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The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution?

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Summary

Traffic noise is known to have a negative impact on bird populations in general, but little is known about the mechanisms by which sound pollution affects bird communities. However, a knowledge of these mechanisms is imperative if we want to account for the differences in susceptibility to traffic noise that exist between species, and may thus be critical for conservation action. To address this issue, population assessments were carried out in a contiguous area of oak-beech forest at differing distances from a much frequented motorway to determine the road effect on the whole bird community. As expected, species richness and diversity decreased towards the motorway, and bird abundance was significantly lower along the motorway than in the control area. However, a few species defied the negative impact of the motorway. The songs of the more abundant passerines were analysed with regard to three frequency parameters to determine whether or not a relationship exists between the song pitch of a species and its sensitivity to noise pollution. A significant relationship was found between dominant frequency and decline in abundance towards the motorway, which indicates that having a higher-pitched song with frequencies well above those of traffic noise makes a bird less susceptible to noise pollution. These results suggest that acoustic masking is one of the mechanisms by which traffic noise negatively affects passerine density along roads.

Keywords: traffic noise, bird song, acoustic masking, sound pollution, population decline.

Zusammenfassung

Die Auswirkungen von Straßen auf Vögel: Ist Gesangsfrequenz ein Faktor für Lärmempfindlichkeit?

Verkehrslärm hat negative Auswirkungen auf Vogelbestände. Sehr wenig ist jedoch bekannt über die Mechanismen, durch welche Lärm zur Beeinträchtigung von Vogelgemeinschaften beiträgt. Dabei ist die Kenntnis eben dieser Mechanismen unerlässlich, wenn man Vorhersagen treffen will bezüglich der Unterschiede in Lärmempfindlichkeit, die es zwischen verschiedenen Arten gibt, beispielsweise im Rahmen von Schutzprogrammen. Um dieser Frage nachzugehen, wurden Bestandserfassungen in einem zusammenhängenden Eichen-Buchenwaldgebiet in unterschiedlichen Abständen zu einer viel befahrenen Autobahn durchgeführt. So konnten die Auswirkungen der Straße auf die gesamte Vogelgemeinschaft erfasst werden. Erwartungsgemäß nahmen Artenreichtum und Diversität

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zur Autobahn hin ab. Ebenso waren Vogelabundanzen entlang der Autobahn signifikant tiefer als im Kontrollgebiet. Dennoch zeigten sich einige Arten nicht beeinträchtigt durch die Autobahn. Um festzustellen, ob zwischen Gesangsfrequenz und Lärmempfindlichkeit ein Zusammenhang besteht, wurden die Gesänge der häufigeren Singvogelarten in Bezug auf drei Frequenzparameter untersucht. Die dominante Frequenz eines Gesanges korrelierte dabei signifikant mit der Bestandsabnahme zur Autobahn hin, was andeutet, dass Vögel mit Gesangsfrequenzen, die weit über den Frequenzen von Verkehrsgeräuschen liegen, weniger lärmempfindlich sind. Diesen Ergebnissen zufolge ist die akustische Überdeckung von Vogelgesang in den Frequenzbereichen von Straßenlärm einer der Mechanismen, durch welche Singvogeldichten entlang von Straßen negativ beeinträchtigt werden.

Introduction

For many years conservation biologists have been highlighting the negative impact roads may have on adjacent habitats and their natural communities (Ellenberg et al. 1981, Leedy & Adams 1982, Begon et al. 1996, Forman & Hersperger 1996, Forman et al. 1997, Reijnen et al. 1995, 1996, 1997, Forman & Alexander 1998, Forman 2000). In birds it has long been recognised that many, though by no means all, species display reduced densities along roads, and much field work has been done to illustrate the road-related decrease of particular species (e. g. Clark & Karr 1979, Räty 1979, van der Zande et al. 1980, Illner 1992) or to demonstrate a general "road effect" on the bird community as a whole (Reijnen et al. 1995, 1996, Reijnen & Foppen 1995, Forman & Deblinger 1998, 1999). Road casualties were shown to contribute significantly to low Barn Owl (*Tyto alba*) population size near roads (Joveniaux 1985). In other species, however, increased mortality through collisions with moving vehicles either could not be detected at all (Reijnen & Foppen 1994) or was deemed insufficient to account for a notable reduction in density (Ellenberg et al. 1981, Leedy & Adams 1982). In fact, Reijnen et al. (1995) found almost no road effect along highways with sparse traffic. They concluded that noise pollution is probably the main factor contributing to avian density decline – a hypothesis that had been put forward by many previous studies (van der Zande et al. 1980, Ellenberg et al. 1981, Leedy & Adams 1982, Illner 1992).

