



Behavioural response of Eurasian Blackcaps to acoustically simulated conspecific and heterospecific male intruders

Alžbeta Darolová¹ · Ján Krištofík¹ · Felix Knauer² · Herbert Hoi³

Received: 6 May 2019 / Revised: 10 October 2019 / Accepted: 31 December 2019
© Deutsche Ornithologen-Gesellschaft e.V. 2020

Abstract

Interspecific territoriality can frequently be observed in the animal kingdom, including birds. One important factor driving the degree of interspecific territoriality is competition for resources. Other influential factors are, for instance, population density, phylogenetic relatedness, fighting asymmetries, and shared predation. Although the degree of competition is usually a composite of several factors potentially influencing competition, it is possible to determine the degree of competition without knowing all influential factors and their importance. In line with this, we used the strength of behavioural interactions between species under standardized experimental conditions. In particular, we investigated the degree of interspecific competition using the territorial song of male Eurasian Blackcaps (*Sylvia atricapilla*) as a low-risk response variable and the crossing flights and nearest approach distance to an intruder as high-risk defence behaviours. To simulate an interspecific intruder, we used male song playbacks of phylogenetic-related and more or less coexisting species. In line with our predictions, we found territorial defence to be most intense against conspecifics (positive control) and virtually non-existent against the allopatric Subalpine Warblers (*S. cantillans*) (negative control). In terms of the defence reaction to sympatric interspecific intruders, the response seemed strongest in relation to the Garden Warbler (*S. borin*) and weakest in relation to the Barred Warbler (*S. nisoria*). Our results further show that the vegetation characteristics of a territory influence behavioural responses to intruders, but only in relation to low-risk defence.

Keywords *Sylvia atricapilla* · Territory defence · Intruder · Interspecific reactions · Intraspecific reaction · *Sylvia* warblers

Zusammenfassung

Territorialverhalten von Mönchgrasmücken gegenüber dem Gesang art eigener und artfremder Eindringlinge

Interspezifische Territorialität ist ein wichtiger Faktor der beim Zusammenleben von Tierarten, unter anderem auch Vogelarten, eine Rolle spielt. Konkurrenzverhältnisse zwischen Arten werden besonders durch die Verfügbarkeit von gemeinsam beanspruchten Ressourcen beeinflusst. Auch Populationsdichte, Verwandtschaft, physische Voraussetzungen oder die Auswirkung gemeinsamer Räuber sind Faktoren welche die Verhältnisse zwischen zwei Arten mitbestimmen können. Welche Bedeutung dabei den einzelnen Faktoren zukommt ist schwer festzustellen. Die Häufigkeit und Intensität von Auseinandersetzungen zwischen Arten kann aber Aufschluss über Konkurrenzverhältnisse liefern und erlaubt

Communicated by S. Kipper.

✉ Alžbeta Darolová
alzbeta.darolova@savba.sk

¹ Institute of Zoology, Slovak Academy of Sciences,
Dúbravská cesta 9, 845 06 Bratislava, Slovakia

² Department of Integrative Biology and Evolution, Research
Institute of Wildlife Ecology, University of Veterinary
Medicine, Savoyenstrasse 1, 1160 Vienna, Austria

³ Department of Integrative Biology and Evolution, Konrad
Lorenz Institute of Ethology, University of Veterinary
Medicine, Savoyenstrasse 1a, 1160 Vienna, Austria

möglicherweise auch Rückschlüsse auf die Bedeutung der einzelnen Faktoren. In diesem Zusammenhang untersuchten wir die Intensität interspezifischer Auseinandersetzungen unter standardisierten Bedingungen. Als Reaktionsparameter wurden dazu einerseits der territoriale Gesang männlicher Mönchsgrasmücken *Sylvia atricapilla*, der repräsentativ für eine geringe Verteidigungsbereitschaft ist, und andererseits die Anzahl der Überflüge knapp über dem Lautsprecher, sowie die nächste Annäherung an den Lautsprecher, beides Parameter repräsentativ für hohe Verteidigungsbereitschaft, verwendet. Die Reaktion von männlichen Mönchsgrasmücken wurde mit Hilfe von standardisierten Playbackexperimenten getestet, wobei ein gleich- oder andersartiger Eindringling durch den territorialen Gesang der jeweiligen Arten simuliert wurde. Entsprechend unseren Vorhersagen war die territoriale Reaktion gegen Artgenossen (Positivkontrolle) am stärksten und gegen die allopatrische Weißbartgrasmücke *S. cantillans* (Negativkontrolle), am schwächsten. In Bezug auf sympatrische interspezifische Eindringlinge ist die Abwehrreaktion gegen die Gartengrasmücke *S. borin* am stärksten und gegen die Sperbergrasmücke *S. nisoria* am schwächsten. Die Ergebnisse zeigen weiters, dass Vegetationseigenschaften das Territorialverhalten, jedoch nur in Bezug auf die Gesangsreaktion, mitbeeinflussen.

Introduction

Resource defence against conspecifics is well documented in the animal kingdom, with varying resource types, including, e.g., food, sites for reproduction, mating partners, and mating sites (Cody 1969; Bartsch et al. 2012; Scordato 2017). Depending on the resource type, territories may vary from permanent “all purpose” territories to short-term defence of, e.g., display sites (Lancot et al. 2000; Morales et al. 2014; Riou and Combreau 2014). Territorial behaviour can also be directed towards other species (Gil 1997; Grether et al. 2009). In addition, this interspecific territoriality may depend on resource competition and more generally, on the niche overlap between coexisting species (Ceresa et al. 2016; Losin et al. 2016). Besides overlapping resource requirements, the intensity of interspecific competition can also depend on other factors, such as the population densities of coexisting species, species community composition, and interspecific breeding synchronization (Port and Johnstone 2013; Scordato 2017). Resource competition should be lower when there is less overlap in the breeding period of different species. Another influential factor could be asymmetries in fighting abilities, e.g., due to differences in body size (Jonart et al. 2007; Martin and Ghalambor 2014) or armament between competing species (Ceresa et al. 2016). Furthermore, phylogenetic relationships among species can co-vary with resource requirements and may additionally influence interspecific interactions (Blackburn et al. 1996; Böhning-Gaese et al. 2003; Szymański and Antczak 2013). Independent of resources, shared predation may negatively influence the existence and survival of less common species (Holt and Kotler 1987). As a result, increased interspecific aggression by rare species towards more common ones can be observed (Hoi and Winkler 1994).

In conclusion, interspecific territoriality can be seen as an adaptive behaviour to reduce competition between sympatric species. However, the degree of competition might be

difficult to assess, given that niche overlap between species is usually based on a variety of resources and is likely to be a composite of several resources additionally influenced by other extrinsic factors mentioned above.

However, assuming that the intensity of aggressive interactions directly reflects the degree of competition, the strength of aggressive interactions between species can be determined and used as a tool to evaluate the overall resource competition and hierarchy among species in a community, without knowing the resource requirements of each species. Studies investigating interspecific interactions are often based on two species only (Thielcke et al. 1978; Gil 1997; Osiejuk and Kuczyński 2000; Kitowski 2003; Matyjasiak 2005; Billerman and Carling 2017; Samplonius 2019).

