

# Impact of military activities on bird species considered to benefit from disturbances: an example from an active military training area in Latvia

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We surveyed the military training area Adazi to evaluate the effects of disturbance caused by military activities on the abundance of protected bird species considered to benefit from disturbances at the site (SCBD). We collected data on the abundance of the selected bird species in a set of representative sample plots during three repeated surveys. In each plot we mapped areas affected by different visually detectable disturbances of military origin and areas covered by EU protected habitat types. Overall abundance and richness of SCBD were calculated for each of the surveyed squares. Generalised linear modelling was used to relate the recorded abundance of each species, and the overall abundance and richness of SCBD, with the available habitat and military disturbance parameters. We evaluated a set of competitive models to identify the most important explanatory variables. The modelling results imply clear positive effects of most of the military activities on the analysed species as well as overall species richness. The variables describing the availability of habitats alone could not explain as large variation in the data as together with the disturbance variables. The results show that the recent (up to one year) and moderately recent (up to two years) disturbances were the most important to maintain the habitats. The results suggest that these species tend to occupy the newly created suitable habitat patches in the next breeding season. At the time of the study, there was no measurable negative effect of the military activities on abundance and richness of the analysed species. However, some negative effects of military activities on species behaviour were observed.



## 1. Introduction

It has been estimated that military training areas cover at least 1% of the Earth's surface (Zentelis & Lindenmayer 2015). Although one may presume that all military activities (either training or warfare) are overwhelmingly “negative” in an ecological context due to their destructive nature, in

reality the consequences of these generate a continuum of outcomes ranging from highly positive to highly detrimental (Lawrence *et al.* 2015, Das-kin *et al.* 2016, Gaynor *et al.* 2016). If used sustainably, the defence sector and nature conservation are compatible. Military training areas have increasingly become recognized as areas of high biodiversity and habitats for many wild organisms,

including threatened or endangered species, as their biodiversity value is often matching or even surpassing that of many areas primarily designed and protected for nature conservation (Stein *et al.* 2008, Warren & Büttner 2008, Aycrigg *et al.* 2015). As these areas occur in all major global ecosystems, they have the potential to increase the global protected area network by at least 25% (Zentelis & Lindenmayer 2015).

Disturbance is a primary cause of spatial heterogeneity in ecosystems (Pickett & White 1985). Historically, traditional farming and small-scale forestry practices had provided a regular disturbance regime needed to maintain extensive and structurally diverse landscapes where patches of arable land and grassland were juxtaposed with more natural habitats (Bignal & McCracken 2000). However, nowadays these traditional practices are often not economically viable and are either replaced by intensive management or the landscape faces abandonment (Stoate *et al.* 2009). Due to the altered disturbance regimes, these formerly extensive open and semi-open landscapes lack their characteristic fine-grained mosaic of habitats and co-occurrence of diverse microhabitats (Benton *et al.* 2003, Báldi & Batáry 2011). This in turn has caused widespread biotic homogenization observed in many taxa and ecological groups, leading to loss of biodiversity at regional and global scales (McKinney & Lockwood 1999, Smart *et al.* 2006). The homogenization of species communities further leads to declining populations of specialist species (Devictor *et al.* 2007, le Viol *et al.* 2012). Lack of appropriate management has also affected many protected nature areas. Thus, species and habitat-specific, often expensive, approaches to restoration and recurring management are necessary (Ostermann 1998, Muller 2002).

Regular military activities using various vehicles and weaponry, are creating disturbances resulting in changes in landscape, topography and vegetation (White & Jentsch 2001). The nature of land based military training creates suitable habitat patches, as well as habitat connectivity, needed for the maintenance of metapopulations of species preferring early successional stages of vegetation (Warren & Büttner 2008). The diversity of microhabitats created by military activities is often greater than that of ploughing or weed and feral

animal management. Thus, military training areas have a potential to provide refuges for the species characteristic of traditional extensive open and semi-open landscapes (Bušek & Reif 2017).

The impacts of vehicle use during military training activities are well documented and result in soil disturbance and vegetation loss, leading to an increase in potential rainfall-related runoff and soil erosion (Wang *et al.* 2007), while also increasing biodiversity and stabilizing ecosystems (Wang *et al.* 2014). It has been shown that tank traffic has considerable immediate impacts on soil structure, reducing earthworm density by 82% and reducing vegetation biomass (Althoff & Thien 2005, Retta *et al.* 2013, Retta *et al.* 2014). However, soon after disturbance, the earthworm density increases to levels greater than before disturbance (Althoff *et al.* 2009).

Disturbance from off-road vehicular traffic moving through complex landscapes varies spatially and temporally, thus creating uneven mosaics of vegetation. It has also been shown that species richness and functional diversity in a dry grassland both increased in response to soil disturbance and rotavation, but not ploughing, and had a persistent positive effect on the occurrence of specialist species of calcareous sandy grassland (Schnoor *et al.* 2015). Tank driving had a short term effect on soil nutrient availability and a significant impact on all plant functional groups, with graminoids recruiting better than rosettes and cryptogams (Jentsch *et al.* 2009). It has been suggested that disturbance up to intermediate levels can be used to maintain biodiversity by enriching the plant species pool (Leis *et al.* 2005).

However, there are limits in the use of prescribed disturbance as it has been reported that no type of soil disturbance caused the plant species composition to develop towards the target vegetation (Schnoor *et al.* 2015). It has also been shown that mimicking the effects of military manoeuvres by the classical restoration measures of dry grasslands is difficult, and only topsoil removal was able to establish vegetation of pioneer species that lasted longer than 3 years (Jentsch *et al.* 2009).

The effects of bombing and shooting on landscape, vegetation and species, have not been equally well documented. Most often such effects have been assessed after actual military conflicts, of which there is evidence of both positive and

negative effects (Lawrence *et al.* 2015, Daskin *et al.* 2016, Gaynor *et al.* 2016).

