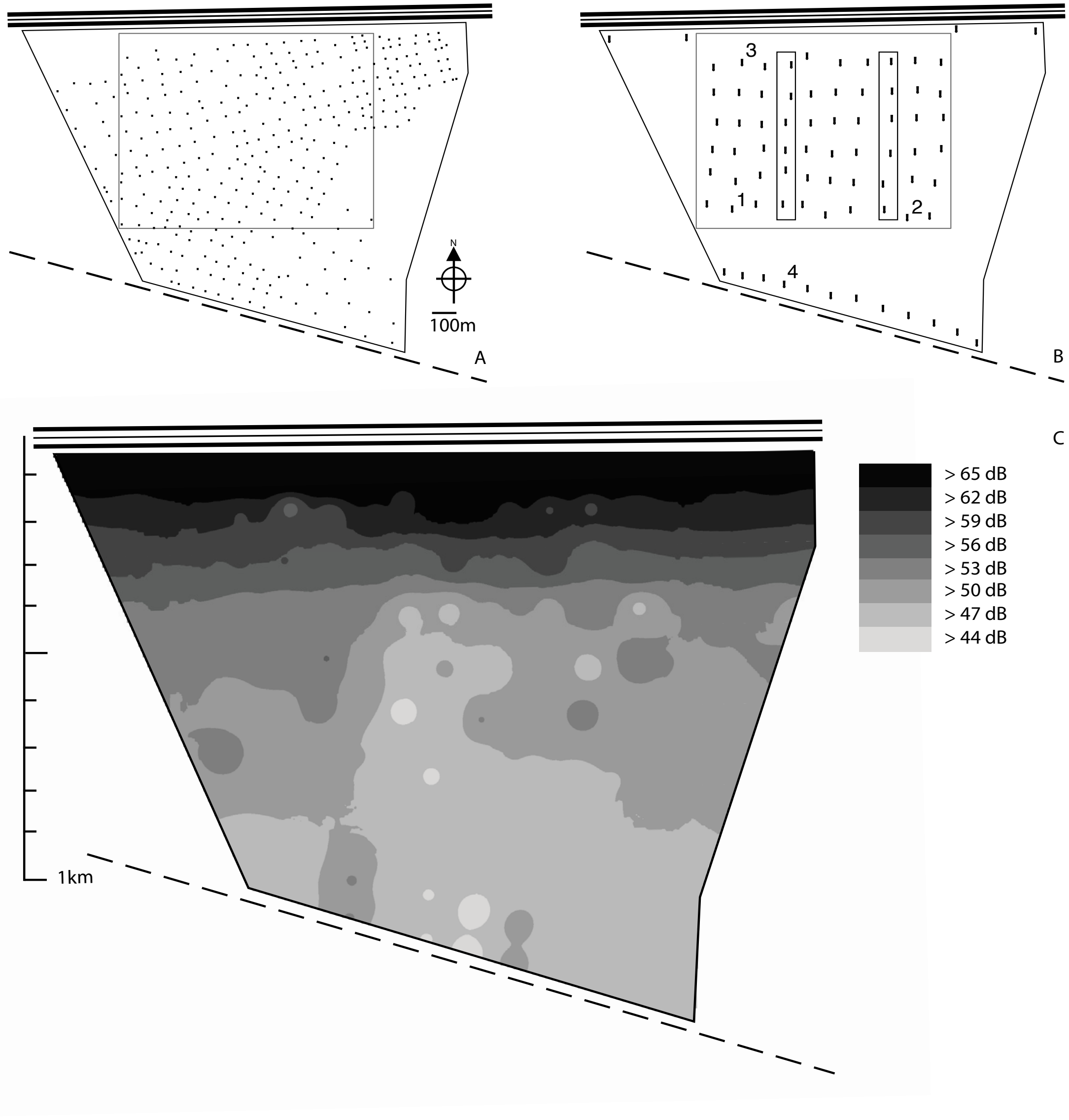


**Figure 6.1.** Maps of the Buunderkamp area showing nest-boxes, sampling locations and noise levels. Motorway (triple line) and railway (dashed line) are shown. (**A**) nest-box distribution (small dots). Only breeding data from nest-boxes within the rectangle was used. (**B**) sampling locations (filled rectangles) along 10 transects (open rectangles, 2 of them shown). Numbers refer to locations of example recordings used in Figure 6.2. (**C**) GIS-map showing spatial variation in sound levels. Traffic noise shows a strong decrease with distance from the motorway (absolute range at sampling locations 46.5–67.8 dB SPL, A-weighted), but there is substantial spatial variation in this decline.

on reproductive success in the field is not straightforward. The effect on breeding numbers may underestimate the impact and provides little insight into the mechanisms by which birds are affected. For example, breeding success and welfare may be impaired, but breeding densities remain high because of compensating effects of noise on predation rates[14] or competition for food[21]. Furthermore, inexperienced or low quality birds may be more likely to occupy noisy areas[11,22]. Therefore, understanding the mechanisms underlying the negative effects of noise is best achieved by focusing on individual life history traits that are components of reproductive success.

The great tit (*Parus major;* Linneaus 1758) is a common species that is currently not under threat, but the availability of long-term data from a population bordering a major highway provides a rare opportunity to investigate whether noise has more subtle effects than simply excluding birds from otherwise suitable habitat. This species prefers artificial nest-boxes to natural cavities[23] even when they are situated in suboptimal habitat. This is probably one reason why great tits breed in substantial numbers in areas adjacent to highways[24], allowing collection of breeding data in noisy areas. Great tit singing behavior has been repeatedly related to noise at both the population[25,26] and individual level[27]. We know that relatively low frequency songs are detected less well when there is traffic-like noise[17], and great tits can switch between song types when exposed to experimental noise (chapter 2)[28]. However, it is unknown whether such behavioral flexibility prevents any negative effects of anthropogenic noise.