This study, therefore, seeks to determine the degree of competition among several sympatric breeding and related species (Böhning-Gaese et al. 2003), where niche breadth and overlap among the species are unclear (Bairlein et al. 1980; Glutz von Blotzheim 1991; Payevski 1999; Böhning-Gaese et al. 2003; Elle 2003). Assuming that the strength of response reflects the degree of competition, we used the Eurasian Blackcap (*Sylvia atricapilla*) as the model (response) species and studied the reaction of unmated territorial males to intruders, simulated by the playback song of conspecifics and five other *Sylvia* species, including the Garden Warbler (*S. borin*), Lesser Whitethroat (*S. curruca*), Common Whitethroat (*S. communis*), Barred Warbler (*S. nisoria*), and Eastern Subalpine Warbler (*S. cantillans*). We predicted that the strongest reaction would be to conspecifics (which set our “positive control”) and that the weakest would be to the Subalpine Warbler (which represented our “negative control”) as they do not coexist in the study area (for details, see the “[Materials and methods](#)” section). Considering what is known about habitat overlap, resource competition and song similarity between the investigated species (for a rough overview, see the “[Materials and methods](#)” section) we would further predict the second strongest reaction towards the Garden Warbler

followed by the Common Whitethroat. As the most dissimilar, reactions should, therefore, be weaker against the Lesser Whitethroat and the Barred Warbler.

For territory defence, birds may use two types of behaviours: on one hand, indirect behaviours (Balsby and Dabelsteen 2003; Grim 2008; Searcy and Beecher 2009; Leedale et al. 2015; Linossier et al. 2015) like male territorial song (Catchpole and Slater 2008) and on the other hand, direct physical defence behaviours (Hof and Hazlett 2010; Linhart et al. 2012; Jones et al. 2016). Acoustic signals are usually energetically less expensive, reduce the need for constant physical defence, and, therefore, reduce the risk of injury (Huntingford and Turner 1987; Slevin et al. 2016). When using acoustic signals to settle territory disputes between species, it would be necessary to identify the species, and assess its fighting motivation and ability, and the defence cost, including energetic costs and the associated risk of injury. This information can then be used to decide whether the second type of behaviours, namely physical defence, should take place.

To determine the degree of interspecific competition, we, therefore, used the territorial song of male Blackcaps as a low-risk response variable and crossing flights and the “nearest approach distance” to an intruder (playback speaker) as a kind of proxy for high-risk defence behaviours. These three behavioural response parameters were observed towards a standardized intruder, simulated by broadcasting the territorial song of six different species.

The phylogenetically related *Acrocephalus* warbler species, breeding in a more or less two-dimensional habitat (namely reed beds), exerts strong interspecific territoriality, directly related to the overlap in habitat requirements (Hoi et al. 1991). Specifically, the motivation to defend a territory has been found to depend on how well-suited the habitat is for individuals of one species in comparison to other species (Hoi et al. 1995; Ceresa et al. 2016). Accordingly, habitat quality also seems to be an important feature in interspecific interactions. In this context, vegetation features (particularly cover) may influence sound transmission in the case of song response (Mockford et al. 2011; Apol et al. 2018) and may enable intruders to approach (hidden by vegetation). They may also be an indicator of the general habitat requirements necessary for nesting and, hence, directly indicate the quality of a breeding site, which is in fact known to be the case for Blackcaps (Hoi-Leitner et al. 1995).

We, therefore, also included the basic vegetation parameters of each territory in the analyses to identify whether they play a role in interspecific interactions over territories.

We discuss the response of male Blackcaps to other species in relation to phylogenetic relatedness and similarities in habitat use, in addition to demonstrating the importance of vegetation in territory defence.

Materials and methods

In this study, we used the Eurasian Blackcap (*Sylvia atricapilla*) as the model species and studied the reaction of unmated territorial males to intruders, simulated by the playback song of the same and five other *Sylvia* species. The study took place in Western Slovakia (16°58'45.31" – 17°15'00.83"E, 48°03'42.26" – 48°27'50.93"N), including Borská and Podunajská nížina lowland and the foothills of the Malé Karpaty Mountains. Experiments were performed from mid-April to mid-June, between 0700 and 1400, in calm weather. In total, 43 territorial male Blackcaps were tested in our study. To reduce the influence of disturbances from neighbouring males interfering with the experiment, we selected localities with medium densities and additionally excluded experiments in which interactions with neighbours have been observed, resulting in deviating sample sizes. The actual sample sizes are indicated in the three figures, respectively.

The study plots used were mainly forest patches and forest edges bordering open meadow areas. Vegetation at the study sites was typical of deciduous lowland forests, including willow (*Salix* sp.), poplar (*Populus* sp.), oak (*Quercus* sp.), field maple (*Acer campestre*), ash (*Fraxinus* sp.), and European beech (*Fagus sylvatica*). Scrub vegetation at the study sites was mainly represented by the common hawthorn (*Crataegus monogyna*) and black elder (*Sambucus nigra*).

Playback experimental design

Directly prior to each experiment, Blackcap territories were identified by repeated observations of singing males and the positions of song posts were determined over a period of 30 min. Based on these findings, a small (about 10×6×3 cm), camouflaged speaker was attached to a pole at a height of 4 m and located at the intersection (territory centre) of at least three observed song posts, near a tree trunk. To avoid disturbance effects, unobtrusive observations (obscured by vegetation) took place at a distance of 10 m from the speaker and started approximately 10 min after having finished the set-up of the playback speaker (all males resumed singing within this period) and starting to hide at the observation site. Male Blackcaps were observed for 2 min prior to the start of the first playback presentation and the number of song strophes, as well as any interaction with neighbouring males, was documented. The number of song strophes resulting from these observations has been used as the reference for “unstimulated” song and for comparison with the song reaction towards different playback stimuli.

The actual playback experiment consisted of a 2-min playback, whereby the speaker was switched on with a remote control. For this period, we determined the number of song strophes produced by each territorial male, the number of flights crossing above the simulated intruder (playback speaker) (for details see later), and the closest observed position of the male to the speaker. Moving Blackcaps are difficult to follow in their territory, so observations prior to and during the experiment were made by two persons. The behaviour of the Blackcaps was noted with a voice recorder and analysed later. The duration of the playback length was chosen according to earlier experiences with this species and the natural behaviour of real intruders.

The experiment represented a repeated design, in which each territorial male Blackcap was tested with six playbacks of male song originating from six *Sylvia* warbler species, respectively. The six species included the conspecific (namely the song of male Blackcaps) and five other related warbler species (namely the Garden Warbler, Lesser Whitethroat, Common Whitethroat, Barred Warbler, and Eastern Subalpine Warbler). The sequence of species presentation was random and the interval between successive playbacks presented to one individual was 30 min. To avoid pseudo-replication effects, each playback type consisted of recordings of the song of five different males, whereby all five males were represented by the same number of strophes. The total number of strophes broadcasted during the 2-min playbacks slightly varied between species playbacks, due to strophe and pause length differences, as follows: 10 strophes for the Blackcap; 15 for the Garden Warbler; 15 for the Lesser Whitethroat; 20 for the Common Whitethroat; 15 for the Barred Warbler; and 15 for the Eastern Subalpine Warbler. For each male included in the playback, we used a song strophe sequence taken from a longer sequence recorded and interlinked one after the other. Therefore, the song strophes of each male occurred only once during the 2 min and the songs of all five males were always broadcast in the same order. Recordings have not been edited, except for the sound pressure level, which was kept the same for all experiments (within the natural range). To generate the playbacks, we used the program Audacity 2.0.5.