Military training activities are known to impact individual species, and it has been shown that many rare and protected species across different parts of the world can benefit from these disturbances (Gazenbeek 2005, Benton *et al.* 2008, Warren & Büttner 2008, Warren & Büttner 2014, Kim *et al.* 2015). The disturbance caused by military training activities may mimic natural disturbances for some species (Rivers *et al.* 2010), and delay or prevent natural succession thus conserving vegetation communities in a state that would otherwise become overgrown with shrubs and trees if left undisturbed (Warren & Büttner 2008, Kim *et al.* 2015).

To date, the number of published studies that have specifically looked at the impacts of active military training on birds is very limited and almost all of them are from the USA. It has been reported that the military training did not cause large changes in the avian community (Rivers *et al.* 2010) or the studied species (Anders & Dearborn 2004, Dobony & Rainbolt 2008). However, conversely, during a period of intensive military training, raptor counts were lower during training than on non-training days (Chueck *et al.* 2001). It has been suggested that military training activities may mimic natural disturbances (Rivers *et al.* 2010) and the positive influence of typical military training on the habitats likely outweighs negative effects (Delaney *et al.* 2011) at least for some species. However, it is likely that impacts on bird communities are still not fully understood. Therefore, more studies are needed to extend the applicability of these results. No evidence has been found of direct impacts of military activity on reproduction of several target passerines in the USA, but it was shown that these activities displace some corvid species (Barron *et al.* 2012) thus potentially reducing predation on nests.

There is a legislation-driven trend of increased cooperation between military stakeholders and nature conservationists in management of military training areas (Gazenbeek 2005, Boice 2006). However, there is also evidence that although often not recognised officially, there are conflicts regarding biodiversity conservation on military installations (Jenni *et al.* 2012). Despite the accumulating evidence of the impact of military activities

on different species, there is limited understanding of these impacts on animal communities, especially in Eastern and Northern Europe. Most of the research in this field has been carried out in the USA. Very few studies have been undertaken in Europe (but see Gazenbeek 2005, Warren *et al.* 2007, Warren & Büttner 2008, Warren & Büttner 2014) and we are unaware of any specifically in the north-eastern part of the Europe.

The aim of our study was to evaluate the impacts of military training on selected bird species in an active military training area. We focused on protected and nationally rare species associated with a complex mix of habitats. Wide moorlands and heathlands are associated with Black Grouse (*Tetrao tetrix*) (Angelstam *et al.* 2000) and European Nightjar (*Caprimulgus europaeus*) (Morris *et al.* 1994). Disturbances caused by military training form different amounts of sparse vegetation and bare soil essential for Woodlark (*Lullula arborea*) (Bowden 1990) and Tawny Pipit (*Anthus campestris*) (Grzybek *et al.* 2008).

This habitat mosaic with scattered trees and military installations provide breeding niches for Common Hoopoe (*Upupa epops*) (Tagmann-Ioet *et al.* 2012) and European Roller (*Coracias garrulus*) (Kiss *et al.* 2012). Heathlands and moorlands of Adazi represent the last remaining breeding site for European Roller in Latvia (Kerus 2015). These species have negative or stable regional population trends (according to the report on Article 12 under Birds Directive 2008–2012 (EIONET Central Data Repository 2014)). The military training area Adazi is of high importance for the conservation of the selected species and it has been suggested that recent increases in their local populations might be a result of increased military training activities (Kerus 2015).

## 2. Material and methods

### 2.1. Study area and sampling design

The military training area Adazi is located in the central part of Latvia (Fig. 1) and covers 7,784 ha. The area has been used for military training since the 1930s. During the 1940s–1980s, the Soviet army actively used the territory. The intensity of military activities declined after Latvia regained

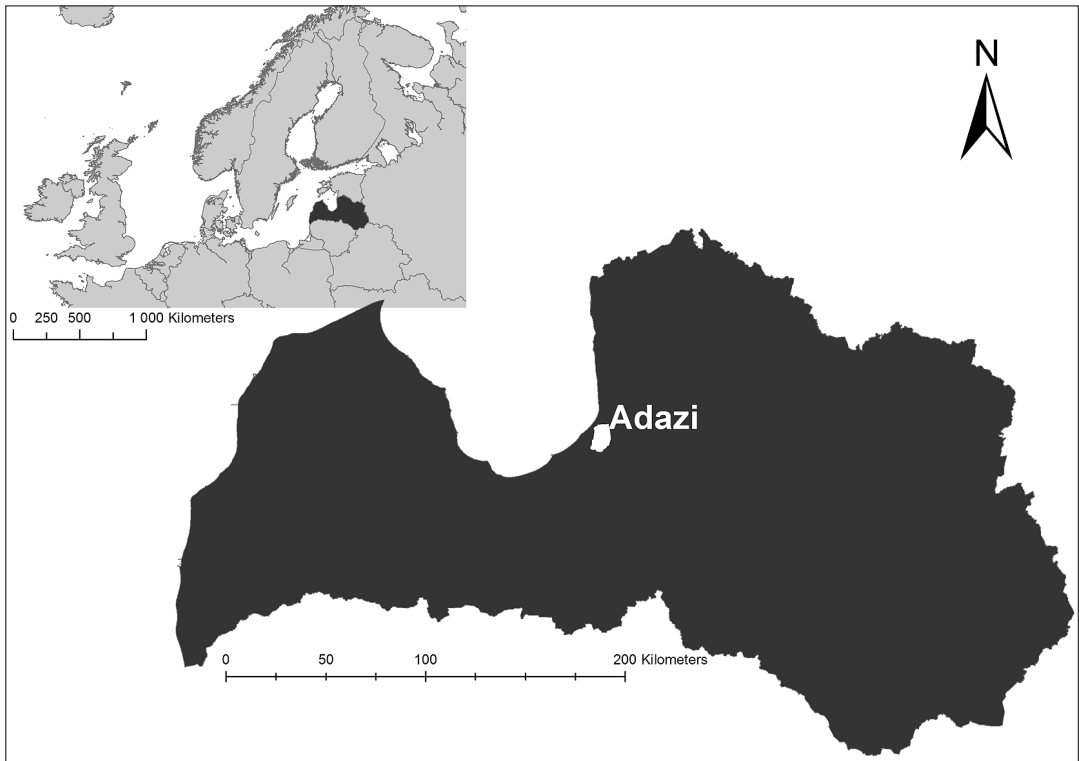


Fig. 1. Location of the study site (Adazi military training area).

independence in 1991, but has increased again since 2010. The current military training involves tactical infantry as well as training with vehicles, use of different (including heavy) weaponry and bombing. Over time, because of wide-scale and large intensity fire events induced by military training, the natural vegetation of dry forests in this area has been replaced with open landscapes dominated by heath and dune habitats.