We studied spatial, temporal and spectral variation in the loudness of traffic noise and bird acoustic behavior in a nest-box population of great tits adjacent to a Dutch highway with a heavy traffic load. Traffic noise and bird song were recorded during two important breeding stages: March, when territories are formed, and April, when eggs are laid and incubated. We used these data, together with habitat and long-term breeding data to explore the following questions: How does traffic noise in habitat adjacent to a highway vary in space? To what extent do traffic noise and bird vocal activity overlap in time and frequency, and does the amount of overlap differ between breeding stages? Is there an impact of traffic noise levels on breeding success? Does seasonal variation in traffic noise affect particular breeding stages? And does spectral overlap between great tit song and traffic noise play a role in the effect on reproductive success? Answers to these questions will be valuable in identifying conservation measures and applying effective noise management in natural areas polluted by traffic noise.

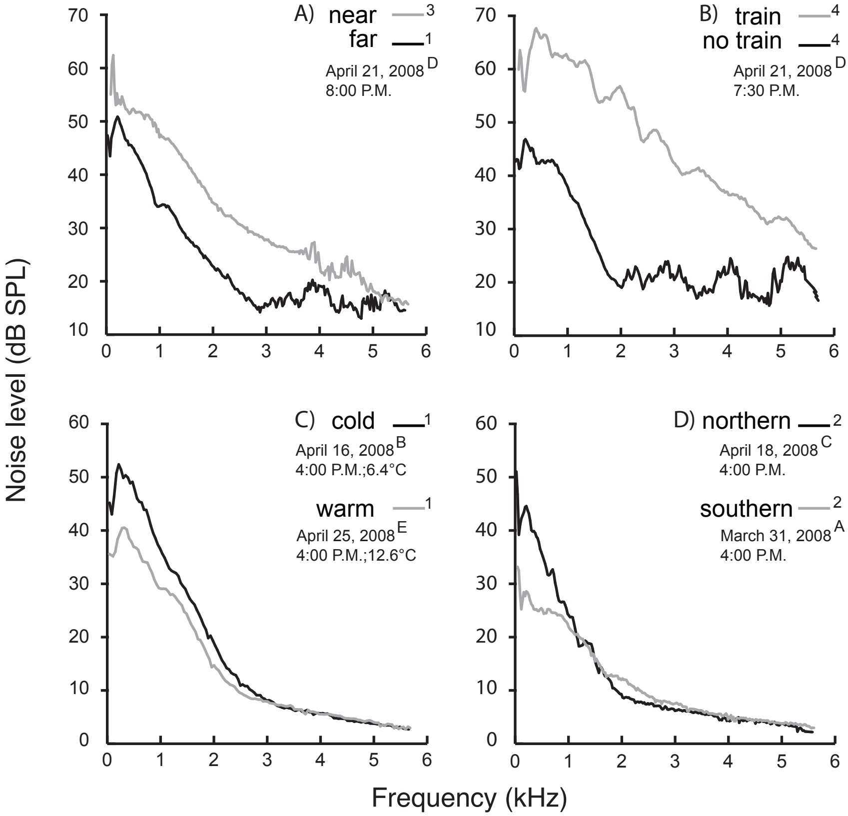


**Figure 6.2.** Variation in sound profiles across different environmental conditions. (**A**) powerspectrographic example comparing sound profiles near to (±100 m), and far from (±700 m), the motorway. At larger distances, the high-frequency components of traffic noise are more attenuated and even disappear above ±3 kHz. (**B**) recordings made near the railway (±100 m from the track and ±1 km from the motorway) shortly before and during the passage of a train. (**C**) comparison of sound profiles on days with different temperatures, but similar wind conditions illustrates large effect of weather conditions on noise levels. (**D**) comparison of sound profiles on days with opposite wind directions, but similar temperature and wind speed. Small numbers refer to locations illustrated in Figure 6.1. Capital letters refer to recording days illustrated in Figure 6.3.

## MATERIALS AND METHODS

### Study site & species

We collected data from a nest-box population of great tits *Parus major* breeding at the Buunderkamp (05°45′E; 52°01′N) in the Netherlands (Figure 6.1A). The area is bounded in the north by a four-lane highway and in the south by a railway line (about 20 trains/hour). The habitat is mixed woodland consisting of plots of varying sizes, and age and species of trees, with *Pinus sylvestris* and *Quercus rubra* dominant (see[29] for further description of the area).

The great tit is a hole-nesting passerine that sings in the frequency range of 2 - 9 kHz[28]. Territory defense starts in mid-January and peaks towards the end of March[23]. Egg-laying in the study population starts in April and is accompanied by a strong increase in dawn singing activity. We used long-term breeding data on great tits for the period 1995 - 2009 during which no major changes have been made in the area that would have affected the spatial spread of noise coming from the highway.

### Noise data acquisition

We made sound recordings between March and May 2008, before major leafing of the deciduous trees. We sampled sound levels along ten transects perpendicular to the highway (Figure 6.1B), with automatic SongMeter recorders (16 bit, 24 kHz sample rate; Wildlife Acoustics Inc.). Exact sampling locations were determined with a GPS (Garmin 60CSx). The sampling transects started 100 m from the mid-line of the highway and six sampling locations at approximately 100 m intervals were chosen within each transect. The transects were spaced 80 - 100 m apart and two transects were sampled simultaneously for 3 - 5 consecutive days. Transects were each sampled twice in a random order, once between 8th and 30th of March, and once between 31st of March and 1st of May. The sampling grid encompassed most of the area, but we used two additional SongMeters to monitor the remaining area. Recorders were attached to large trees (> 40 cm in diameter) at 2 m above the ground with the recording microphone directed towards the highway. Recording levels for the microphones were adjusted to a sensitivity ranging from 0.0 - 1.5 dBV/pa (reaching full scale between 92.5 - 94.0 dB SPL) and amplitude levels were adjusted according to the effective sensitivity of each individual Song Meter recorder. Recorders were randomly swapped between sampling locations to control for any remaining variation in recording levels. Recorders were scheduled to record for 30 seconds at 30 minute intervals, day and night.