In our experiment, the song of conspecifics was used as a positive control. Except for the Eastern Subalpine Warbler, all the other species breed within the wider study area of the Blackcap, although not necessarily in the immediate vicinity. The only species with a distant breeding range (a minimal distance of 400 km from our study site to NE Italy, Slovenia, Bosnia Herzegovina, Croatia, Bulgaria, Greece, and Turkey) (Brambilla et al. 2008b) and, hence, not representing a direct competitor, is the Eastern Subalpine Warbler. As a result and based on the predictions presented in the introduction, we used this species as a negative control.

To test the behavioural reaction of male Blackcaps to conspecifics or different species, two categories of dependent variables were used: (i) the number of male song strophes produced during the whole playback duration (2 min) as an indicator of territorial occupancy and an advertisement of territory ownership (song rate is an important characteristic and indicator of the quality of male Blackcap song) (Hoi-Leitner et al. 1995); and (ii) two parameters, namely the number of “crossing flights” and the nearest approach of a male to the simulated intruder (speaker) as an indicator of direct and alert willingness to defend the territory. During the playback presentation, the number of “crossing flights” was calculated as the number of flights which a male performed crossing the speaker within a distance of 1 m. The “nearest approach distance” (m) was the closest position of each territorial male to the speaker.

Song features of the investigated species

Blackcap song strophes usually consist of two parts, an introductory warble part (harsh sounds) of varying length, followed by a louder part of pure fluting tones (Garcia 1981; Bergmann and Helb 1982). They imitate other passerines, including the Garden Warbler. Thus, the song of the Garden Warbler is most similar to that of Blackcaps, although their warble part seems more even-flowing, subdued, and more sustained, containing more syllables. The two species also have similar strophe length (approximately 4 s), but Blackcaps have shorter pause lengths (about 3 s, for details, see Cramp and Brooks 1992). The Lesser Whitethroat appears to be the most distinct in terms of song, producing shorter strophes (strophe length about 2 s) consisting of two parts, but with a unique loud wooden rattling repetition (second part), which is only sometimes preceded by short warbling or chattering (first part), audible only at closer distances. Similarly, short is the strophe of the Common Whitethroat, but without any distinct strophe partitioning. Males produce strophes consisting of rapidly uttered more or less musical warble syllables. Given males frequently repeat copies of the same strophe, their song appears to be more stereotypical. In the Lesser and Common Whitethroat, song pause lengths are longer than strophe lengths (reviewed in Cramp and Brooks 1992). The song of the Barred Warbler, in comparison to the other species, is relatively complex, with no distinct separation and not much variation. Their strophe length is intermediate (about 4 s, Cramp and Brooks 1992). Finally, Subalpine Warbler song strophes resemble those of the Common Whitethroat, but their strophes are more sustained and musical, with prolonged notes. Uniquely, their song includes a fairly conspicuous high-pitched whistle at the start and consistent whistles which gently descend later on (Cramp and Brooks 1992).

Besides these descriptive differences, it is not known how important they may be for Blackcap response. The six investigated species also show some common features, which makes them particularly interesting for examining inter-specific territorial behaviour. All of them exhibit distinct song strophes clearly separated by a pause, with little variation in song duration and similar ranges in song frequency (between about 1.5 to 7.5 kHz, Cramp and Brooks 1992). Males advertise their song from song posts, while the Barred Warbler and Common Whitethroat frequently perform song flights as well (Cramp and Brooks 1992).

Habitat requirements of the investigated species

Blackcaps are highly arboreal, preferring more or less mature forests, but they also require shrubby undergrowth that is not overly dense (reviewed in Cramp and Brooks 1992). They have overlapping territories with Garden Warblers, which have very similar habitat requirements, except Blackcaps have a greater preference for shady, mature trees, often with less dense foliage, in which they are freely visible.

Garden Warblers sometimes also share their territories with the Lesser and Common Whitethroat, but in contrast, the Garden Warbler is primarily a woodland species, although in comparison with Blackcaps, it generally prefers more open canopies accompanied by fairly dense and tall scrub, or a shrub layer.

The Lesser Whitethroat flourishes in intermediate habitats between extensive closed forest and open country, resorting to well-spaced, often tall, bushes, shrubs, hedgerows, and the like, but often including tree song posts.

The Common Whitethroat requires an ample but discontinuous well-mixed and open cover of tall herbage, low bushes, and shrubs, usually on more or less dry, level or gently sloping and fairly sunny terrain. They sometimes share their habitat with the Barred Warbler. Both clearly avoid wetland areas and forests.

The Barred Warbler inhabits narrow shelterbelts and plantations, clearings in broad-leaved and mixed woodlands with plenty of undergrowth (especially of thorny bushes) and can be also seen, in common with the Garden Warbler, namely in bushy terrain overgrown with young trees and dotted with single higher trees which are used as song posts.

Finally, the Subalpine Warbler breeds in typical Mediterranean regions containing dense, xerophytic, often prickly scrub on sunny hillsides and maquis, and even extremely dry places may be occupied.

In conclusion, habitat requirements among species seem to overlap to varying degrees, but the species most similar to the Blackcap in this regard seems to be the Garden Warbler, followed by the Lesser Whitethroat. The Common Whitethroat appears to be the most different in terms of habitat requirements. On the other hand, there is also remarkable

within-species variation, which makes resource competition ranking ambiguous. Given that the information gathered from strophe similarity and habitat requirements is not clear-cut, we performed this experiment to shed further light on interspecific competition between Blackcaps and the other species.

Additionally, to examine the importance of habitat quality for each male territory, three vegetation parameters were determined: (i) average tree height (m); (ii) average scrub height (m); and (iii) overall vegetation cover (%), including the area of the territory covered by tree and scrub vegetation. Vegetation cover was estimated as the percentage of the area covered with trees or scrub within a 30 m radius of the territory centre, based on the observation of several males' song posts (see earlier). All tree and scrub heights were determined within the same 30 m radius. Tree and scrub heights were determined using a field laser rangefinder. Average tree and scrub heights were then used in the analyses.

Statistical analyses

Experiments which elicited the reaction of real neighbouring individuals were excluded from the analyses.

To determine the reaction of male Blackcaps to simulated intruders, we used three behavioural parameters as the dependent variables: (i) number of song strophes; (ii) number of crossing flights; and (iii) nearest approach distance to the playback. Three vegetation parameters were used as independent variables and included the experiment date (point in the breeding season) as a non-parametric covariate (spline).

We used additive linear regression models in an information-theoretic approach (Burnham and Anderson 2002). For all potential models, the Akaike weights were estimated and (based on the sum of the Akaike weights of all models containing a variable) the relative variable importance (RVI) was calculated. The RVI is the probability of a given variable being in the model that best explains the data. Variables with RVI values > 0.9 are very likely, and variable values around 0.7 are "likely" to be in the best model, whereas the situation for variables with RVI values about 0.5 is "uncertain", and variables under 0.2 are "very unlikely" to be in the best model (see Burnham and Anderson 2002). In this study, each territorial Blackcap male was tested with six playbacks of male song originating from six *Sylvia* Warbler species, respectively. Therefore, data originating from such a design constitute multiple measurements on the same individual. This means that the data are not independent of each other within each individual. Biologically speaking, there could be individual effects hidden in these data. Therefore, we accounted for this data structure by including the individuals as random effect in the model, a standard approach to handle data with such a structure.

R (R Core Team 2016), mgcv (Wood 2017), and MuMIn (Barton 2018) software packages were used for the statistical analyses.

Furthermore, to directly interpret the model results, we calculated the 95% confidence intervals of the parameter estimates for the six species in relation to the three response variables, respectively. We then used the overlap or non-overlap in the 95% confidence intervals in pairwise comparisons between species to determine the occurrence of significant differences between species pairs. Reactions in this case can be seen to be exclusive or overlap from one or from both sides (species).