Little research has focused on the way in which traffic noise affects bird populations. Noise pollution is likely to be of particular relevance to avian communities because these comprise a considerable percentage of species that rely on acoustic signals for mating, predator evasion and so forth. Reijnen & Foppen (1994) showed that male Willow Warblers (*Phylloscopus trochilus*) experience difficulties in mate attraction near highways, which points to the masking of male song by noise as a possible mechanism, but elsewhere the same authors argue that disturbance of vocal communication is probably not a general mechanism in causing reduced densities (Reijnen et al. 1995). They and others (Illner 1992, Reijnen et al. 1997) suggest that a major additional factor may be the stress that noise pollution exerts on body functions.

Equally, the reason some species defy the negative impact of traffic noise while others do not remains obscure (Reijnen et al. 1995). Population density is not necessarily a reliable indicator of habitat quality (Fretwell 1972, van Horne 1983) and can be unexpectedly high in suboptimal habitat provided that overall population density is high (Glas 1962, O'Connor & Fuller 1985), for instance in unusually productive years. Therefore, Reijnen & Foppen (1995) pointed out that it is unsafe to dismiss a road effect if a species fails to display reduced densities near roads. On the other hand, a more likely scenario would be one where members of a bird community differ in their susceptibility to traffic noise either because of inherent differences in stress tolerance, or because of differing amounts of overlap between the frequency range of their songs and that of traffic noise (Reijnen et al. 1995). The latter should be true if sound masking is the major factor of disturbance, and this – though intuitively appealing – has never been rigorously tested.

Behavioural research shows that birds may adopt new modes of vocal behaviour as a response to increasing noise: Bergen & Abs (1997), for instance, found that Great Tits (*Parus major*), Blue Tits (*Parus caeruleus*) and Chaffinches (*Fringilla coelebs*) in areas with considerable traffic noise start singing earlier in the morning than elsewhere. Brumm & Todt (2002) demonstrated that Nightingales (*Luscinia megarhynchos*) are able to compensate for some of the interference from background noise by regulating vocal amplitude. Bergmann (1993) mapped local variations of chaffinch calls in the city of Osnabrück (Germany) and found that most individuals in areas with considerable traffic noise resorted mainly to a high-pitched subset of the total call repertoire of chaffinches. He put forward the hypothesis that such modified call use may be an adaptation to enhance acoustic communication in the presence of traffic noise. More recent studies do not support Bergmann's hypothesis, however. Skiba (2000) demonstrated that chaffinches in areas with heavy traffic in three German cities do not use the higher-pitched calls of their repertoire more preferencially than chaffinches from other areas. It can be deduced that most birds have probably not had sufficient time to modify their frequency range as an adaptation to an increasingly noisy environment.

In this study, I evaluate the impact of traffic noise from a motorway on the avian community of a temperate oak-beech forest. I argue that lower frequencies are more likely to lie within the frequency range of traffic noise and thus be masked by it. By comparing the community adjacent to a motorway with that in an area with little sound pollution, I demonstrate that traffic noise tends to exert a greater influence on species with low-frequency songs than on species with higher-pitched songs.