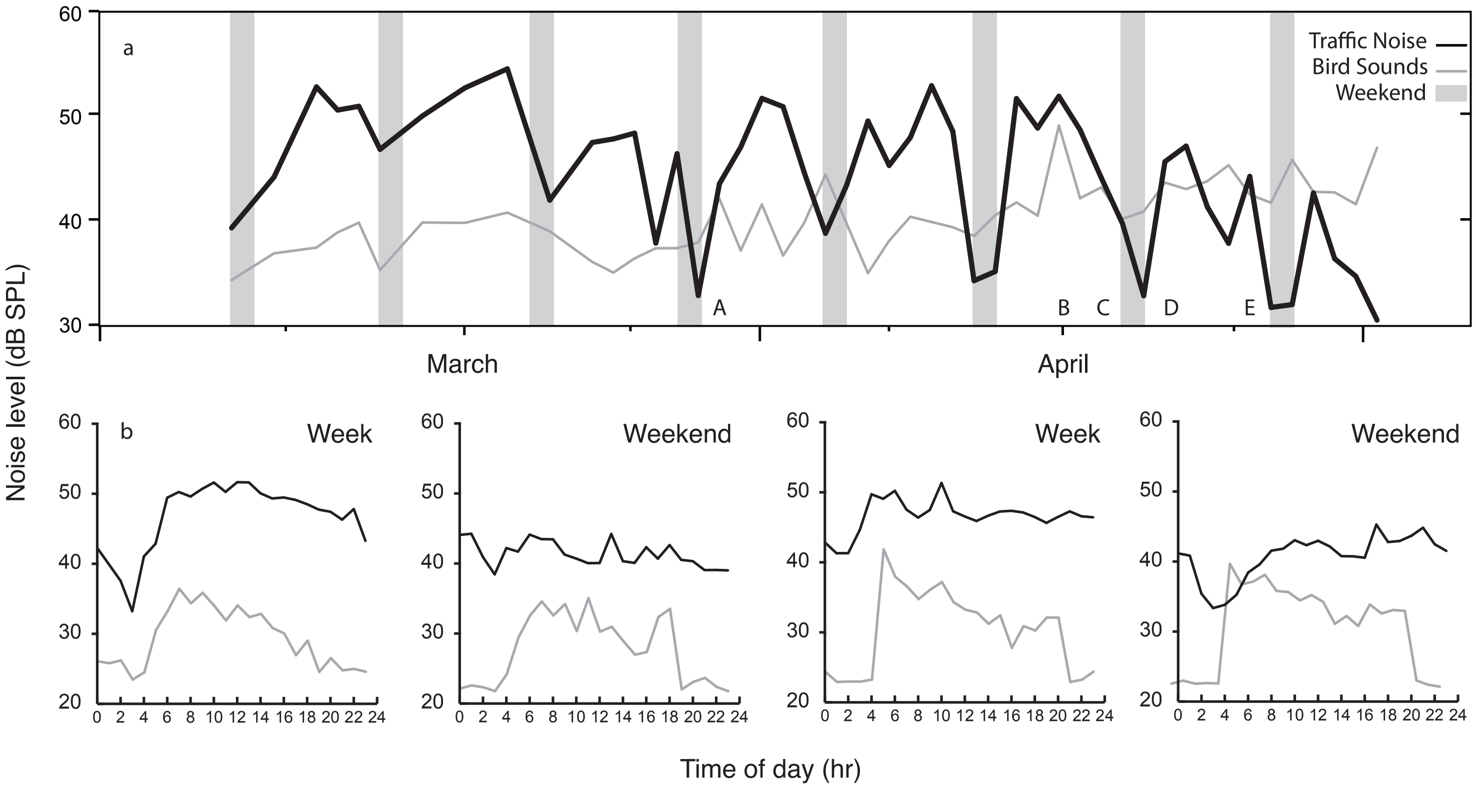


**Figure 6.3.** Temporal patterns in traffic noise levels and bird vocal activity. Recordings made at distances of 400–700 m from the motorway, averaged over 1 or 24 h intervals. We compared amplitude fluctuations in the 1 and 4 kHz band, which are mainly influenced by traffic and bird vocal activity respectively. (**A**) seasonal pattern in sound levels between March and May 2008. Recordings made at dawn during peak singing activity. Traffic noise levels decrease throughout the season, but show substantial variation due to changes in traffic activity (week days being noisier than weekend days) and changes in weather conditions. Bird vocal activity increases throughout the season. (**B**) daily pattern in traffic noise and bird sound levels during either the period of great tit territory defense (8–16 of March, left two graphs) or egg-laying (19–27 of April, right two graphs), on weekdays or at the weekend.

We analyzed sound recordings in the computer program Matlab (Mathworks Inc.). We measured overall sound levels (using an A-weighted filter), and also sound levels in four adjacent octave-bands, centered at frequencies of 0.5, 1.0, 2.0, and 4.0 kHz. Sound measurements were averaged over either 30-minute or 24-hour intervals, and/or sampling locations, depending on the type of analysis.