Since 2004, most of the military area Adazi has been designated a Natura 2000 site, mainly for protection of heath habitats and associated species. The military training can take part at any time of the year. The current daily activities involve a few tens to a few hundreds of field personnel, concentrated in certain parts of the area. Additionally, there are annual international training activities involving up to several thousand soldiers which cause various disturbances throughout the area. Despite regular disturbance, because of the open landscape and complex terrain created and maintained by the military training, the area is of high importance for the conservation of several animal

species such as Rattle Grasshopper (*Psophus stridulus*), Smooth Snake (*Coronella austriaca*), Black Grouse, European Roller, Tawny Pipit and others (Kerus 2015).

The two decades of decreased military activity in the 1990s and 2000s resulted in large parts of the formerly open areas becoming overgrown with vegetation. Because of the importance of the site for rare and protected species and habitats, several habitat restoration projects have been undertaken since 2005, mainly targeted at restoration of heath and dune habitats but also providing nest-boxes for locally rare hole-nesting bird species such as European Roller and Common Hoopoe.

To evaluate the effects of disturbance by military activities on protected bird species and heath habitats, a representative area of military training zone was surveyed. To achieve this, the study area was divided into 500x500 meter squares, thus creating a sampling grid consisting of 487 cells. Of these, 44 squares were randomly selected as sampling areas (Fig. 2). The selected squares represented a gradient of different intensity of military



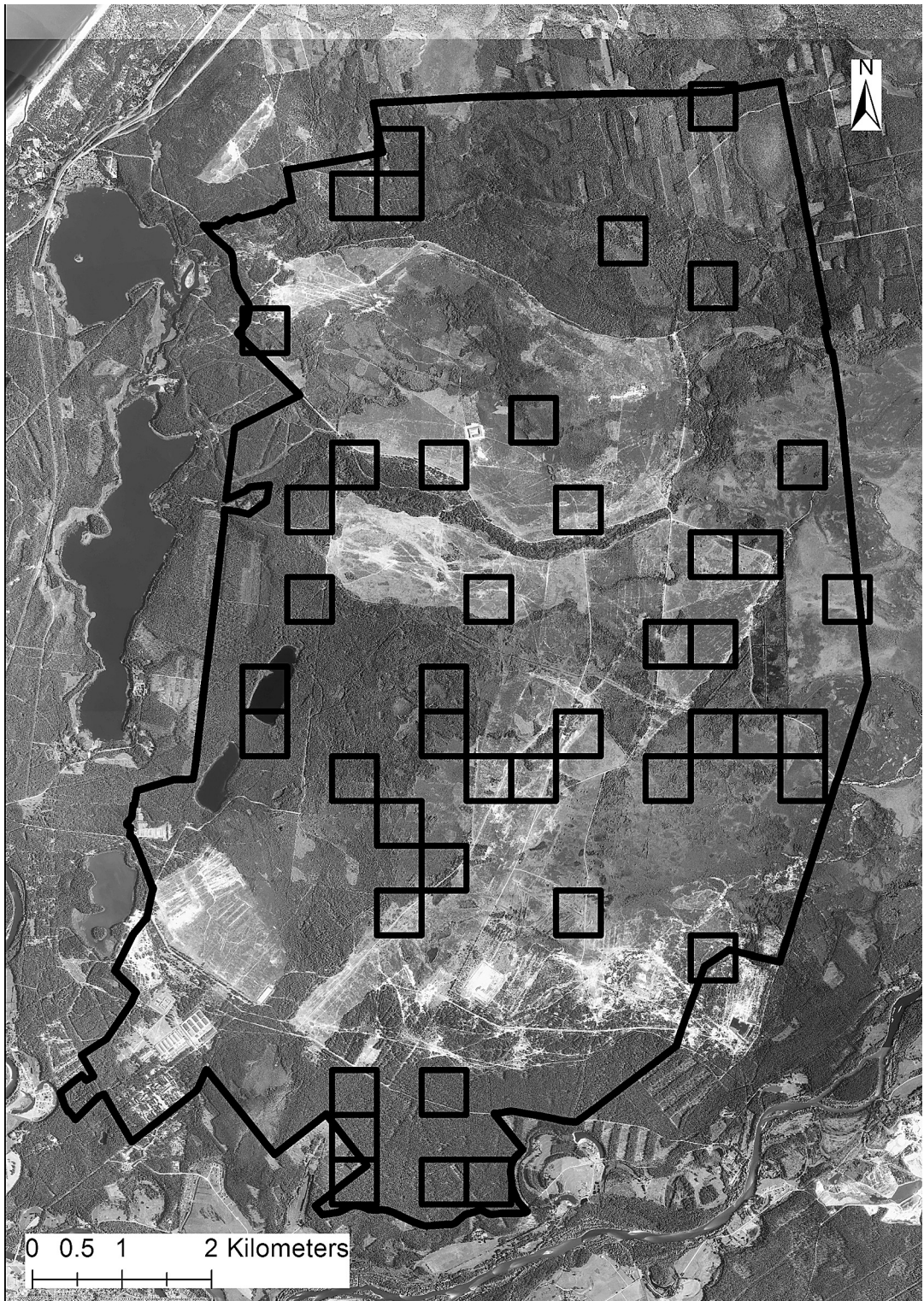


Fig. 2. The border of the Adazi military training area and the selected sample plots.



activities, from intact mature forest through patchy mosaics of trees, shrubs and heath to open areas with sparse vegetation generated by military activities such as bombing, burning, digging trenches and use of heavy military vehicles. Of the selected 44 squares, no traces of military activities were found in 8 squares. The rest of the squares had varying amounts of visible military impact. The total area of recorded military impacts combined covered more than 88% in the most affected square.