Methods

Study transects

With more than 50,000 vehicles per day in 1990 (Zahn 1992), the A3 motorway between the Kist and Rottendorf exits near Würzburg (Bavaria) is one of the most heavily frequented highways in southern Germany. This traffic is due mainly to the merging

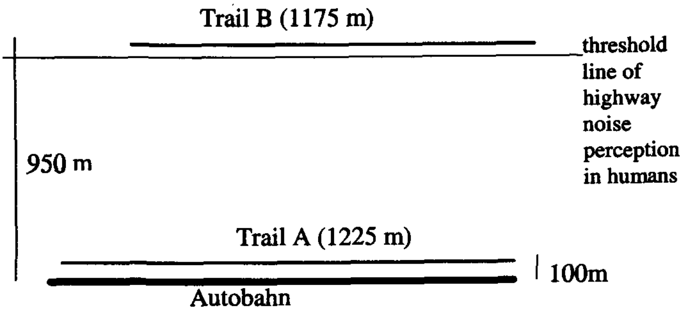

Fig. 1. The arrangement of transects A and B with respect to the motorway (not to scale).
Abb. 1. Die Anordnung beider Transekte in Bezug auf die Autobahn (nicht maßstabsgetreu).

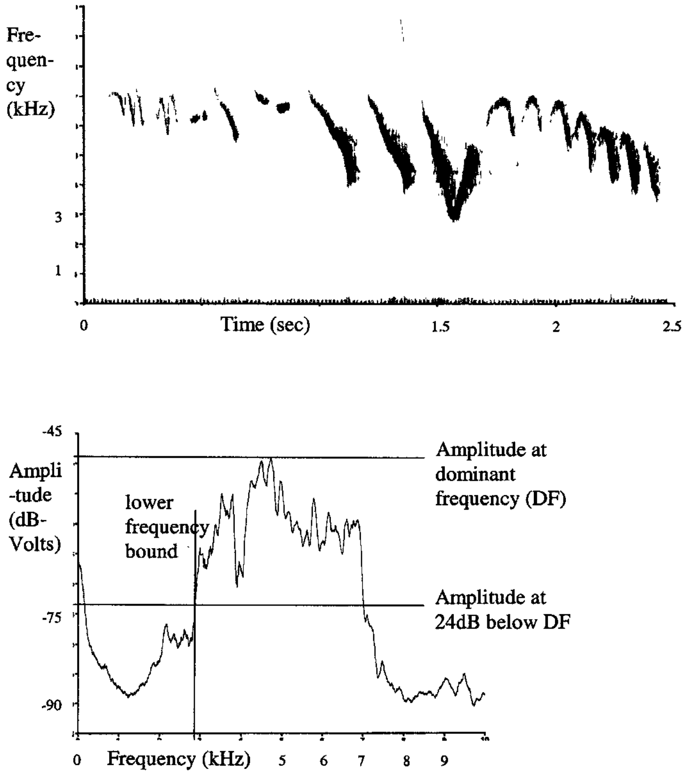

Fig. 2. The sonogram (above) and frequency spectrum (below) of the song of the Tree Creeper (*Certhia familiaris*). As illustrated in the frequency spectrum, the lower frequency bound was defined as the lowest frequency 24 dB below the dominant frequency (DF). The upper frequency bound can be computed by analogy.

Abb. 2. Das Sonagramm (oben) und Frequenzspektrum (unten) des Gesangs des Waldbaumläufers (*Certhia familiaris*). Wie im Frequenzspektrum gezeigt, wurde die tiefste (und analog dazu auch die höchste) Frequenz 24 dB unter der dominanten Frequenz gemessen.

of various motorways coming from four different directions into this short two-laned motorway segment. There are frequent traffic jams, a high numbers of vehicles, and a large proportion of trucks, all of which combine to create high intensity noise pollution.

Between Kist and Heidingsfeld the motorway crosses a sizeable contiguous area of deciduous forest for a distance of approximately 6 km. Within this forest, I extensively surveyed a 1 225 m stretch of a trail (Trail A, Fig. 1) running parallel to the motorway at a distance of roughly 100 m for breeding birds throughout one breeding season between 21.4. and 19.6.1999. During the same period a second transect was surveyed in the same way. This control transect consisted of a 1 175 m stretch of forest trail (Trail B, Fig. 1) roughly parallel to the motorway at a distance of 950 m, just barely beyond the sound threshold where traffic noise can no longer be heard by humans. These 950 m happened to coincide well with the 1 000 m sound threshold value for woodland given in Reijnen et al. (1995).