Results

Our results suggest that the number of song strophes produced by the male Blackcap (unstimulated, prior to playback presentation) seems to depend on tree and scrub height in the territory, as well as the time in the breeding season (Table 1). All three parameters have relative importance values (RVI) around 1, which suggests that they are very likely to be included the best model and are, therefore, important determinants of the unstimulated production of the male Blackcap song strophes. The positive parameter estimates suggest that the number of song strophes increases with vegetation height (tree and scrub height) (Table 1).

As expected, during the playback presentation simulating the singing of male territorial intruders (conspecifics and five other species of the genus *Sylvia*), we found differences in the number of song strophes of unmated male Blackcaps (Fig. 1). During song playbacks, the number of strophes was generally reduced (Table 1) in comparison to

song production prior to the playback challenge, whereby the average number of unstimulated song strophes is indicated by the dashed line and the upper and lower standard error by dotted lines (see Fig. 1). Relative variable importance indicated which species (RVI=0.85) were likely to be included in the best model to explain the variation in the number of song strophes. Post hoc comparisons using the standard errors of the parameter estimates indicated that the difference between species was probably due to the response to conspecific song, rather than to the song of other species (Fig. 1; Table 2a). The Blackcap song response differs from the response towards the Common Whitethroat, Barred Warbler, and the Subalpine Warbler, as the response towards the Subalpine Warbler in contrast also differs from the response towards conspecifics. Thus, males reduce the number of song strophes more significantly when confronted with conspecific song than the song of the other three species. Most interestingly, Blackcaps' song response did not differ towards Garden Warblers and Lesser Whitethroats, and the song response did not differ among the five heterospecific species (Table 2a).

Based on the relative variable importance, vegetation cover (RVI=0.83) and season (0.80) also seems likely to be in the best model and to influence the song response. The positive parameter estimates suggested a slight but positive effect of increasing vegetation cover on the number of song strophes and an increase in the number of song strophes with the season (Table 1).

Examination of the parameters reflecting direct territory defence (such as crossing flights) again revealed the high importance of species (Table 1). Species only showed a high RVI value (1) in relation to crossing flights, whereas for the nearest approach distance, the point in the season also

Table 1 Relative Variable Importance (RVI) and parameter estimates (beta coefficients) for different independent variables including the six playback types (species) separately, tree- and shrub height, and vegetation cover of the territory in relation to behavioural response of male Blackcaps in terms of number of song strophes, crossing flights, and nearest approach distance towards the playback

	# Song strophes		Crossing flights		Min. distance		# Unstim. song strophes	
	Estimate	RVI	Estimate	RVI	Estimate	RVI	Estimate	RVI
SA	5.11270	0.85	1.30794	1.00	4.43053	1.00	0.005	0.005
SB	3.03223	0.85	− 1.03552	1.00	2.21548	1.00	0.005	0.005
SCU	3.14526	0.85	− 1.48814	1.00	7.32894	1.00	0.005	0.005
SCO	2.13758	0.85	− 1.42815	1.00	5.08107	1.00	0.005	0.005
SN	2.71127	0.85	− 1.51287	1.00	5.67678	1.00	0.005	0.005
SCANT	1.23084	0.85	− 1.60181	1.00	7.79622	1.00		0.005
Tree height	− 0.07650	0.47	0.00673	0.28	0.01641	0.26	0.06795	0.99
Scrub height	0.19801	0.61	− 0.04821	0.47	− 0.16095	0.34	0.30114	1.00
Veg. cover	0.03283	0.83	0.00665	0.59	− 0.00814	0.28	− 0.00496	0.31
Date	Spline	0.80	Spline	0.38	Spline	1.00	Spline	1.00

Additionally, parameter estimates for vegetation parameters are given for male song not stimulated by the playback. Important results based on RVI (≥ 0.8) are in bold

SA=*Sylvia atricapilla*, SB=*S. borin*, SCU=*S. curruca*, SCO=*S. communis*, SN=*S. nisoria*, and SCANT=*S. cantillans*

Fig. 1 Number of song strophes of male Blackcaps when reproducing song of male conspecifics SA = *Sylvia atricapilla*, and of males of five other *Sylvia* Warbler species, including SB = *S. borin*, SCU = *S. curruca*, SCO = *S. communis*, SN = *S. nisoria*, and SCANT = *S. cantillans*. Given is average (\pm standard error) number of song strophes in 2 min for each playback species and the average unstimulated strophe production (prior to the first playback challenge) is indicated by a dashed line and the standard errors by dotted lines. Sample sizes for each playback type are given in parenthesis

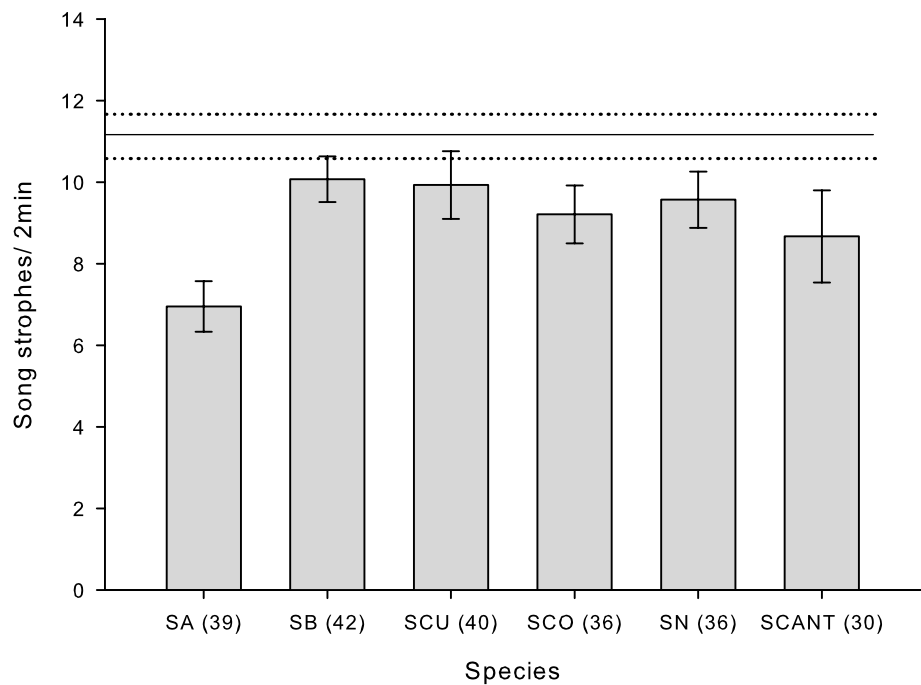


Table 2 Results of pairwise comparisons based on parameter estimates and their 95% confidence intervals of three different behavioural response parameters of male Blackcaps towards simulated intruders using playback presentations of song of conspecifics (SA = *Sylvia atricapilla*) and five different *Sylvia* Warbler species, including SB = *S. borin*, SCU = *S. curruca*, SCO = *S. communis*, SN = *S. nisoria*, and SCANT = *S. cantillans*