## 2.2. Field data collection

Birds were surveyed on three visits within the breeding season, during periods when military training did not take place. Two of the surveys were carried out during the first five hours after sunrise and the other at night between sunset and sunrise. The first morning survey took place between May 10 and May 15 and the second between June 20 and June 25. The night visit took place between May 25 and June 3. The route used by the observer was chosen so that no area in each sampling square was further than 50 m away from the observer. However, to ensure high detection probability regardless of terrain and habitats, the observers were allowed to adopt more extensive coverage if needed. The locations of all the observed birds were recorded on detailed maps.

Surveys were designed and carried out to collect data on six bird species recognised as being important in the nature conservation context and considered likely to benefit from military disturbances on the site (Kerus 2015): Black Grouse, European Nightjar, European Roller, Common Hoopoe, Woodlark and Tawny Pipit. Encountered birds considered as relating to possible breeders were interpreted in terms of territories, while those not related to breeding were recorded separately as individuals and were not used in data analyses. As the sedentary Black Grouse has a lek-based mating system and observations of females are equally important as males for evaluating the species' habitat, all observed individuals were recorded and analysed.

EU protected habitats and visible signs of military activities were mapped in August and September. Borders of each patch were delineated as a

polygon on a map. The main habitats of interest were heath habitats, primarily "2320 Dry sand heaths with *Calluna* and *Empetrum nigrum*". Habitat quality was assessed for each of the mapped heath habitat patches. After digitising the habitat borders, an area was calculated for all patches within the selected squares.

Visible signs of military activities were mapped using a detailed classification system that recorded the cause of the disturbance and its age. However, as there were only few patches recorded in many of the original classes, the disturbances were later grouped into fewer, partly overlapping, categories that were used as possible predictors in the analyses (Table 1).

## 2.3. Species considered to benefit from disturbance: abundance and richness

To estimate suitability of the squares to the whole group of the considered species, two additional measures were derived for each surveyed square: 1) the overall abundance of the species considered benefiting from disturbances in the site (SCBD) was calculated as a sum of abundances of all SCBD and 2) the richness of SCBD was the number of these species present in the square. As the dataset contained zeros (there were squares with no SCBD species recorded) we could not use any of the diversity indices to merge the abundance and richness components into a single diversity measure.

## 2.4. Data analysis

We created a data matrix where each sample plot was a case and which contained all the variables describing visible impacts of military activities and EU protected habitat types (Table 1). Maximum count (abundance) was calculated for each species recorded in each sample plot. Data analysis and statistical tests were carried out in statistical software R 3.2.3. (R Core Team 2014) and its packages. The GIS analyses were performed using ArcGIS 10.4 (ESRI 2016).

To explain the influence of EU protected habitats and various military disturbances on the abundance of species and the overall abundance and

Table 1. Predictors used to explain variation in occupancy and abundance of the modelled species.

Variable	Description	Proportion in sampling plots	
		Mean	Range
EU protected habitats			
J2320	Dry sand heaths with <i>Calluna</i> and <i>Empetrum nigrum</i> (2320)	30.8	0–98.2
J2330	Inland dunes with open <i>Corynephorus</i> and <i>Agrostis</i> grasslands (2330)	0.16	0–5.7
J4010	Northern Atlantic wet heaths with <i>Erica tetralix</i> (4010)	10.6	0–87.5
J2130	Fixed coastal dunes with herbaceous vegetation (grey dunes) (2130*)	1.1	0–15.9
J7120	Degraded raised bogs still capable of natural regeneration (7120)	2.3	0–100
J9010	Western Taiga (9010)	1.5	0–47.4
J9080	Fennoscandian deciduous swamp woods (9080)	0.1	0–6.4
J91D0	Bog woodland (91D0)	0.002	0–0.1
All_heath	All EU protected habitats with heath or grass vegetation	42.67	0–98.24
All_EU_forest	All EU protected forest	1.67	0–47.35
All_EU_habs	All EU protected habitats	43.52	0–98.24
Disturbances caused by military activities			
Fresh_1	Any recent (up to 1 year old) disturbances	0.61	0–6.11
Fresh_2	Any moderately recent (between 1 and 2 years old) disturbances	0.66	0–19.88
Fresh_12	Any recent to moderately recent (up to 2 years old) disturbances	1.27	0–20.00
All_dist	Any disturbances (regardless of age)	3.3	0–88.08
Open_1	Any recent (up to 1 year old) disturbances creating open landscape	0.56	0–6.11
Open_2	Any moderately recent (between 1 and 2 years old) disturbances creating open landscape	0.57	0–19.88
Open_12	Any recent to moderately recent (up to 2 years old) disturbances creating open landscape	1.13	0–19.88
Open_123	Any (regardless of age) disturbances creating open landscape	1.67	0–80.68
Open_3	Old (more than 2 years old) disturbances creating open landscape	1.48	0–80.68
μTerrain_1	Any recent (up to 1 year old) disturbances, altering the microterrain (bombing craters, trenches, ditches, etc.)	0.005	0–0.14
μTerrain_2	Any moderately recent (between 1 and 2 years old) disturbances, altering the microterrain (bombing craters, trenches, ditches, etc.)	0.011	0–0.49
μTerrain_12	Any recent to moderately recent (up to 2 years old) disturbances, altering the microterrain (bombing craters, trenches, ditches, etc.)	0.016	0–0.49
μTerrain_3	Old (more than 2 years old) disturbances, altering the microterrain (bombing craters, trenches, ditches, etc.)	2.57	0–27.47
μTerrain_123	Any (regardless of age) disturbances, altering the microterrain (bombing craters, trenches, ditches, etc.)	2.59	0–27.47
Overgrown	Visible older disturbances overgrown with bushes and trees	1.4	0–16.0
Water	Craters or trenches filled with water	0.26	0–5.63

richness of SCBD, a generalized linear modelling approach (Nelder & Wedderburn 1972) was used. We fitted Poisson family models using a log-link function. To deal with uncertainty in the model selection process we used information-theoretic approach and multi-model inference. Instead of selecting only a single “best model” for each species, we used a set of “competitive models” to describe relationships between species abundance and the

explanatory variables (Burnham & Anderson 2002). We fitted two separate groups of models for each species as well as for overall abundance and richness of SCBD. The first group was “habitats only” models where only EU protected habitat variables were allowed. The second group was “military” models where variables describing different military activities were used in addition to the habitat variables.