Bird survey

Surveys were carried out as ordinary line transect counts (see Bibby et al. 1992 for exact methodology). Sixty hours were spent in the field, roughly the same amount of time per distance surveyed along each transect (though overall time investment for transect A was slightly higher, see below). Of seven census walks in each plot, four were carried out at dawn and three at dusk. The time interval between two censuses was always more than four days and only once (in June – before the final census walk) as long as three weeks. All walks took place during sunny or slightly cloudy weather without rain or heavy winds.

Raptors and owls were ignored entirely because of their low density and bad detectability, which combine to make them unsuitable for a study of this scale (see Thiollay 1989). Likewise, species exclusively inhabiting forest edges were not taken into account during the census walks. Among the breeding birds of the forest interior, the European Starling (*Sturnus vulgaris*) and the Woodpigeon (*Columba palumbus*) were omitted, the main reasons being the former's coloniality and the far-reaching vocalisations of the latter blurring its abundance patterns.

Care was taken to select comparable habitat for each transect: Both transects lie within a large contiguous area of homogenous oak-beech forest interspersed with little patches of conifer plantation. Conifer stands covered less than 10 % of the study area, but their proportion within the tree community of Trail B was around 60 % above that of Trail A. Accordingly, acoustic analysis (see below) was carried out only with generalist forest birds that can be found in deciduous forest as well, not with conifer specialists. There were no nest-boxes or comparable artificial breeding aids in any of the transects.

Acoustic analysis

I analysed the songs using commercially available recordings of Central European birds (Roché 1990) and SIGNAL sound analysis software (Engineering Design, Belmont, Massachusetts). I measured three different song parameters (see Fig. 2 for details on computation):

1.) dominant frequency as calculated by SIGNAL over the whole song (DF)
2.) lower frequency bound at 24dB below the song's DF
3.) upper frequency bound at 24dB below the song's DF; 24dB below a song's DF was found to be a good average threshold to delimit the louder and presumably more influential elements of songs.

All passerines with courtship vocalisations (generally referred to as "songs") were included in the analysis as long as they were represented by at least 8 pairs in both transects (with the exception of two strict conifer specialists, the Coal Tit (*Parus ater*) and the Firecrest (*Regulus ignicapillus*) because of their clumped, grossly uneven and predictable distribution). Only songs were used in the acoustic analysis, mainly because of their key function in reproduction and territory maintenance. Also, preliminary analysis of the data showed that songs, being far more complicated and diverse in structure than calls in most species, often exhibit a broader range of frequencies that generally encompasses that of all the calls. In species that have more than one song type, dominant frequency was calculated for the song type that was most frequently heard in the field. The upper and the lower frequency bounds, in contrast, were derived from that song type which yielded a maximum or minimum value respectively, as long as the song type had been heard in the field with some regularity.

In the analysis of bird song, body mass has to be taken into account as a potential confounding variable (Ryan & Brenowitz 1985). Body masses of all the species were obtained from Dunning (1993). Where sexes differ noticeably in body mass, only male figures were used for statistical analysis.

Statistical analysis and study design

I used S-Plus 2000 (Lucent Technologies, Inc.) for statistical analysis. Species richness, average bird abundance (i. e. the sum of all bird abundances averaged), diversity and equitability (i. e. the evenness with which the species are distributed, see Begon et al. 1996) were calculated for each transect as given in Tab. 1. Individual bird abundances of both transects were compared with a Wilcoxon signed rank test. Linear regressions with the change in abundance from transect B to A as a dependent variable were conducted on dominant frequency, lower and upper frequency bound respectively. However, only species that were represented by at least 8 pairs in transects A and B together were included in calculations that involve the change in abundance from one transect to the other because the inclusion of less abundant species would seriously diminish the accuracy of the calculations if only a single pair had gone unnoticed or had been counted twice during

Table 1. For each transect, area, total number of bird pairs, total bird abundance (= birds of any species per hectare), species richness, average abundance (= total abundance divided by species richness), Simpson's reciprocal diversity and Simpson's equitability are given; for these last two parameters see Begon et al. (1996).

Tab. 1. Für jedes Transekt ist die Fläche, die Gesamtzahl an Vogelpaaren, die Gesamtabundanz (über alle Arten hinweg), der Artenreichtum, durchschnittliche Abundanz (d. h. Gesamtabundanz dividiert durch Artenreichtum), Simpsons reziproker Diversitätsindex und Simpsons Äquitabilitätsindex angegeben; bez. letzterer beider Parameter, siehe Begon et al. (1996).