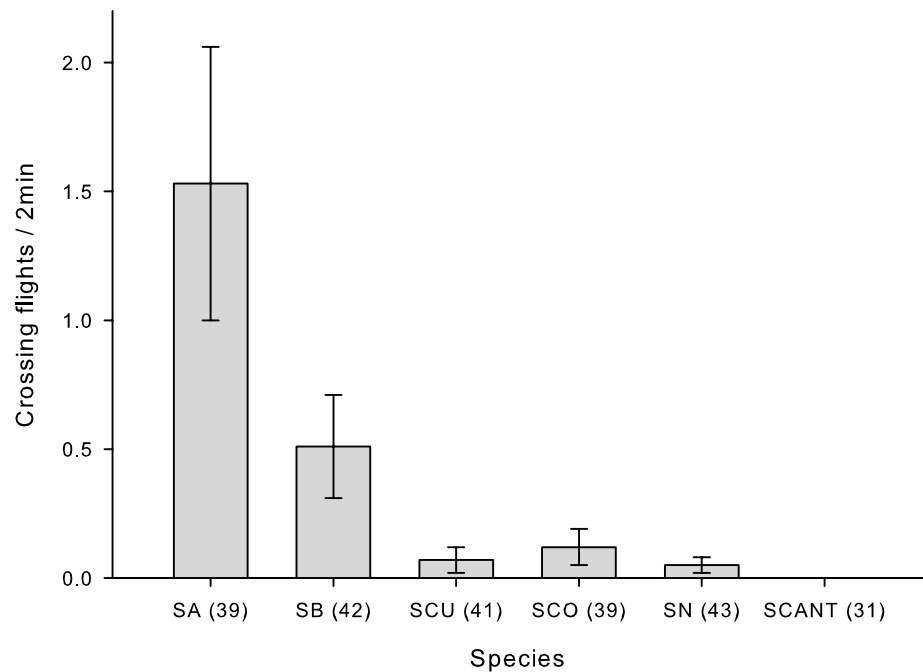
	SA	SB	SCU	SCO	SN	SCANT
(a)						
SA	0	–	–	–	–	+
SB	–	0	–	–	–	–
SCU	–	–	0	–	–	–
SCO	+	–	–	0	–	–
SN	+	–	–	–	0	–
SCANT	+	–	–	–	–	0
(b)						
SA	0	+	+	+	+	+
SB	+	0	–	–	–	–
SCU	+	–	0	–	–	–
SCO	+	–	–	0	–	–
SN	+	–	–	–	0	–
SCANT	+	+	–	–	–	0
(c)						
SA	0	–	+	–	–	+
SB	–	0	+	+	+	+
SCU	+	+	0	–	–	–
SCO	–	+	–	0	–	–
SN	–	+	–	–	0	–
SCANT	+	+	–	+	–	0

Responses of male Blackcaps are separated into (a) song response in terms of number of song strophes produced during the playback (2 min) and direct defence behaviours in terms of (b) crossing flights above the speaker, and (c) nearest approach distance – minimal distance to the speaker. Significant (non-overlapping interval ranges between each pair of species) differences in the responses are indicated by +

seems likely to be included the best model (Table 1). Post hoc comparisons, using the overlap in 95% confidence intervals, again suggested that this species difference was mainly

due to the different response to conspecifics in comparison to other species (Fig. 2). The number of crossing flights occurred significantly more often towards conspecifics

Fig. 2 Number of crossing flights over the playback speaker when reproducing song of male conspecifics SA = *Sylvia atricapilla*, and of males of five other *Sylvia* Warbler species, including SB = *S. borin*, SCU = *S. curruca*, SCO = *S. communis*, SN = *S. nisoria*, and SCANT = *S. cantillans*. Given is average (\pm standard error) number of crossing flights in 2 min for each species. Sample sizes are given in parenthesis

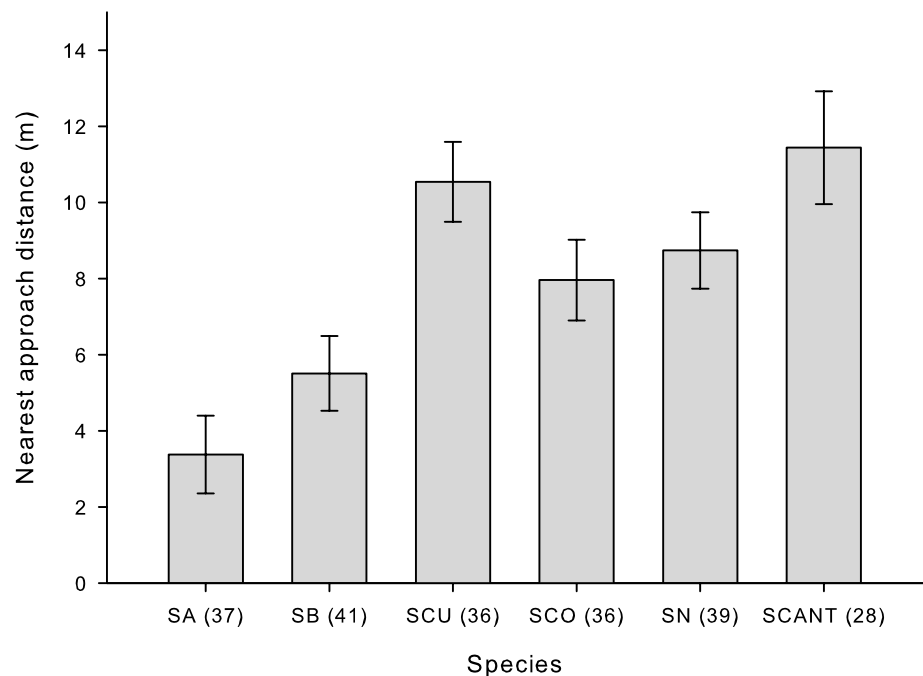


than any other species (Table 2b) and these differences are obvious from both directions (Table 2b). All other pairwise comparisons were found to be insignificant, except between the Garden Warbler and the Subalpine Warbler. Blackcaps perform more crossing flights towards the Garden Warbler than towards the Subalpine Warbler (Fig. 2, Table 2b).

Similarly, male Blackcaps approached significantly closer to conspecific song than to the song of all other species except the Garden Warbler (Fig. 3). Pairwise results

also support this finding that there was a significant difference between the proximity of male Blackcaps to Lesser Whitethroat and Subalpine Warbler, but not to the Garden Warbler, Common Whitethroat, and Barred Warbler (Table 2c). Furthermore, the approach distance of Blackcaps further differs towards the four other species, but not the Garden Warbler. Thus, the approach response to Garden Warblers was as close as the response to conspecifics.

Fig. 3 Nearest approach distance towards the playback speaker when reproducing song of male conspecifics SA = *Sylvia atricapilla*, and of males of five other *Sylvia* Warbler species, including SB = *S. borin*, SCU = *S. curruca*, SCO = *S. communis*, SN = *S. nisoria*, and SCANT = *S. cantillans*. Given is the average (\pm standard error) nearest approach distance observed in 2 min, separately for each species. Sample sizes are given in parenthesis



In terms of habitat parameters, the results reveal low RVI values. For crossing flights as well as the nearest approach distance to the speaker, habitat parameters are uncertain or unlikely to feature in the best model. The highest RVI value was found for crossing flights in relation to vegetation cover, but an RVI value of 0.59 is still too low to derive any implications as a predictor for the crossing flight frequency.

Finally, according to the RVI value, season also seems to be included in the best model, at least for the nearest approach distance to the simulated intruder (Table 1). Male Blackcaps approached closer to the speaker later in the season. Crossing flights, however, seemed to be independent of the point in the season.

The crossing flight number and nearest approach distance to the playback revealed high RVI values for species (for both $RVI = 1$, Table 1), but for the nearest approach distance, season also seemed to yield the highest relative importance values ($RVI = 1$).