We used 76 sampling locations to visualize spatial variation in noise levels for the Buunderkamp in the computer program ArcGis (version 9.0, ESRI). Sixty locations from the sampling transects and 16 additional sampling locations were plotted onto a geo-annotated reference map from which noise maps were derived with the Spatial Analyst toolbox. Spatial resolution was set at 5m and raster values between sampling locations were calculated with a weighted distance interpolation tool (IDW). Additionally we calculated distances for all nest boxes and sampling locations to the nearest mid-point on the highway.

We assessed the temporal overlap between traffic noise and vocal bird activity throughout the season and at different times of day. At our study site most of the non-anthropogenic sound comes from vocalizing birds with the majority of acoustic energy in the range of 2 - 8 kHz. We selected a subset of sampling locations at distances over 400 m from the highway where there is little traffic noise present in the 4 kHz octave band so temporal variation in sound levels was mainly related to the vocal activity by birds. For these locations, we compared sound levels, averaged over 1 or 24 hour intervals, in the 1 kHz band (mainly due to traffic noise) with those in the 4 kHz band (mainly due to bird activity, including great tits).

## Long-term breeding data

Great tit breeding data were collected between 1995 and 2009 by the Netherlands Institute of Ecology (NIOO-KNAW). We used data from both large and small nest-boxes within the sampling grid (Figure 6.1A) on laying date, clutch size, number of hatchlings, number of fledglings and fledging mass (average weight of chicks for the brood when chicks are 15 days old) for all first great tit clutches over this period, except for 2007 and 2008 when data were excluded because of an unrelated experiment. Additional data on female identity, female age and fledging mass were only available for 1995-1999, 2001 and 2009.

For analysis of breeding performance we used only first clutches (categorized using female identity or because laying date was within 30 days of the first laying date for a given year). For

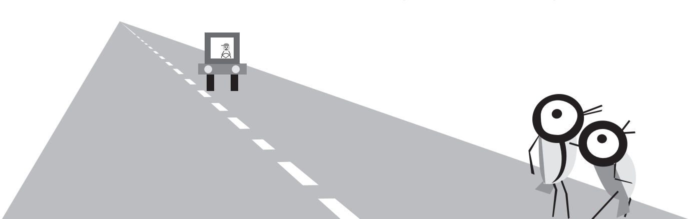


**Table 1.** Results from mixed model showing effect of weather condition on overall noise levels. Sampling location (N = 60) was added as random factor. Only first order interactions are reported.

| Source | d.f. | F | P |
|---|---|---|---|
| Distance | 5 | 6.61 | <0.001 |
| Wind direction (N vs S) | 1 | 10.92 | 0.001 |
| Daily Temperature | 1 | 9.65 | 0.002 |
| Wind speed* | 1 | 29.30 | <0.001 |
| Distance x Wind direction | 5 | 3.81 | 0.002 |
| Distance x Daily Temperature | 5 | 2.73 | 0.019 |
| Distance x Wind speed* | 5 | 1.75 | 0.12 |
| Wind direction x Daily Temperature | 1 | 1.32 | 0.25 |
| Wind direction x Wind speed* | 1 | 10.38 | 0.001 |
| Daily Temperature x Wind speed* | 1 | 11.26 | 0.001 |
| * log-transformed | | | |

analyses of laying date we used only clutches for which this could be reliably calculated. We were interested in the mechanisms underlying breeding success and therefore focused on life history traits that reflected decisions made by the birds. For the analysis of clutch size we therefore excluded clutches that were not incubated, because including nests that were abandoned (either through a decision by the parents, or predation of the parents) would introduce unwanted heterogeneity in the data. Similarly, we excluded nests where no chicks hatched or fledged from the analyses of the number of hatchlings and fledglings, respectively, because it was usually unknown whether failure was caused by death of all the embryos or chicks, abandonment by the parents or predation of the parents (away from the nest).

## Weather & habitat data

We assessed habitat characteristics, including tree density, tree diameter and species composition, at the level of woodland plots (0.2-1.0 ha). We measured tree density and diameter and noted tree species at each of the 60 sampling locations, and at the two nest boxes nearest to these locations. We calculated the percentage of deciduous trees per plot and averaged tree density and diameter over all locations within a plot. We used weather data on daily wind direction and speed, and temperature, recorded by the Royal Netherlands Meteorological Institute (KNMI) at de Bilt (situated ± 50 km to the west of the Buunderkamp).

## Statistical analysis

We analyzed all data using SPSS (version 17.0) and log-transformed variables when necessary to meet model assumptions. Temporal variation in daily and seasonal sound levels were explored using repeated measures ANOVAs with sound level grouped by sampling location as the dependent variable and time of day or date as an explanatory variable. Additionally, we compared recordings made on weekdays with recordings from weekends with type of day as a fixed factor.

We examined the effect of daily weather conditions on the propagation of noise with full factorial linear mixed models. To test for the effect of wind direction we discriminated between days with northerly (coming from the direction of the highway) and southerly winds (going towards the direction of the highway). Wind direction was included as a fixed factor, and sample location as a random factor. Distance to the highway, wind speed, and daily temperature were included as covariates.