	Transect A (motorway)	Transect B (control)
Area A [ha]	24.5	23.45
Total number of bird pairs T	202.5	244.5
Species richness S [number of species]	22	26
Total bird abundance T/A [pairs/ha]	8.27	10.43
Average bird abundance T/(A*S) [pairs/ha]	0.376	0.401
Simpson's reciprocal diversity index; $D = 1/\Sigma P^2$ (where P = proportion of pairs/species contributed to total)	10.94	13.25
Simpson's equitability E = D/S	0.50	0.51

Table 2. The change in abundance from transect B to A of species with a total of at least 8 pairs in the study area (species that are considered in the vocal analysis are printed in bold).

Tab. 2. Abundanzänderungen von Transekt B nach A aller Arten mit einer Mindestanzahl von 8 Paaren im Untersuchungsgebiet (in der Frequenzanalyse berücksichtigte Arten sind fett gedruckt).

Species	Change in abundance from B to A (%)
Great Spotted Woodpecker (*Dendrocopos major*)	–76
Winter Wren (*Troglodytes troglodytes*)	–37
European Robin (*Erithacus rubecula*)	–4
European Blackbird (*Turdus merula*)	–33
Song Thrush (*T. philomelos*)	–38
Blackcap (*Sylvia atricapilla*)	–30
Chiffchaff (*Phylloscopus collybita*)	–58
Firecrest (*Regulus ignicapillus*)	–26
European Nuthatch (*Sitta europaea*)	–59
Tree Creeper (*Certhia familiaris*)	–9
Blue Tit (*Parus caeruleus*)	90
Great Tit (*Parus major*)	–30
Coal Tit (*P. ater*)	–54
Hawfinch (*Coccothraustes coccothraustes*)	82
Chaffinch (*Fringilla coelebs*)	26

the census. I calculated the area and the abundance of all species along each trail making two assumptions:

1) The average spatial limit at which a bird could be detected acoustically from the trail was estimated at 100 m, a figure which several tests at the beginning of the census showed to be fairly accurate within this mature secondary deciduous forest. Even if this proposed detection limit deviates from the true value, the comparability of the results does not suffer, since the spatial denominator of each abundance value will shift away from the true abundance in the same direction and by the same factor with all species. 2) The detection rate for breeding birds was presumed to be equal in every plot. This assumption is obviously incorrect, since traffic noise can be expected to have some negative impact on the acoustic detection of birds along Trail A. However, the effect on the accuracy of bird detection near the motorway was probably negligible, as the sound recognition of birds was only moderately impaired during the early morning hours, when traffic was still low compared to just a short time after the morning censuses. During the walks a conscious effort was made to make frequent stops and invest more time in bird detection along those sections of Trail A where traffic noise remained constantly high for a longer period. Therefore, I am confident that the survey's

Table 3. Body masses (from Dunning 1993) and measurements of the song parameters investigated for the 12 species included in vocal analysis; DF = dominant frequency measured over the whole song, LB = lower bound at –24dB, UB = upper bound at –24dB; for a more detailed description of song parameters see Methods and Fig. 2.

Tab. 3. Körpermassen (aus Dunning 1993) und Messwerte der Gesangsparameter der 12 Arten, die in der Frequenzanalyse berücksichtigt sind; DF = dominante Frequenz (über den gesamten Gesang gemessen), LB = tiefste Frequenz 24 dB unter der dominanten Frequenz, UB = höchste Frequenz 24 dB unter der dominanten Frequenz; siehe Methoden und Abb. 2 bez. genauerer Details zur Beschreibung der Gesangsparameter.