All explanatory variables were standardized (centred and scaled) before using them in the models. A correlation matrix was generated to check for possible strong correlations between the explanatory variables. Out of 702 correlations, 60 exceeded 0.50. To reduce model overfitting and to maintain ecological meaning we did not allow these highly correlated variables in the same model. We also did not allow pairs of variables where each described very similar effects as one another (e.g., “Any recent (up to one year old) disturbances” and “Any recent to moderately recent (up to two years old) disturbances”) in the same model, even if the correlation between them was not strong.

Different combinations of the variables, allowing a maximum of five variables in a model, were tested using automated model selection procedure in the R package “MuMIn” (Barton 2016). We used Akaike information criteria adjusted for small sample size (AICc) for comparing model performance. We considered models with  $\Delta\text{AICc}$  scores less than two to be competitive (Burnham & Anderson 2002). We individually checked all competitive models for multicollinearity (Fox & Monette 1992). The variance-inflation factor did not exceed two in any of the predictors of these models. For evaluating the performance of individual variables, we used model averaging and the conditional average of competitive models in which the variable was present (Burnham & Anderson 2002). Generalized coefficient of determination (pseudo  $R^2$ ) was calculated for the best model of each species, as suggested by Nagelkerke (1991).

### 3. Results

#### 3.1. Factors influencing species abundance

Of the surveyed 44 sample squares, we recorded nine territories of Tawny Pipit in seven squares, 20 individuals of Black Grouse in 13 squares, six territories of Common Hoopoe in five squares, 23 territories of Woodlark in 18 squares and 25 territories of European Nightjar in 13 squares. As there were only three observations of European Roller in three squares, we did not use this species for modelling. Nevertheless, we included the species

for calculating the richness and overall abundance of the SCBD.

Black Grouse did not form any larger aggregations (leks) within the study area and most of the observed calling males were solitary.

The best GLM models explaining abundance of the analysed species using only the variables describing the EU protected habitats, captured *ca.* 9 to 52 percent of the variation in data depending on species. However, the best models that included also the variables describing the military activities captured *ca.* 24 to 67 percent of the variation in data (Supplementary Tables 1–5). For every species, the “military” model outperformed the “habitats only” model.

In all of the competitive “habitats only” models for Tawny Pipit, at least one of the EU protected habitats with heath or grass vegetation appeared as an important positive predictor. However, the inclusion of variables describing military activities noticeably improved the model (Supplementary Table 1). While the extent of the EU protected heath habitats was still important, the competing models also included different military variables. Among them, any disturbances (regardless of age) creating open landscape appeared most frequently and was present in the best model.

The habitats with heath and grass vegetation (either “Dry sand heaths with *Calluna* and *Empetrum nigrum* (2320)” or all such habitats combined) were positive predictors also in the competitive “habitats only” models for Black Grouse (Supplementary Table 2). In addition to the habitats with heath and grass vegetation, all the competitive “military” models included also recent disturbances altering the micro-terrain and at least one other “military” variable.

Common Hoopoe in its competitive “habitats only” models also preferred the habitats with heath and grass vegetation while avoided the EU protected forests. In none of the models where the forest variable was present this relationship was significant (Supplementary Table 3). This is not surprising as the EU protected forests are only a fraction of all forests present in the study areas, and we assume this relationship will have been much stronger if the area of all forests had been used as a predictor.

A quarter of the competitive “military” models also included the EU protected forests as a non-



Table 2. Summary of the GLMs explaining the richness of the “species considered to benefit from disturbances” with military disturbed areas and habitats of EU importance.

Parameter	Conditional averaged models				Variable importance		Best model	
	Coefficient	SE	Z-value	P-value	No. models with variable	Relative importance	AICc	Pseudo R <sup>2</sup>
“Habitats only” model								
<b>Intercept</b>	0.1308	0.1539	0.825	0.40961	3		121.41	0.3548653
<b>J2130</b>	0.2093	0.1002	2.028	0.04257 *	3	1.00		
<b>J2320</b>	0.5270	0.1781	2.875	0.00403 **	2	0.75		
All_EU_forest	-0.1369	0.1860	0.714	0.47523	1	0.21		
“Military” model								
<b>Intercept</b>	0.07080	0.15890	0.432	0.66572	22		114.80	0.4840772
<b>μTerrain_12</b>	0.21500	0.07981	2.618	0.00886 **	13	0.61		
<b>Fresh_1</b>	0.28273	0.11205	2.451	0.01425 *	10	0.52		
All_dist	0.32827	0.14996	2.127	0.03345 *	9	0.40		
<b>Open_123</b>	0.34828	0.14162	2.389	0.01691 *	6	0.35		
All_heath	0.41948	0.24339	1.692	0.09057.	9	0.33		
Open_1	0.28694	0.10914	2.553	0.01067 *	6	0.26		
μTerrain_2	0.20042	0.07771	2.510	0.01208 *	5	0.25		
Open_12	0.34456	0.12061	2.784	0.00536 **	6	0.22		
μTerrain_3	-3.04520	5.00678	0.604	0.54574	5	0.18		
J2130	0.15493	0.11539	1.302	0.19284	4	0.17		
J2320	0.28592	0.20961	1.330	0.18351	4	0.17		
μTerrain_123	5.84452	5.32770	1.086	0.27751	3	0.11		

significant negative predictor, while the “Fixed coastal dunes with herbaceous vegetation (2130)” appeared in all of them as a significant positive predictor. All of the “military” models included either “moderately recent” or “recent to moderately recent” disturbances, altering the micro-terrain as a positive predictor often accompanied with another “military” variable (Supplementary Table 3).