We constructed a set of linear mixed models for each life history trait and compared them using a model selec-

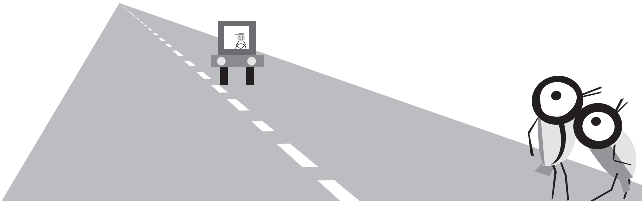


**Table 2.** Life history model selection procedure based on traffic noise, distance and/or habitat features using Akaike's information criterion. Overall noise level (**Noise**), distance to the highway (**dH**), tree diameter (**d**), tree density (**t**) and percentage of deciduous trees (**%d**) were entered as main effects in mixed models. Only models with a Δ AIC < 4.0 are shown for each life history trait.

| Dependent trait | Model | AIC | Δ AIC | Akaik weight |
|---|---|---|---|---|
| Laying date | d+t | 3523.81 | 0.00 | 0.52 |
| (N = 542) | d | 3525.61 | 1.80 | 0.21 |
| | Noise+d+t | 3526.86 | 3.06 | 0.11 |
| Clutch size | Noise+d | 1727.51 | 0.00 | 0.32 |
| (N = 505) | Noise+d+t | 1727.92 | 0.41 | 0.26 |
| | Noise | 1729.43 | 1.92 | 0.12 |
| | d | 1730.05 | 2.54 | 0.09 |
| | d+t | 1730.41 | 2.90 | 0.07 |
| | Noise+t | 1730.41 | 2.90 | 0.07 |
| Number of hatchlings | d | 917.53 | 0.00 | 0.36 |
| (N = 470) | d+t | 917.71 | 0.18 | 0.33 |
| | Null | 920.18 | 2.65 | 0.10 |
| | t | 921.05 | 3.53 | 0.06 |
| | Noise+d | 921.19 | 3.66 | 0.06 |
| | Noise+d+t | 921.38 | 3.85 | 0.05 |
| Number of fledglings | d | 1956.24 | 0.00 | 0.29 |
| (N = 387) | d+t | 1956.65 | 0.42 | 0.24 |
| | Noise+d | 1957.61 | 1.37 | 0.15 |
| | Noise+d+t | 1958.08 | 1.85 | 0.12 |
| | Null | 1958.98 | 2.74 | 0.07 |
| | t | 1959.22 | 2.99 | 0.07 |
| Fledging mass | Noise+d+t+%d | 2070.29 | 0.00 | 0.52 |
| (N=215) | Noise+d+t | 2072.26 | 1.96 | 0.19 |
| | Noise+d+t+dH+%d | 2072.86 | 2.57 | 0.14 |

tion approach based on Akaike's information criterion[30]. Models always included nest-box type (large or small), sampling location and breeding year as random factors. Depending on the model, we also included other reproductive traits as explanatory variables (cf. [31]). For instance, clutch size can correlate with laying date and an effect of noise on clutch size could be indirectly caused by an effect of noise on laying date. Including laying date in the clutch size model therefore allows us to test for a direct effect of noise. For the number of hatchlings we included clutch size and for the number of fledglings we included number of hatchlings in the models. For the fledging mass model we included both clutch size and laying date as these factors are known to have a large effect on fledging mass (e.g.[31]).

In a first analysis we compared models that included overall noise levels, distance to the highway, tree density, tree diameter and percentage deciduous trees as explanatory factors. Models contained single factors or in combination with other factors as main effects as we had no a priori knowledge that interactions among factors would be of importance. The total set contained 32 models to be compared for each trait, including the Null model. We calculated for each explanatory factor the probability that it would be in the best approximating model using Akaike weights (see e.g.[.32,33]). We used the subset of models with a delta-AIC < 4.0 from the top model to get model-averaged estimates and standard errors each factor (cf. [30]). In a second analysis we focused on temporal overlap between noise sampling period and breeding stage. We used the models with delta-AIC < 4.0 from the previous analysis and only exchanged the overall noise with noise levels sampled either in March or in April. In a third analysis, we repeated this procedure, but focused on the spectral overlap with song and explored whether noise in a certain frequency range (0.5, 1.0, 2.0, or 4.0 octave band, or overall noise) better explained variation of the data.

Breeding performance is known to be age-dependent[23,31] and we therefore re-ran analyses for which we found strong support using the subset of data for which female age was known. Female identity was added as a random factor and female age (first year or older) as a fixed factor.

## RESULTS

### Spatial patterns in noise levels

Overall sound levels gradually decreased with distance from the highway ($F_{5,54} = 200.5$, $P < 0.001$) with an average drop of 20 dB SPL (A-weighted) over less than 500 m (Figure 6.1C). Furthermore, high frequencies attenuated faster than low

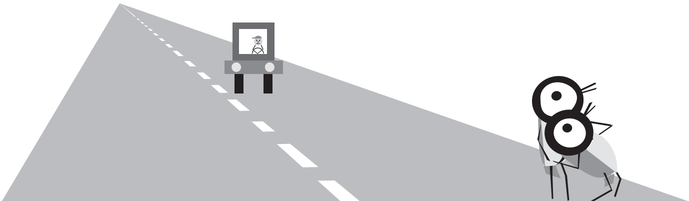


**Table 3.** Results from model selection procedure showing selection probabilities (calculated across the whole model set) and parameter estimates (using a subset of the models with Δ AIC < 4.0 and model averaging procedures; see text and Table 2). Only factors that were used for model averaging are shown.

| Dependent trait/ independent parameter | Selection probability | B | SE |
|---|---|---|---|
| Laying date | | | |
| Tree diameter | 0.92 | -1.07 | 3.92 |
| Tree density | 0.70 | 0.34 | 0.93 |
| Noise | 0.18 | 0.044 | 0.075 |
| Clutch size | | | |
| Noise | 0.80 | -0.053 | 0.021 |
| Tree diameter | 0.75 | 0.18 | 1.23 |
| Tree density | 0.42 | 0.17 | 0.25 |
| Number of hatchlings | | | |
| Tree diameter | 0.81 | 0.72 | 1.64 |
| Tree density | 0.46 | -0.05 | 0.35 |
| Noise | 0.14 | -0.039 | 0.030 |
| Number of fledglings | | | |
| Tree diameter | 0.80 | -0.75 | 0.83 |
| Tree density | 0.45 | -0.18 | 0.15 |
| Noise | 0.33 | -0.044 | 0.020 |
| Fledging mass | | | |
| Tree diameter | 0.99 | 145.1 | 151.7 |
| Tree density | 0.99 | -10.87 | 26.96 |
| Noise | 0.93 | -3.14 | 2.67 |
| Distance to highway | 0.22 | 0.005 | 0.11 |
| Percentage deciduous | 0.16 | 0.56 | 0.39 |