Species	DF (Hz)	LB (Hz)	UB (Hz)	Body Mass (g)
Winter Wren – *Troglodytes troglodytes*	4 500	3 050	6 750	9.3
Blackcap – *Sylvia atricapilla*	2 850	2 000	5 900	15.5
Chiffchaff – *Phylloscopus collybita*	3 950	2 650	5 700	7.5
Robin – *Erithacus rubecula*	4 200	2 100	5 150	18.2
Song Thrush – *Turdus philomelos*	2 500	1 950	4 600	68.9
Blackbird – *Turdus merula*	2 450	1 300	4 600	113
Blue Tit – *Parus caeruleus*	4 700	1 550	6 300	13.3
Great Tit – *Parus major*	4 000	1 600	5 300	19
European Nuthatch – *Sitta europaea*	3 100	1 850	5 850	22
Tree Creeper – *Certhia familiaris*	4 750	2 900	7 000	9
Chaffinch – *Fringilla coelebs*	3 350	1 900	5 250	21.9
Hawfinch – *Coccothraustes coccothraustes*	5 200	4 150	7 250	54
Results of linear regression with change in abundance from B to A: **p-value** (F, df, n in brackets)	**0.046** (5.182, 11, 12)	**0.382** (0.835, 11, 12)	**0.160** (2.308, 11, 12)	**0.952** (0,004, 11, 12)

accuracy for transect A should be approximately equal to that for the control transect. The fact that survey results from working days were not significantly different from weekend surveys is another indication that the assumption of equal detectabilities in both transects is not unreasonable – noise pollution is greatly reduced on weekend mornings when commuters are missing and truck traffic is prohibited on German motorways (see Discussion for more details).

Results

Bird abundance in both transects

Species richness, average bird abundance and diversity were lowest along transect A (Tab. 1). Equitability was found to be roughly equal in transects A and B (Tab. 1). Across the community, bird abundances in the motorway transect A were significantly lower than in the control transect B ($p = 0.040$, $T = 50$, $n = 20$; Wilcoxon signed rank test, data log transformed because of unequal variance). However, although a significant overall decrease in bird abundance towards the motorway transect could be shown, several species clearly deviated from this pattern (Tab. 2).

Difference in abundance in the context of vocal features

The measurements of the three vocalisation parameters investigated and the resulting statistics of their linear regressions with the changes in abundance from transects B to A (p, F, df, n) are presented in Tab. 3. The decline rate for birds from the control transect B to the motorway transect A increased significantly (Fig. 3; Tab. 3) with decreasing dominant frequency (DF). Dominant frequency showed no significant relationship with avian body mass,

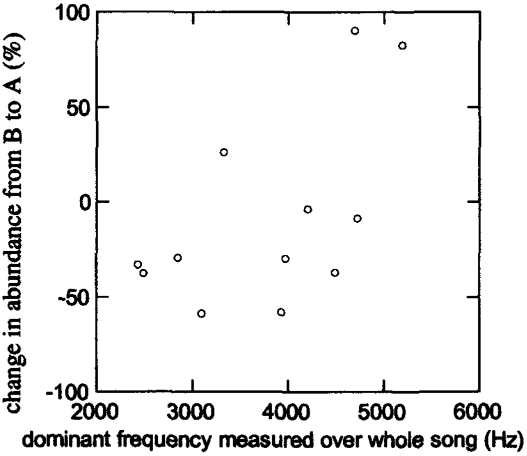

Fig. 3. Linear regression of dominant frequencies vs. decline in abundance from transect B to A; species with lower dominant frequencies show a more marked decrease in abundance towards the motorway.
Abb. 3. Lineare Regression der dominanten Frequenzen gegen Abundanz-Abnahme von Transekt B nach A; Arten mit geringerer dominanter Frequenz weisen eine deutlichere Abundanz-Abnahme zur Autobahn hin auf.

though it was fairly well within the range of near-significance ($p = 0.092$; $F = 3.47$, $df = 11$, $n = 12$; linear regression). Equally, body mass did not exhibit any relationship whatsoever with rates of decline towards transect A (see Tab. 3 for details on statistics). Neither the lower frequency bound at 24dB below DF nor the upper frequency bound exhibited any notable relationship with change in abundance (Tab. 3).