The relative variable importance of the vegetation parameters in relation to crossing flights and the nearest approach distance is low (Table 1), and as such, these do not seem to feature in the best model.

Accordingly, the reaction, including the song and physical defence of male Blackcaps, is determined by the playback type (species), whereas vegetation (i.e., vegetation cover) only influences the song reaction of males.

Discussion

We found differences in the interspecific response to other species in terms of the song strophes produced. A territorial response in terms of song has been already demonstrated for Blackcaps (Leedale et al. 2015; Linossier et al. 2015), but, here, we can also show that the song strophe number varies depending on the vegetation features of the territory. In contrast, the frequency and proximity of approaches to intruders depended on the intruder species, but did not vary in relation to the vegetation characteristics of territories. Our results further suggest that the territorial response is far more intense in relation to conspecifics than other species and is least intense in relation to the Subalpine Warbler, which is not coexisting.

In response to territorial intruders, birds are usually thought to increase their song rate (Cuthill and MacDonald 1990; Nelson and Poesel 2011; Szymkowiak and Kuczyński 2017). In contrast to this assumption, our results (in terms of counter-singing during playback stimulations) revealed a reduction in song production (Fig. 1, Table 1). The high RVI values suggest that variation in male song response depends to a large extent on the species and a reduction in the number of song strophes is in fact most evident in relation to conspecifics (Fig. 1). Post hoc comparisons suggested that

the number of song strophes produced towards conspecifics was significantly reduced in comparison to the Common Whitethroat, Barred, and Subalpine Warblers, whereby the difference to the Subalpine Warbler is even obvious from both directions (see Table 2a). However, the song reaction, namely the reduction in song strophes, was similarly strong and did not differ for the Garden Warbler and Lesser Whitethroat. The results of this study are, therefore, in line with our predictions, which, considering habitat requirements, song similarity, and relatedness (see “Materials and methods” section), assumes that male Blackcap territorial reactions would be the strongest towards conspecifics (our positive control), regarding heterospecifics, almost as strong towards the Garden Warbler, more or less intermediate to the three other heterospecific species. Finally, weakest reaction should be shown towards the Subalpine Warbler (representing our negative control). As the Subalpine Warblers do not occur in the study area, our Blackcap population should not be familiar with this species. The next possible breeding locality of Subalpine Warblers is in fact about 400 km away in north east Italy. Thus, this species do not represent a competitor for reproductive resources. In this context, it might be interesting to see whether male Blackcaps overlapping with Subalpine Warblers in breeding areas would reveal a stronger territorial reaction (Brambilla et al. 2007, 2008a).

Why should males reduce their song rate during playbacks? One explanation could be that males may need to determine the characteristics of an intruder acoustically, which may require them to listen to information transferred by the intruder (given that no visual cues were included in our set-up). This identification process may include accessing the precise location, as well as the identity of the intruder, which may then be used to evaluate its importance as a competitor. The information content to be assessed may be even larger in the case of intraspecific intruders, including information about more specific features. Furthermore, interspecific intruders only create competition for food and nesting resources, whereas in the case of conspecific intruders, there is also competition for mating partners and/or loss of paternity; a complete loss of breeding opportunities may even be a threat. Consequently, in the case of conspecific intruders, gathering information may require more time, resulting in longer periods of listening. Thus, song reduction might be best explained by the time needed for listening before full singing is resumed. There is no indication that male Blackcaps change the song rate or the number of syllables produced and, consequently, would sing faster in response to song playbacks of conspecifics (see Matyjasiak 2005). In the case of playback experiments, the length of this assessment period may be longer than under natural circumstances, given that males lack a visual cue (intruder). Consequently, the lower number of strophes produced during our observations could partly be a result of visually missing an

intruder. In fact, Matyjasiak (2005) showed that also presenting visual cues had an effect on male territorial song and he demonstrated that male Blackcaps are able to link song to the visual cues of a species. Another alternative explanation could be that, for instance, the volume of the playback song in our study was too loud, scaring off territorial males. However, this is unlikely, given that the playbacks reproduced were within the natural range in terms of sound volume and the sound pressure level was the same for the playback song of all species. Finally, as pointed out by Helfer and Osiejuk (2015), there could be also a potential effect of the artificial playback, as the counter-singing overlap is not controlled, which might influence communication differently to real-life intruders. Finally, we cannot exclude another possible factor influencing male song reaction, namely that the response of male Blackcaps is influenced by the nature of the playback design. When males are able to recognize song strophes of several males within the playback sequence, our multi-male design could scare them off. However, the ability to differentiate song strophes of individual males may vary between hetero- and conspecifics which may partly explain the differences found. In spite of that, we chose this multi-male song playback type over single male playbacks to exclude the possibility of pseudo-replication. Variation in song of single intruder males might generate another probably bigger source of variation in the response which we wanted to avoid.

Regarding direct defence reactions to intruders, the results are similar (Figs. 2 and 3). Again, the results are in line with our prediction. The number of crossing flights during the playback presentation towards conspecifics (positive control) was significantly higher than towards all other species and male Blackcaps did not show crossing flights towards Subalpine Warblers (negative control) at all (Fig. 2). However, the number of crossing flights of male Blackcaps tended to be more frequent towards the most similar species, namely the Garden Warbler than the Subalpine Warbler (Table 2b).

In terms of how close a territorial male approaches a simulated intruder, we again found a clear response pattern. Males approached closest to conspecifics and the least closely to Subalpine Warblers (Fig. 3). Post hoc comparisons revealed that the nearest approach distance significantly differed between conspecific song playbacks and the Lesser Whitethroat, as well as the Subalpine Warbler and this holds from both points of view (Table 2c). The fact that the nearest approach distance additionally differs between the Garden Warbler and the four remaining species (Table 2c) again suggests that the male Blackcap response towards Garden Warblers is more similar to their conspecific response than to the others (Fig. 3).

Assuming that the reactions observed in this study indicate the degree of competition between Blackcaps and different heterospecific species, they can be ranked as follows: the

strongest response, as already mentioned, was found towards conspecifics, but Blackcaps also show interspecific defence behaviour towards Garden Warblers (Matyjasiak 2005); a weaker response was elicited by the Lesser Whitethroat, whereas the two remaining species, namely the Common Whitethroat and the Barred Warbler, provoked even less of a response and the least response was observed against the Subalpine Warbler. This result is in line with several possible causal explanations. Male defence intensity, for instance, seems to be partly reflected in phylogenetic relatedness (Böhning-Gaese et al. 2003) as the Garden Warbler is the closest relative to the Blackcap. However, the Common Whitethroat would be the second-closest relative, whereas the Lesser Whitethroat and Barred Warbler are phylogenetically more distant. Considering the descriptive information available regarding habitat requirements (see “Materials and methods” section), habitat similarity and, hence, niche overlap, may also somehow explain the results, given that Blackcaps and Garden Warblers inhabit similar habitats, whereas Common and Lesser Whitethroats, as well as Barred Warblers, usually inhabit drier or more open localities (Glutz von Blotzheim 1991). Furthermore, our findings regarding fighting asymmetries partly explain the results, given that the Barred Warbler, the larger and hence, less vulnerable species, is less likely to be approached by male Blackcaps.

Finally, incorrect species identification may also influence the territorial response (Murray 1981). In this context, song similarity between species could also partly explain a territorial response. The song of different warbler species is quite similar, so song response between related species is not surprising. However, given that we do not know which criteria are important for species identification, judging similarities on the basis of physical acoustic parameters would probably be subjective.