frequencies ($F_{3,59} = 12.03$, $P < 0.001$; Figure 6.2A). There was substantial spatial variation in traffic noise, independent of distance to the highway (Figure 6.1C): different locations at medium (>300 m) to large (>700 m) distances from the highway differed by more than 9 dB SPL (A-weighted) in noise level (Figure 6.1C). Train noise can be very loud (see e.g. Figure 6.2B) but, in contrast to highway noise, is transient and average daily noise levels near the railway line were among the lowest (Figure 6.1C).

### Weather-dependent noise levels

Wind direction, wind speed and daily temperature all had an effect on overall sound levels (see Table 1). Furthermore, wind direction and temperature interacted with distance to the highway (Table 1). We reanalyzed a subset of recordings made at distances of 400 – 700 m from the highway to explore the effect of weather conditions on sounds in different octave bands. Both temperature ($F_{1,59} = 27.78$; $P < 0.0001$) and wind direction ($F_{1,59} = 5.27$; $P = 0.001$) interacted with frequency, with the strongest effect at lower frequencies and large distances from the highway. For instance, at 700 m from the highway, sound levels below 1 kHz could increase by over 10 dB SPL on cold days or days with northerly winds (Figure 6.2C,D).

### Temporal fluctuations in traffic noise overlap with bird activity

Traffic noise levels changed throughout the season ($F_{1,59} = 7.57$ $P = 0.008$) with March being noisier and more variable than April (Figure 6.3A). Additionally, noise levels on weekdays were significantly higher than at the weekend ($F_{1,59} = 4.87$ $P = 0.032$; Figure 6.3). Noise levels showed a strong daily pattern ($F_{1,59} = 8.776$ $P = 0.005$), with a clear drop between 0:00 and 4:00 AM, but no distinct rush-hour peaks (Figure 6.3B).

Screening of recordings revealed that, at distances over 400 m from the highway, variation in sound levels in the 4 kHz band was indeed mainly influenced by bird vocal activity, and we therefore used recordings at these distances to assess seasonal and daily overlap of traffic noise and bird vocal behavior. Bird vocal activity as measured at the peak of the dawn chorus increased throughout the season (4 kHz-band; $F_{1,59} = 7.88$, $P < 0.001$) whereas traffic noise during this time period decreased (1 kHz-band; $F_{1,59} = 5.13$, $P < 0.001$; Figure 6.3A). Bird vocal behavior showed a temporal shift between early March and late April due to changes in the time of sunrise, but despite this, the temporal overlap with traffic noise remained remarkably high on weekdays (Figure 6.3B), probably due to the change from winter to summer time (i.e. clock time advancing by

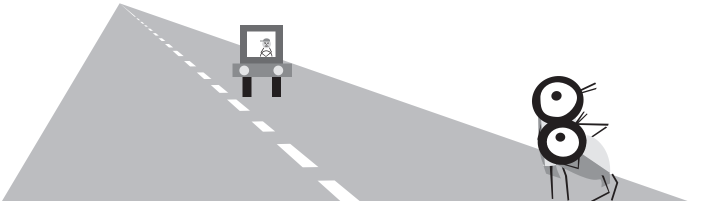


**Table 4.** Results from model selection procedure focusing on temporal variation in noise. Models as used in Table 2 were adjusted to include noise levels recorded either in March or April.

| Dependent trait | Model | AIC | Δ AIC | Akaike weight |
|---|---|---|---|---|
| Laying date | d+t | 3523.81 | 0 | 0.52 |
| (N = 542) | d | 3525.61 | 1.80 | 0.21 |
| | Noise April+d+t | 3527.03 | 3.23 | 0.10 |
| | Noise March+d+t | 3527.30 | 3.49 | 0.09 |
| | Noise April+d | 3528.85 | 5.05 | 0.04 |
| | Noise March+d | 3529.14 | 5.34 | 0.04 |
| Clutch size | Noise March+d | 1725.97 | 0 | 0.25 |
| (N = 505) | Noise April+d | 1726.20 | 0.23 | 0.22 |
| | Noise April+d+t | 1726.56 | 0.59 | 0.19 |
| | Noise March+d+t | 1726.79 | 0.82 | 0.17 |
| | Noise March | 1728.05 | 0.17 | 0.09 |
| | Noise April | 1728.11 | 2.08 | 0.09 |
| Number of hatchlings | d | 917.53 | 0 | 0.36 |
| (N = 470) | d+t | 917.71 | 0.18 | 0.33 |
| | Null | 920.18 | 2.65 | 0.09 |
| | t | 921.05 | 3.53 | 0.06 |
| Number of fledglings | Noise April+d | 1955.34 | 0 | 0.32 |
| (N = 387) | Noise April+d+t | 1956.08 | 0.74 | 0.22 |
| | d | 1956.24 | 0.89 | 0.21 |
| | d+t | 1956.65 | 1.31 | 0.17 |
| Fledging mass | Noise April+d+t+%d | 2070.16 | 0 | 0.39 |
| (N=215) | Noise Marchl+d+t+%d | 2071.12 | 0.96 | 0.24 |
| | Noise April+d+t | 2072.30 | 2.14 | 0.13 |
| | Noise March+d+t | 2073.01 | 2.85 | 0.09 |
| | Noise April+d+t+dH+%d | 2073.13 | 2.97 | 0.09 |
| | Noise March+d+t+dH+%d | 2073.84 | 3.68 | 0.06 |

one hour on 30 March). Peak activity of avian vocal behavior showed the least overlap with traffic noise during the weekends, especially in late April (Figure 6.3B).