Discussion

The motorway's impact on the bird community

In the present study bird diversity, average bird abundance, and species richness all displayed noticeably lower values along the motorway transect than in the control transect (Tab. 1). Bird abundance across the community was shown to be significantly lower in transect A than in the control transect. As the habitat is essentially the same along both transects, these data demonstrate a negative effect of the motorway on the bird community and add to the mounting body of evidence that bird densities tend to decline along roads. As numerous previous authors have stated (van der Zande et al. 1980, Ellenberg et al. 1981, Leedy & Adams 1982, Illner 1992, Reijnen et al. 1997), traffic noise is very likely to contribute greatly to this road effect, especially in woodland and forest (Reijnen et al. 1995), where other variables such as visual stimuli operate at only very short distances from the road. Factors other than the road, such as the density of paths or the frequency of hikers or cyclists, can be ruled out as confounding variables because they would predict an increase of bird abundance towards the motorway. Equally, no relationship between body mass and change in abundance could be shown.

The influence of dominant frequency on the sensitivity to traffic noise

The significant overall decline notwithstanding, a few species remained largely unaffected by the presence of the motorway or even increased in abundance towards it (Tab. 2). This observation suggests different levels of sensitivity to traffic noise across the bird community.

Skiba (2000) showed that the sound of heavy traffic is generally very uniform, despite minor site-dependent differences in the exact distribution of the peaks of dominant frequency. In all of his samples the sound intensity of heavy traffic exhibits one well-marked peak between 0 and 1 kHz with a subsequent series of slightly lower peaks between 1.5 and 4 kHz. Generally, traffic noise does not exhibit any frequencies higher than 5 kHz (Skiba 2000). Most bird vocalisations, in contrast, are in the range from 2 to 9 kHz (present study).

In the present study, dominant song frequency (DF) exhibited a significant relationship with the change in abundance of the corresponding species from the motorway to the area beyond its sound threshold (Fig. 3). This relationship strongly suggests that noise pollution has a more pronounced negative impact on birds with lower-pitched vocalisations.

The lower and upper frequency bounds of bird song were not found to be good predictors of sensitivity to traffic noise. The causes are difficult to determine: One may insist that the lower frequency bound should not be discounted because it indicates whether a song exhibits frequencies within the range of traffic noise. On the other hand, a measure for lowest frequency will not predict the amount and the frequency of sound intensity above it, which is more crucial. The opposite can be said with respect to the upper bound by analogy.

Song frequency is known to depend heavily on the body mass of the singer (Wiley 1991). In the species set investigated here, however, the relationship between mass and dominant frequency was only near-significant. Equally, body mass showed no relationship with the abundance trends themselves (Tab. 3). A scenario that envisages body mass as an agent that reduces bird abundance towards the motorway has to be put aside as highly unlikely, since there is no *a priori* reason to believe that differences in body mass should determine the level of sensitivity to the road effect.

Differences in bird detectability between the two transects, on the other hand, are a more critical confounding variable. If traffic noise in transect A considerably biased the detection of birds, the results obtained would be an artefact arising from the very masking effect they are being put forward to demonstrate. However, reduced detectability of bird song in transect A is highly unlikely to have had a significant impact on the census, as traffic noise was generally low in the early morning hours (04.00–06.00), which is when all morning censuses took place. Additionally, half of the census walks were conducted at weekends, when truck traffic is prohibited on German motorways and commuters are missing (see Methods). The results from weekend morning censuses (when traffic was lowest) and working day evening censuses (when traffic was highest) did not differ notably with respect to bird individuals recorded, which points to a low noise bias on census work. Moreover, analysis of the census results from transect B, which was completely unaffected by traffic noise, showed that abundance estimates would generally not have changed greatly if two or three of the seven census walks had been omitted. If we now disregard the results from both weekend morning census walks along transect A (the two walks that should have contributed the least proportion of noise-biased data), abundance estimates do not change at all for 18 species, and do so only slightly for the remaining 4 species. This strongly supports the assumption that noise bias during census work was negligible.

Arguing that bird detection was not considerably impaired at low traffic during the early morning could be interpreted as a contradiction to the masking effect of noise on bird song, since bird communication should consequently not be impaired either at that time. In fact, it has even been shown that some species shift their singing activity to a time of day when noise level is low (Bergen & Abs 1997), while others can compensate for part of the masking effect by increasing the intensity of song (Brumm & Todt 2002). However, it is justifiable to assume that high noise levels at most times of the day will not be devoid of impact, even if noise is somewhat reduced in the mornings. Equally, it should be considered that the change of vocal behaviour in response to noise, such as commencing vocal activity earlier in the morning or singing louder, is probably costly in terms of fitness and may have long-term repercussions.