In conclusion, the degree of interspecific competition seems to be related to several factors, but at this point, it is not possible to separate the respective contributions of these evolutionary forces to the ultimate outcome.

Finally, our results also suggest that the habitat features of a territorial bird can be important in relation to the intruder response, which has been also demonstrated in a different set of warbler species inhabiting reed beds (Hoi et al. 1991). Hoi et al. (1991) showed that territory occupancy is partly independent of fighting asymmetries and depends on the habitat requirements of a given species. In this paper, we can additionally show that habitat may influence the type of territorial behaviour. In particular, we can show that performing low-risk defence (reflected by number of song strophes) seems to be related to the vegetation cover (Table 1). First, unstimulated male song seems to be related to vegetation parameters, namely tree height (Table 1); in which males with higher trees in their territories sing more strophes. Second, also when challenging a male with an intruder song,

the male song response is elevated in territories with higher vegetation cover. In such a situation, Blackcaps even seem to change their song structure (Leedale et al. 2015). In this context, Linossier et al. (2015) found that Blackcap song consists of two parts: whereby the introductory (warble part) seems to be directed towards females and the second, so-called whistle part, is directed towards competitors. In response to an intraspecific intruder, male Blackcaps, not surprisingly, can even lengthen the whistle part of their song (Leedale et al. 2015).

In contrast, it seems that performing high-risk behaviour (e.g., physically approaching an intruder) is not associated with the vegetation parameters investigated. The decision to attack might probably more likely depend on the threat an intruder constitute, rather than environmental cues. For instance, male physical defence was mainly observed towards conspecifics and with them the threat reaches a higher level (risk of losing the female partner or paternity), and in that moment, the importance of vegetation features of the territory should be irrelevant. Furthermore, during an attack or defence approach, males might be focused on that and less sensitive to circumstances in the surrounding, like environmental cues.

Future studies are necessary to examine the song response in more detail, e.g., changes over time and the latency of response. It may also be important to investigate whether (and which) structural changes in the song response might occur in relation to interspecific contests, which may shed light on the parameters that are important for species identification. Finally, it would be useful to investigate how the breeding density of different competing species influences the intensity of interspecific aggression.

Acknowledgements This study was funded by Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic and the Slovak Academy of Sciences (VEGA Grant Nr. 2/0097/16).

Compliance with ethical standards

Ethical statement Experiments comply with the current laws of the Slovak Republic.

References

- Apol CA, Sturdy CB, Proppe DS (2018) Seasonal variability in habitat structure may have shaped acoustic signals and repertoires in the black-capped and boreal chickadees. *Evol Ecol* 32:57–74. <https://doi.org/10.1007/s10682-017-9921-4>
- Bairlein F, Berthold P, Querner U, Schlenker R (1980) Die Brutbiologie der Grasmücken *Sylvia atricapilla*, *borin*, *communis* und *curruca* in Mittel- und N-Europa. *J Ornithol* 121:325–369. <https://doi.org/10.1007/BF01643331>
- Balsby TJS, Dabelsteen T (2003) Male calling between courtship sequences in Whitethroats: a way to counter intrusions from neighbouring rivals. *Behav Process* 63:149–157. [https://doi.org/10.1016/S0376-6357\(03\)00052-4](https://doi.org/10.1016/S0376-6357(03)00052-4)
- Barton K (2018) Package ‘MuMIn’. <https://cranr-project.org/web/packages/MuMIn/MuMIn:18>
- Bartsch C, Weiss M, Kipper S (2012) The Return of the intruder: Immediate and later effects of different approach distances in a territorial songbird. *Ethology* 118:876–884. <https://doi.org/10.1111/j.1439-0310.2012.02081.x>
- Bergmann HH, Helb HW (1982) Stimmen der Vögel Europas, BLV Verlagsgesellschaft, München
- Billerman SM, Carling MD (2017) Differences in aggressive responses do not contribute to shifts in a sapsucker hybrid zone. *Auk* 134:202–214. <https://doi.org/10.1642/AUK-16-142.1>
- Blackburn TM, Lawton JH, Gregory RD (1996) Relationships between abundances and life histories of British birds. *J Anim Ecol* 65:52–62. <https://doi.org/10.2307/5699>
- Böhning-Gaese K, Schuda MD, Helbig AJ (2003) Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *J Evol Biol* 16:956–965. <https://doi.org/10.1046/j.1420-9101.2003.00605.x>
- Brambilla M, Reginato F, Guidali F (2007) Habitat use by Moltoni's Warbler *Sylvia cantillans moltonii* in Italy. *Ornis Fenn* 84:91–96
- Brambilla M, Janni O, Guidali F, Sorace A (2008a) Song perception among incipient species as a mechanism for reproductive isolation. *J Evol Biol* 21:651–657. <https://doi.org/10.1111/j.1420-9101.2008.01523.x>
- Brambilla M, Vitulano S, Spina F, Baccetti N, Gargallo G, Fabbri E, Guidali F, Randi E (2008b) A molecular phylogeny of the *Sylvia cantillans* complex: Cryptic species within the Mediterranean basin. *Mol Phylogenet Evol* 48:461–472. <https://doi.org/10.1016/j.ympev.2008.05.013>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Catchpole CH, Slater PJB (2008) Bird song. Biological themes and variations, 2 edn. Cambridge University Press, Cambridge
- Ceresa F, Belda EJ, Gómez J, Miñana JJ, Soler L, Villarroja J, Monrós JS (2016) Differences in time and space use between two sympatric *Acrocephalus* warblers with similar diets. *Bird Study* 63:172–180. <https://doi.org/10.1080/00063657.2016.1182466>
- Cody ML (1969) Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* 71:222–239. <https://doi.org/10.2307/1366300>
- Cramp S, Brooks DJ (1992) The birds of the Western Palearctic, vol VI. Warblers. Oxford Univ. Press, Oxford
- Cuthill IC, Macdonald WA (1990) Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. *Behav Ecol Sociobiol* 26:209–216. <https://doi.org/10.1007/BF00172088>
- Elle O (2003) Quantifizierung der integrativen Wirkung von Ökotonen am Beispiel der Habitatwahl der Mönchsgrasmücke und der Dorngrasmücke (*Sylvia atricapilla* und *S. communis*, Sylviidae). *J Ornithol* 144:271–283. <https://doi.org/10.1046/j.1439-0361.2003.03019.x>
- Garcia EFJ (1981) An experimental and observational study of interspecific territoriality between the blackcap *Sylvia atricapilla* (Linnaeus) and the Garden Warbler *Sylvia borin* (Bodeart). D. Phil thesis, University of Oxford
- Gil D (1997) Increased response of the short-toed treecreeper *Certhia brachydactyla* in sympatry to the playback of the song of the common treecreeper *C. familiaris*. *Ethology* 103:632–641. <https://doi.org/10.1111/j.1439-0310.1997.tb00174.x>
- Glutz von Blotzheim UNH (1991) Handbuch der Vogel Mitteleuropas, Bd. 12/II. Passeriformes, (3. Teil) Sylviidae. AULA Verlag, Wiesbaden