### Negative effect of traffic noise on breeding performance

Overall noise levels received strong support in the model selection procedure for clutch size and fledging mass models and moderate support for the number of fledglings model (Table 2 and 3). Tree diameter and tree density received strong support in all life history models (Table 2 and 3), but the effect was not consistent across models and the variance was high (Table 3). Distance to the highway and percentage deciduous trees received weak support in the fledging mass model (Table 2 and 3) and virtually no support in the remaining life history models.

Overall noise levels had an independent negative effect on clutch size, with females laying on average about 10% fewer eggs across a noise gradient of 20 dB SPL (A-weighted) (Table 3). Reanalyzing the top clutch size model to include female identity and age confirmed the effect of noise ($F_{1,268} = 7.82$, $P = 0.007$), but failed to show an effect of female age on clutch size ($F_{1,268} = 0.20$, $P = 0.82$). Noise levels had a negative effect on fledging mass (Table 3), but in none of the top models was the effect significant (all $P > 0.2$).

### Temporal and spectral variation in noise predicts smaller clutches and fewer fledglings

Refining the models with noise sampled either in March or in April did not change the level of support, except for the number of fledglings model (Tables 4 and 5). Noise sampled in April was about 7 times more likely to explain variation of the data compared to noise sampled in March (Table 5). Higher noise levels in April correlated with lower numbers of fledglings (Table 5). We re-ran the top model to include clutch size instead of the number of fledglings as fixed factor. Clutch size had a large effect on the number of fledglings (B = 0.57 ± 0.070; $F_{1,364} = 65.51$, $P < 0.0001$), but we found noise sampled in April to have an additional negative effect (B = -0.061 ± 0.027; $F_{1,364} = 5.09$, $P = 0.028$) as well.

Finally, we found that variation in noise levels in the 2 kHz octave band best explained variation in clutch size, although overall noise and noise in the 0.5 and 1.0 kHz band also received moderate support (Table 6a). Noise in the 2 kHz band frequency range overlaps the lower part of great tit song in our study population and had a negative effect on the number of eggs laid by females (Table 6b).

**Table 5.** Temporal variation in noise is related to breeding performance. Selection probabilities and parameter estimates of noise recorded either in March or April from model selection procedures are shown (see text and Table 4).

| Dependent trait | Noise parameter (sampling period) | Selection probability | B | SE |
|---|---|---|---|---|
| Laying date | March | 0.13 | 0.007 | 0.050 |
| | April | 0.14 | 0.024 | 0.059 |
| Clutch size | March | 0.50 | -0.038 | 0.020 |
| | April | 0.50 | -0.040 | 0.020 |
| Number of hatchlings | March | 0.07 | -0.027 | 0.027 |
| | April | 0.09 | -0.032 | 0.029 |
| Number of fledglings | March | 0.08 | -0.033 | 0.019 |
| | April | 0.55 | -0.051 | 0.019 |
| Fledging mass | March | 0.39 | -1.97 | 1.80 |
| | April | 0.61 | -3.16 | 2.48 |

**Table 6.** Spectral overlap between noise and song predicts clutch size. (**A**) model selection using clutch size models with strong support in previous analysis (see text and Table 2). Only models with a Δ AIC < 4.0 are shown. (**B**) Selection probabilities for noise in different frequency ranges and parameter estimates after model averaging. Only results for noise variables are shown.

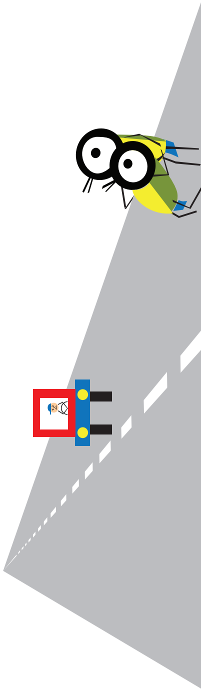
**A**

| Model (Noise frequency range) | AIC | Δ AIC | Akaike weight |
|---|---|---|---|
| 2 kHz band+d+t | 1726.59 | 0 | 0.28 |
| overall (A-weighted)+d+t | 1727.92 | 1.33 | 0.15 |
| 0.5 kHz band+d+t | 1728.14 | 1.54 | 0.13 |
| 1 kHz band+d+t | 1728.62 | 2.02 | 0.10 |
| 4 kHz band+d+t | 1729.57 | 2.98 | 0.06 |
| 2 kHz band+d | 1730.27 | 3.67 | 0.05 |

**B**

| Noise frequency range | Selection probability | B | SE |
|---|---|---|---|
| 2 kHz band | 0.38 | -0.058 | 0.016 |
| overall (A-weighted) | 0.20 | -0.053 | 0.021 |
| 0.5 kHz band | 0.18 | -0.070 | 0.022 |
| 1 kHz band | 0.15 | -0.064 | 0.018 |
| 4 kHz band | 0.09 | -0.069 | 0.027 |

**Collecting field data**; clockwise: female incubating on nest during weekly routine check; finished clutch containing 12 eggs, measuring chicks, blood sample for genetic paterniry analysis.



## DISCUSSION

We recorded high traffic noise levels in forest bird breeding habitat related to the proximity of a highway. However, we also found spatial variation in noise levels independent of distance to the highway that allowed us to demonstrate a negative relationship between noise levels and the reproductive success of great tits. Furthermore, noise levels varied substantially with the time of day, season and weather conditions, and both temporal and spectral overlap with vocalizing birds is high under a wide range of conditions. Finally, we found noise levels in April to have a negative effect on the number of fledglings, while noise variation in the frequency with most spectral overlap with great tit song best predicted a negative effect on clutch size.