Other factors

Though a significant relationship between dominant frequency and reduction in density towards the motorway could be demonstrated, the species-specific differences in abundance decline from B to A are most probably caused by additional factors as well. The most important of these is possibly a difference in the availability of particular microhabitats between transects A and B. In fact, part of this factor has been taken into account by considering generalist forest birds only in the analysis, and by excluding species with limited microhabitat requirements within the census area, such as edge inhabitants (which were exempt from the whole census). By the same token, the Coal Tit, and the Firecrest were excluded from acoustic analysis, although they occurred with more than 8 pairs. Discounting these two species was deemed necessary because they are restricted entirely to conifer stands, and their distribution is therefore clumped and grossly uneven. Taking them into account would render the relationship between dominant frequency and decline from B to A near-significant, so their exclusion can be criticised as *a posteriori* reasoning, but it is important to stress that transect B contained approximately 60 % more patches of conifer plantation, so the higher abundance of these species in transect B comes as no surprise (though the total extent of conifer plantations in the study area was below 10 %). It must be noted that all the other species that were sufficiently abundant to be considered for acoustical analysis showed a steady and even distribution over the transects, the Coal Tit and the Firecrest being the only species that were absent in most parts and super-abundant in the remainder. This and the general homogeneity of the deciduous parts of the forest indicate that microhabitat can most probably be neglected as a significant confounding variable, as long as the two conifer inhabitants are counted out.

A marked increase in abundance towards the motorway was found in three species. This increase cannot be accounted for by vocal features. Here, again, it becomes evident that other factors, possibly species-specific, are also at work in determining abundance patterns. Interpretation of one of these, however, is possibly not that difficult after all: The Blue Tit has an abundance nearly twice as high in transect A as in B. However, the dependence of the Blue Tit and Great Tit on the same kinds of resources in part is well-established (Tokeshi 1999). To evade interspecific competition and to render possible their coexistence within the same habitat, these two species have undergone a long evolutionary process of resource partitioning and niche differentiation through the establishment of size differences. But wherever the bigger Great Tit has to abandon suitable habitat (here presumably because of motorway noise), the smaller Blue Tit gets the opportunity to occupy a wider resource spectrum and therefore has higher reproductive success. This hypothesis requires further confirmation, but it certainly offers one plausible explanation for the rise in abundance of the blue tit towards the motorway. Note that the abundance patterns of the two common tit species in this study are in seeming contrast to Junker-Bornholdt et al. (1998) who found no differences between breeding populations of the same two species along a newly constructed highway and two control areas. However, nest-boxes were interspersed throughout their study area. These constitute a habitat asset that may have been absent from surrounding areas and may therefore have recruited birds from outside. Moreover, the authors admit that sound pollution remained at a relatively low, stable level throughout the study period. These factors invalidate any comparisons between their results and those presented here.

The implications of increasing sensitivity to traffic noise with decreasing song pitch

Differences in dominant song frequency are probably not solely responsible for the noticeable differences in abundance distributions among the species investigated. For instance, the abundance of virtually all species, however generalist they may be, is governed by the absence or presence of certain microhabitat structures that may or may not have been evenly distributed throughout the selected transects. Nonetheless, in this study dominant song frequency was a powerful predictor of the differences in abundance patterns. Acoustic signals are of paramount importance for the survival and reproduction of most passerines. Traffic produces a sound background that greatly impairs communication in a few species, whilst other species appear to suffer less from this impact.

This investigation was based on a single set of study and control transects, so further confirmation of the results would be desirable. It would be especially interesting to see if the relationship between dominant frequency and decrease in abundance holds across different habitats and if other meaningful sound parameters can be found. Likewise, physiological investigations into the differences of auditory perception among species may uncover complementary evidence (see Klump 2001).

Finally, these findings indicate that the masking effect that noise exerts on bird song is an important mechanism by which road traffic affects bird density. Though other authors (Illner 1992, Reijnen et al. 1995, 1997) have come to think of other factors (e. g. stress) as more important, the results of this study show that the masking effect does contribute substantially to forest songbird decline along roads.

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