- Grether GF, Losin N, Anderson CN, Okamoto K (2009) The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biol Rev* 84:617–635. <https://doi.org/10.1111/j.1469-185X.2009.00089.x>
- Grim T (2008) Are blackcaps (*Sylvia atricapilla*) defending their nests also calling for help from their neighbours? *J Ornithol* 149:169–180. <https://doi.org/10.1007/s10336-007-0257-7>
- Helfer B, Osiejuk TS (2015) It takes all kinds in acoustic communication: a new perspective on the song overlapping phenomenon. *Ethology* 121:315–326. <https://doi.org/10.1111/eth.12356>
- Hof D, Hazlett N (2010) Low-amplitude song predicts attack in a North American wood warbler. *Anim Behav* 80:821–828. <https://doi.org/10.1016/j.anbehav.2010.07.017>
- Hoi H, Winkler H (1994) Predation on nests: a case of apparent competition. *Oecologia* 98:436–440. <https://doi.org/10.1007/BF00324234>
- Hoi H, Eichler T, Dittami J (1991) Territorial spacing and interspecific competition in three species of reed Warblers. *Oecologia* 87:443–448. <https://doi.org/10.1007/BF00634604>
- Hoi H, Kleindorfer S, Ille R, Dittami J (1995) Prey abundance and male parental behaviour in *Acrocephalus* warblers. *Ibis* 137:490–496. <https://doi.org/10.1111/j.1474-919X.1995.tb03258.x>
- Hoi-Leitner M, Nechtelberger H, Hoi H (1995) Song rate as a signal for nest site quality in Blackcaps (*Sylvia atricapilla*). *Behav Ecol Sociobiol* 37:399–405. <https://doi.org/10.1007/BF00170587>
- Holt RD, Kotler BP (1987) Short-term apparent competition. *Am Nat* 130:412–430. <https://doi.org/10.1086/284718>
- Huntingford FA, Turner AK (1987) *Animal conflict*. Chapman and Hall, London
- Jonart LM, Hill GE, Badyaev AV (2007) Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. *Anim Behav* 74:1675–1681. <https://doi.org/10.1016/j.anbehav.2007.03.012>
- Jones JA, Tisdale AC, Tucker JL, Bakermans MH, Larkin JL, Smalling CG, Siefferman L (2016) A case of mistaken identity: understanding the stimulus of agonism between two wood warblers. *Anim Behav* 114:81–91. <https://doi.org/10.1016/j.anbehav.2016.01.024>
- Kitowski I (2003) Inter-specific and temporal differences in brood defence of adult Montagu's Harriers *Circus pygargus* and Marsh Harriers *Circus aeruginosus* against Foxes *Vulpes vulpes* and avian intruders during the post-fledging dependency period. *Biota* 4:57–66
- Lancot RB, Sandercock BK, Kempnaers B (2000) Do male breeding displays function to attract mates or defend territories? The explanatory role of mate and site fidelity. *Waterbirds* 23:155–164
- Leedale AE, Collins SA, de Kort SR (2015) Blackcaps (*Sylvia atricapilla*) increase the whistle part of their song in response to simulated territorial intrusion. *Ethology* 121:403–409. <https://doi.org/10.1111/eth.12349>
- Linhardt P, Slabbekoorn H, Fuchs R (2012) The communicative significance of song frequency and song length in territorial chiffchaffs. *Behav Ecol* 23:1338–1347. <https://doi.org/10.1093/beheco/ars127>
- Linossier J, Courvoisier H, Aubin T (2015) The two parts of the blackcap song: acoustic analysis and male responses to playbacks. *Behav Process* 121:87–92. <https://doi.org/10.1016/j.beproc.2015.10.007>
- Losin N, Drury JP, Peiman KS, Storch C, Grether GF (2016) The ecological and evolutionary stability of interspecific territoriality. *Ecol Lett* 19:260–267. <https://doi.org/10.1111/ele.12561>
- Martin PR, Ghalambor CK (2014) When David beats Goliath: the advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLoS ONE* 9:e108741. <https://doi.org/10.1371/journal.pone.0108741>
- Matyjasiak P (2005) Birds associate species-specific acoustic and visual cues: recognition of heterospecific rivals by male Blackcaps. *Behav Ecol* 16:467–471. <https://doi.org/10.1093/beheco/ari012>
- Mockford EJ, Marshall RC, Dabelsteen T (2011) Degradation of rural and urban great tit song: Testing transmission efficiency. *PLoS ONE* 6:e28242. <https://doi.org/10.1371/journal.pone.0028242>
- Morales MB, Casas F, García de la Morena E, Ponjoan A, Calabuig G, Martínez-Padilla J, García JT, Mañosa S, Viñuela J, Bota G (2014) Density dependence and habitat quality modulate the intensity of display territory defence in an exploded lekking species. *Behav Ecol Sociobiol* 68:1493–1504. <https://doi.org/10.1007/s00265-014-1758-z>
- Murray BG (1981) The origin of adaptive territorialism. *Biol Rev* 56:1–22
- Nelson DA, Poesel A (2011) Song length variation serves multiple functions in the white-crowned sparrow. *Behav Ecol Sociobiol* 65:1103–1111. <https://doi.org/10.1007/s00265-010-1120-z>
- Osiejuk TS, Kuczyński L (2000) Song functions and territoriality in Eurasian Treecreeper *Certhia familiaris* and Short-toed Treecreeper *Certhia brachydactyla*. *Acta Ornithol* 35:109–116
- Payevski VA (1999) Breeding biology, morphometrics, and population dynamics of *Sylvia* warblers in the Eastern Baltic. *Avian Ecol Behav* 2:19–50
- Port M, Johnstone RA (2013) Facing the crowd: Intruder pressure, within-group competition, and the resolution of conflicts over group-membership. *Ecol Evol* 3:1209–1218. <https://doi.org/10.1002/ece3.533>
- R Core Team (2016) A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. <https://www.r-project.org/>
- Riou S, Combreau O (2014) Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*. *J Ornithol* 155:959–967. <https://doi.org/10.1007/s10336-014-1082-4>
- Samplonius JM (2019) Interspecific aggression declines seasonally in breeding great tits *Parus major*. *Ethology* 125:159–163. <https://doi.org/10.1111/eth.12830>
- Scordato ESC (2017) Geographical variation in male territory defence strategies in an avian ring species. *Anim Behav* 126:153–162. <https://doi.org/10.1016/j.anbehav.2017.01.001>
- Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. *Anim Behav* 78:1281–1292. <https://doi.org/10.1016/j.anbehav.2009.08.011>
- Slevin MC, Raybuck DW, Boves TJ (2016) Prothonotary Warblers (*Protonotaria citrea*) Break their beaks during attacks on wooden conspecific decoys. *Wilson J Ornithol* 128:193–197. <https://doi.org/10.1676/1559-4491-128.1.193>
- Szymański P, Antczak M (2013) Structural heterogeneity of linear habitats positively affects Barred Warbler *Sylvia nisoria*, Common Whitethroat *Sylvia communis* and Lesser Whitethroat *Sylvia curruca* in farmland of Western Poland. *Bird Study* 60:484–490. <https://doi.org/10.1080/00063657.2013.840555>
- Szymkowiak J, Kuczyński L (2017) Song rate as a signal of male aggressiveness during territorial contests in the wood Warbler. *J Avian Biol* 48:275–283. <https://doi.org/10.1111/jav.00969>
- Thielcke G, Wüstenberg K, Becker PH (1978) Reaktionen von Zilpzalp und Fitis (*Phylloscopus collybita*, *Ph. trochilus*) auf verschiedene Gesangsformen des Zilpzalps. *J Ornithol* 119:213–226. <https://doi.org/10.1007/BF01644590>
- Wood SN (2017) Generalized additive models: an Introduction with R, 2nd edn. Chapman and Hall/CRC texts in statistical science.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.