The two competitive “habitats only” models for Woodlark consisted of only one explanatory variable – either “Inland dunes with open *Corynephorus* and *Agrostis* grassland (2330)”, or all habitats with heath and grass vegetation combined; both of them being significant or near-significant positive predictors.

However, none of the competitive “military” models included any habitat variables. In these, the moderately recent disturbances creating open landscape appeared most frequently as positive predictors altering the micro-terrain, followed by recent to moderately recent disturbances. These

two were the only variables present in the “best” model (Supplementary Table 4).

Even the “best” of the “habitats only” models for European Nightjar performed very weakly with no significant predictors and explaining just slightly more than 8% of the variation in the data. Most of these models included “Degraded raised bogs (7120)” as a non-significant negative predictor. The “military” models performed considerably better. Most of them included moderately recent disturbances creating open landscape, along with any of the variables describing recent to moderately recent disturbances altering the micro-terrain as positive predictors (Supplementary Table 5).

### 3.2. Factors influencing “species considered to benefit from disturbances” score

At least one of the species considered to benefit from disturbances was recorded in 33 of the se-

Table 3. Summary of the GLMs explaining the relationship of the overall abundance of the “species considered to benefit from disturbances” with military disturbed areas and habitats of EU importance.

Parameter	Conditional averaged models				Variable importance		Best model	
	Coefficient	SE	Z-value	P-value	No. models with variable	Relative importance	AICc	Pseudo $R^2$
“Habitats only” model								
<b>Intercept</b>	0.56970	0.13086	4.224	2.4e–05 ***	3		174.31	0.622238
<b>J2130</b>	0.17093	0.07731	2.146	0.0319 *	3	1.00		
<b>J2320</b>	0.70722	0.15305	4.485	7.3e–06 ***	3	1.00		
All_EU_forest	–0.15335	0.15745	0.945	0.3449	1	0.26		
J7120	–0.16738	0.21000	0.773	0.4395	1	0.22		
“Military” model								
<b>Intercept</b>	0.41698	0.14437	2.797	0.005151 **	19		144.52	0.8268505
<b>J2320</b>	0.59466	0.18827	3.078	0.002084 **	19	1		
$\mu$ Terrain_2	0.20756	0.05967	3.387	0.000707 ***	13	0.70		
$\mu$ Terrain_1	0.36999	0.10225	3.532	0.000412 ***	10	0.58		
All_dist	0.28615	0.12726	2.185	0.028856 *	8	0.46		
<b>Open_12</b>	0.34595	0.11008	3.068	0.002152 **	6	0.31		
<b><math>\mu</math>Terrain_12</b>	0.17640	0.05610	3.052	0.002272 **	6	0.30		
Open_1	0.27078	0.08938	2.945	0.003226 **	4	0.27		
Fresh_1	0.26740	0.08875	2.926	0.003437 **	5	0.27		
J2130	0.12283	0.08712	1.366	0.171885	5	0.22		
Open_123	0.29671	0.12889	2.238	0.025228 *	4	0.19		
Fresh_12	0.29686	0.08862	3.250	0.001153 **	4	0.15		
$\mu$ Terrain_123	0.16948	0.10408	1.577	0.114866	2	0.11		

lected 44 squares. Of these “positive” squares, almost half (15) held only one territory (or individual in the case of Black Grouse) of one species. There were three more squares with only one species but more than one territory. Two or more species were recorded in the rest of the squares (15). The maximum recorded species richness was five in two squares and the maximum recorded abundance of SCBD was ten in one of the squares.

The best “habitats only” GLM explaining the richness of the species considered to benefit from disturbances captured *ca.* 35% of the data variation while the “military” model explained *ca.* 48% (Table 2). All the competitive “habitats only” models included the EU protected habitat type “Fixed coastal dunes with herbaceous vegetation (grey dunes) (2130\*)” and two of the three models held also the habitat type “Dry sand heaths with *Calluna* and *Empetrum nigrum* (2320)” as a significant or near-significant positive predictor. The

two habitat variables were not among the most frequent predictors in the competitive “military” models. Among the “military” variables, the variable describing recent to moderately recent disturbances altering the terrain (“ $\mu$ Terrain\_12”) was present in more than half of the competitive models.

The best GLM explaining the overall abundance of the species considered to benefit from disturbances captured *ca.* 62% of the data variation (Table 3). All the competitive “habitats only” models included both the EU protected habitat type “Dry sand heaths with *Calluna* and *Empetrum nigrum*” (J2320) and “Fixed coastal dunes with herbaceous vegetation (grey dunes)” (2130\*) as a significant positive predictors. The habitat type “Dry sand heaths with *Calluna* and *Empetrum nigrum*” (J2320) was present also in all the competitive “military” models. Of the variables describing the military activities, at least one of the

Table 4. Relative importance of variables (number of significant relations with presence of the species and frequency of their appearing in GLMs).