### Explaining noise impact on reproductive success

We found an impact of traffic noise on avian reproductive success manifest by smaller clutches and fewer fledged chicks in the noisier areas. We also explored relationships between breeding traits and temporal and spectral overlap of noise, which could provide some insight into the mechanisms by which birds are affected. We believe there are at least four possible mechanisms, all related to signal masking to some degree, which could explain how anthropogenic noise has a negative impact on avian reproductive success.

The first explanation is related to interference with acoustic assessment of mate quality. Female birds are known to rely on song in assessment of male quality and subsequent investment decisions[34]. High noise levels could reduce perceived song quality and cause females to breed later, allocate less energy to the eggs or provide less maternal care to the chicks. Our data show that spectral overlap between noise and great tit song best predicts patterns in clutch size, suggesting that noise may indeed interfere with song-based assessment of male quality and subsequently lower female investment.

The second explanation for the effect of traffic noise on reproductive success could be related to the non-random distribution of individuals across the habitat. Birds may perceive a noisy territory as being of lesser quality[5] and therefore try to avoid these areas. For instance, both Reijnen & Foppen[11] and Habib, *etal*[22] found less experienced birds breeding in more noisy territories. We did not find traffic noise or clutch size to covary with female age and we have no insight into distribution and performance of lower quality individuals (e.g. immigrants, who are known to produce smaller clutches;[23]), but it is likely that noise may play an important role at the time that individuals are settling and defending territories.

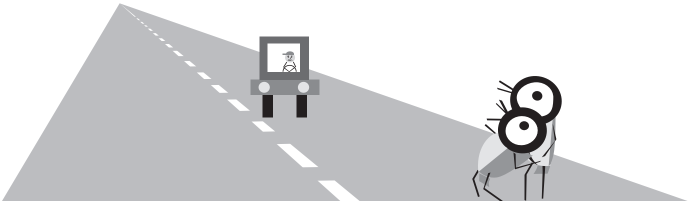
The third explanation is that increased noise levels could also cause physiological stress due to reduced foraging opportunities, because prey are less easy to detect[6], or because more time has to be spent scanning for predators[35]. Individuals living in noisy areas may therefore have less energy to invest in their eggs and offspring.

And finally, the fourth explanation could be that noise can have an impact on parent-offspring communication and adults may therefore not be able to meet their chicks' demands[36]. We did not find a significant effect on fledging mass, but we did find that high noise levels in April have a negative effect on the number of fledglings, independent of clutch size. Whether this is related to higher stress levels, reduced foraging or decreased communication is difficult to disentangle, but it does suggest that noise interference could affect food provisioning to the chicks.

### Explaining traffic noise heterogeneity

The opportunity to test for an impact of traffic noise on avian reproductive success relied on the heterogeneity of noise levels independent of distance to the highway. Many earlier studies have designed ways to predict spatial and temporal variation of traffic noise, using a combination of field data and theoretical modeling[37]. However, these models have tended to focus either on noise data at the source (taking traffic and road variables into account; e.g.[38,39]) or on transmission data (e.g.[20]). The few models that have integrated these aspects have assumed that the areas adjacent to highways are environmentally homogeneous[37]. In contrast, our study reveals a high level of heterogeneity at a local scale that should be taken into account when trying to understand the impact of noise on bird breeding populations.

In addition to revealing the pattern of noise heterogeneity, we were able to provide some insight into the causal explanations for the noise variation in space, time, and frequency. We found substantial spatial variation throughout our study area that was not related to the distance to the highway. The effect was most pronounced at a few hundred meters from the highway, with nearby areas differing by over 9 dB in mean noise levels. Transmission of traffic noise is known to depend on highway architecture, and ground and vegetation structure[40]. However, the architecture of the highway does not vary over the length adjacent to our study area and the spatial noise heterogeneity that we found is most likely to be caused by variation in tree densities in the areas close to the highway[19]. Noise levels close to the highway source are known to depend on traffic load[39] which can vary between day and night, and between weekdays and the weekend[15]. Noise amplitude is also strongly related to traffic speed[41], which is probably why we did not detect a clear rush-hour peak in noise, because traffic during the rush-hour is often much slower



or even stationary. Finally, we not only confirmed that lower frequency sounds were transmitted over a larger area than higher frequency sounds but that relatively low frequencies were also more influenced by changing weather conditions.

## CONCLUSIONS AND APPLICATIONS

We have shown that traffic noise levels in roadside forest vary substantially in space, time and frequency, which allowed us to reveal a negative relationship with reproductive success in a common species. Great tit females laid fewer eggs and pairs fledged fewer young in noisier areas. As the impact of noise is potentially even higher for species vocalizing at lower frequencies than great tits our data could have significance for the conservation of species that are less abundant or under threat. Consequently, we believe that integration of data on species-specific acoustic behavior with noise prediction models and actual field measurements could be a useful approach in exploring ways to protect threatened birds in noise-polluted wildlife sanctuaries.

Mitigation measures to reduce the negative impact of noise on breeding birds could include sound barriers[5], alternative, more sound-efficient transport by buses through nature reserves[42] or closing roads during acoustically critical phases in the breeding cycle[43]. Traffic noise could also be reduced by introducing a 'noise tax' for a given time of day or season based on the type of car or tires and the average vehicle speed - factors that are known to affect noise levels[41]. It is clear that the trade-off between ecological and economic values will play a crucial role in the implementation of these kinds of applications. Furthermore, sufficient insight into species-specific acoustic behavior and noise distribution data is typically still lacking. Nevertheless, we hope our results help to raise awareness of the potentially negative impact of anthropogenic noise on breeding birds in general.

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