Variable	Number of species with the variable in chosen species models	Direction of the effect in the species models	Frequency in the sets of chosen species models	Direction of the effect in the abundance of SCBD models	Frequency in the set of chosen abundance of SCBD models	Direction of the effect in the SCBD species richness models	Frequency in the set of chosen SCBD species richness models
<b>“Habitats only” models</b>							
J2320	5	+	8	+	3	+	3
J2130	3	+	6	+	3	+	2
All_heath	4	+	4				
All_EU_forest	2	–	4	–	1	–	1
J7120	1	–	1	–	1		
<b>“Military” models</b>							
μTerrain_2	4	+	14	+	13	+	5
μTerrain_12	4	+	12	+	6	+	13
Fresh_1	4	+	5	+	5	+	10
J2130	2	+	15	+	5	+	4
J2320	2	+	10	+	19	+	4
Open_1	2	+	10	+	4	+	6
All_dist	2	+	8	+	8	+	9
All_heath	2	+	5			+	9
μTerrain_1	2	+	4	+	10		
Open_12	2	+	2	+	6	+	6
Open_123	1	+	9	+	4	+	6
Water	1	–	4				
Open_2	1	+	3				
Overgrown	1	–	2				
All_EU_forest	1	–	2				
Fresh_12	1	+	1	+	4		
μTerrain_123				+	2	+	3
μTerrain_3						–	5

variables describing recent to moderately recent disturbances altering the terrain (“μTerrain\_2”, “μTerrain\_1” or “μTerrain\_12”) was present in all models, most often accompanied with one of the variables measuring disturbances creating open landscape.

### 3.3. Relative importance of the predictor variables

As many of the candidate predictors were inter-related, many of the species or group models were very similar and differed one from another just by replacing individual variables largely describing the same phenomena. However, the relative frequency of each variable in the competitive models

allows us to draw conclusions about their importance.

Of the 11 candidate explanatory variables describing the area of different EU protected dune, heath, mire and forest habitats occurring in the study plot, only five appeared in the competitive species’ “habitats only” models (Table 4). Of these, the most frequent was the habitat type “Dry sand heaths with *Calluna* and *Empetrum nigrum*” (“J2320”) appearing as a positive predictor in the models of all analysed species. The “Fixed coastal dunes with herbaceous vegetation (grey dunes)” (“J2130”) and all habitats with heath and grass vegetation combined (“All\_heath”) were also frequent positive predictors, appearing in models of three and four species, respectively.

The variables describing all EU protected fo-



rest habitats and “Degraded raised bog” (“J7120”) only appeared as negative predictors in the models of two and one species, respectively. The same variables except “All\_heath” appeared also in the competitive “habitats only” models explaining the overall abundance of SCBD. The competitive models explaining the richness of SCBD used only the two heath and dune habitats (“J2320” and “J2130”) as positive predictors and all EU protected forest habitats as negative predictors.

Although the same habitat variables (except “J7120”) also appeared in a part of the “military” models, the number of species each of them was relevant for did not exceed two. Of the 16 candidate explanatory variables quantifying the impact of military activities, 12 variables appeared in at least one of the competitive models for at least one of the species (Table 4). However, only seven of them were present in the models for more than one species. Most of the “military” variables appeared as positive predictors in the models, except the craters or trenches filled with water (“Water”) and older disturbances overgrown with bushes and trees (“Overgrown”). The variables describing recent to moderately recent disturbances altering the terrain (“ $\mu$ Terrain\_2” and “ $\mu$ Terrain\_12”), as well as any recent (up to one year old) disturbance caused by a military activity (“Fresh\_1”), were used in models for most (four) of the species (Table 4).

The sets of competitive models explaining overall abundance and richness of SCBD used 10 and 9 of the available “military” variables, respectively. All of them appeared as positive predictors in the models, except more than two years old disturbances altering the micro-terrain ( $\mu$ Terrain\_3), which was negative in five of the models explaining the richness of SCBD. There was good agreement in variable importance among the different sets of models: variables appearing more frequently in the species’ models were also frequent in the models explaining overall abundance and richness of SCBD (Table 4).

#### 4. Discussion

The modelling results (comparison of the “habitats only” and “military” models in Tables 2–3 and Supplementary Tables 1–5) imply clear positive

effects of most of the military activities on the analysed species. This is not surprising as almost all of them contributed to the creation or maintenance of a fine scale mosaic of sandy patches on a rugged terrain that is preferred breeding or feeding habitat for most of the species (del Hoyo *et al.* 1999, del Hoyo *et al.* 2001, del Hoyo *et al.* 2004). The only variables showing negative effects were those that either did not result in sandy patches (too deep craters and trenches that filled with water) or were abandoned and thus were becoming overgrown with trees and bushes.

Not surprisingly, the variables describing the availability of locally common open dune or heath habitats (“J2320”, “J2130” or “All\_heath”) appeared as significant predictors in all the competitive “habitats only” models for all the species as well as for the overall abundance and richness of SCBD. However, these habitats alone could not explain as large variation in the data as they could together with the disturbance variables. In fact, the sample squares with no or very few signs of recent military disturbances did not hold any of SCBD despite the presence of open dune or heath habitats. This is an important indication that military training activities have been playing an important role in serving as a source of management of these habitats for the analysed species. Activities altering the micro-terrain, as well as recently (up to one year old) disturbed areas, had the highest importance among all military variables. It is plausible that primary drivers of species presence and abundance were still dune and heath habitats, while military disturbances helped to improve habitat quality by providing favourable habitat management (Jentsch *et al.* 2009) through heterogeneous disturbance. Heterogeneous disturbance hypothesis suggests that biodiversity is maximized where multiple kinds, frequencies, severities, periodicities, sizes, shapes, and/or durations of disturbance occur concomitantly on a landscape in a spatially and temporally distributed fashion (Warren *et al.* 2007).

In our study area, the heterogeneous disturbances were creating good feeding sites for insectivorous birds as well as lekking sites for Black Grouse. Yet, through unequal use of terrain for military activities, they also preserve less disturbed sites for breeding in a favourable open landscape. Many of the different types and ages of dis-

turbances co-occurred in the same sample plots thus obscuring their individual signals. For example, the bombing and firing did not only create a rough terrain and removed the vegetation directly in the target zone, but frequently caused a fire that partially removed the vegetation in larger areas. Similarly, areas where bombing or digging of trenches took place were often accessed by heavy military vehicles that created additional sandy patches. Thus, a patchy landscape was formed consisting of a mosaic of habitat patches at different stages of vegetation succession, originating from different disturbances.

The results show that all recent (up to one year) and moderately recent (up to two years) disturbances appeared more often and more consistently in the models than those describing the same kind of activities regardless of their age (Table 4). The variables quantifying only disturbances older than two years either did not appear in the competitive models or, in one case, appeared as a negative predictor. This suggests that the recent to moderately recent disturbances have been essential in maintaining the habitats for the analysed species and, without them habitat quality may deteriorate within a few years. A similar effect has also been shown for the protected habitats themselves via disturbance-related effects on structural diversity and preservation of openness (Sutherland & Hill 1995), and particularly on succession species (Jentsch *et al.* 2009). The variable quantifying any kind of recent (up to one year old) disturbances (“Fresh\_1”) appeared among the predictors of the competitive models for most of the analysed species (Table 4).

Also, recent (up to 1 year old) disturbances creating open landscape (“Open\_1”) was among the frequent positive predictors, and appeared more often in the models than variables that include older activities of this kind. This allows us to suggest that either the intensity of military activities that typified the study period did not create even a short-term negative effect on territory occupancy of the disturbance-dependent species, or the duration of this effect was too short to measure in our study.

The results rather suggest that these species already tend to occupy the newly created suitable habitat patches in the next breeding season regardless of disturbance levels, as has been suggested

for Tawny Pipit (Grzybek *et al.* 2008, Meffert & Dziock 2012) and Woodlark (Wright *et al.* 2007).

Nevertheless, the highest military activity rates (the international NATO trainings) in our study site overlapped with bird breeding season in June. The large-scale trainings were relatively short in duration during the study period – a few weeks of high military activity followed by several weeks of low-level activity. Unfortunately, we are not able to assess if the described situation may create an ecological trap for the disturbance dependent species in providing an attractive breeding habitat where subsequent breeding success was too low to maintain the populations (Schlaepfer *et al.* 2002). As the annual monitoring does not provide any evidence of declines of these species on the site in recent years (Aunins & Avotins 2016), we assume that the positive effects of maintaining the habitat in favourable condition outweigh the potential negative impact of the current level of military activities on breeding success.

Despite the favourable effects on habitat quality, some negative effects of military activities on species behaviour were observed. In particular, despite the large population in Adazi, Black Grouse males were observed displaying only solitarily or in very small lekking groups (up to three individuals). It has been suggested that such a shift from lekking to solitary displaying indicates decreasing effective population sizes (Svobodova *et al.* 2011). However, presently, there are no indications of a population decline of Black Grouse in the area (Aunins & Avotins 2016).

After the collapse of the USSR more than two decades ago, the military activities in Adazi military training area took place on a small scale and with low intensity thus leaving large areas of abandoned land. Abandoned military training areas in Eastern Europe have been reported as emerging biodiversity hotspots (Reif *et al.* 2011, Cizek *et al.* 2013). However, the habitats at the earliest successional stages, and those important for highly specialized and threatened bird species and often those of the highest conservation value, tend to be negatively affected by the abandonment (Reif *et al.* 2013). Similarly, the parts of the Adazi military training area where no military activities occurred became important for maintaining populations of different forest and mire species as well as the protected forest and mire habitats. At the same time,

the populations of the species associated with open areas and open dune and heath habitats were affected negatively as encroachment of bushes and trees rendered the open areas unsuitable and reduced the habitat area.

Thus, special habitat restoration activities (for example, LIFE06 NAT/LV/ 000110 “Restoration of Biological Diversity in Military Training Area and Natura 2000 site Adazi”) were needed to prevent decline of the protected species. During the recent years, the intensity of the military training has increased, and as this study shows, the species preferring open dune and heath habitats benefit from the disturbances generated. During the data collection for this study, there were no measurable signs of negative effects of the military activities on abundance and richness of the analysed species. However, the short duration of the study did not allow for analysis of changing habitat conditions resulting from the military activities. In the future, it would be important to quantify the effects of yearly changes in availability and quality of the habitats, and the role of different military activities on population dynamics of species considered to benefit from anthropogenic disturbance.

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### **Sotaharjoitusalueiden merkitys diversiteetille: aktiivisten harjoitusten vaikutus häiriöstä hyötyviin lintulajeihin Latviassa**

Tässä tutkimuksessa selvitettiin Adazin sotaharjoitusalueella sotaharjoitusten vaikutusta häiriöstä hyötyviin lintulajeihin. Aineistoa valittujen lintulajien runsaudesta kerättiin toistuvasti 44 tutkimusruudulta. Jokaiselta tutkimusruudulta kartoitettiin sotaharjoituksista aiheutuneen häiriön määrä sekä ruudulle osuvat, EUn luokitusten mukaiset suojellut populaatiot. Häiriöstä hyötyvien lintulajien

runsaus ja monimuotoisuus laskettiin kullekin tutkimusalueelle ja näiden yhteyttä populaatioihin ja sotaharjoitusten aktiivisuuteen (häiriön määrä) analysoitiin yleistetyillä lineaarisilla malleilla. Kilpailuvista malleista valittiin tärkeimmät selittävät tekijät.

Havaittiin, että sotaharjoituksilla oli positiivinen yhteys sekä tutkittuihin lajeihin että lajirunsauteen. Habitatuuttuuttajat ja häiriömuuttajat yhdessä selittivät vaihtelua paremmin kuin habitatuuttuuttajat yksinään. Viimeaikaiset häiriöt (yhden tai kahden vuoden sisällä tapahtuneet) säilyttivät parhaimmin heterogeenisen populaation. Tulosten mukaan lajit suosivat uutta, häiriötoiminnan seurauksesta syntyneitä populaatioita seuraavana lisääntymiskautena. Tutkimuksessa ei löydetty sotaharjoitusten aiheuttavan haitallisia vaikutuksia tutkimuslajien runsauteen tai määriin, mutta havaittiin haitallisia vaikutuksia lajien käyttäytymiseen.

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### **Online supplementary material**

Tables S1 to S5 show summary of GLMs explaining species abundance in relation to the EU protected habitats (Habitats only model) and with military disturbances (Military model).