



## Association between mowing regimes and abundance of the Bull Bush Cricket (*Polysarcus denticauda*)

Susanne Hermann<sup>1</sup> | Peter Detzel<sup>2</sup> | Thomas Bamann<sup>3</sup> | Nils Anthes<sup>4</sup>

<sup>1</sup>Gewerbestr. 64, 79194 Gundelfingen, Deutschland

<sup>2</sup>Zum Langwieser See 13, 70599 Stuttgart, Deutschland

<sup>3</sup>Regierungspräsidium Tübingen, Konrad-Adenauer-Str. 20, 72072 Tübingen, Deutschland

<sup>4</sup>Animal Evolutionary Ecology, Institute of Evolution and Ecology, University of Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany

Correspondence: Susanne Hermann; e-mail: susanne.hermann@posteo.de  
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### Abstract

This study investigates whether the abundance of the critically endangered Bull Bush Cricket, *P. denticauda*, associates with mowing dates in preceding years, the availability of uncut refuge patches, or the coverage of open soil and matted vegetation cover. We used a correlative approach in populations spanning from small – and presumed “marginal” – to individual-rich – and presumed “stable” – local populations, as derived from recent surveys. *P. denticauda* numbers were determined via repeated acoustical surveys along predefined transects in 2020. Mowing regimes in 2018 were reconstructed from own observations in 2020 and farmer judgement. The cover of open soil and matted vegetation was measured using a wooden frame with 40 sticks contacting the meadow ground. Additionally, we compared estimated population sizes derived from an acoustical transect survey to those from a capture-mark-recapture analysis of this species. This analysis revealed an underestimation of the population size of *P. denticauda* by a factor of 1.36 when conducting an acoustical transect estimation. The abundance of *P. denticauda* did not vary significantly with previous mowing dates or the availability of uncut refuge patches and peaked at intermediate values of open soil and matted vegetation cover. We found a high estimated mean effect size for the availability of uncut refuges and propose to implement these as core conservation strategy for the Bull Bush Cricket. Further, we debate how mowing effects may have gone undetected given substantial population fluctuations of *P. denticauda* and discuss how the negative effect of postponed mowing on the habitat suitability and there-

fore survival of *P. denticauda* can be overcome with yearly alternating implementation of uncut refuge patches and an early pasture as alternative management practice.

**Keywords:** grassland management, matted soil cover, mowing, population size species conservation

## Zusammenfassung

**Zusammenhang zwischen Mahdregimes und der Abundanz der Wantschaftschrecke (*Polysarcus denticauda*).** In dieser Studie wurden erstmals Abundanzen der stark gefährdeten Wantschaftschrecke, *P. denticauda*, in Zusammenhang mit späteren ersten Mahdzeitpunkten und der Verfügbarkeit von Mahdstreifen als Rückzugsraum sowie dem Prozentanteil offenen und verfilzten Bodens gebracht. Für den korrelativen Ansatz wurden 15 Populationen zwischen kleinen – und angenommen „marginalen“ – bis hin zu großen – und angenommen „stabilen“ – Lokalpopulationen aus jüngst erhobenen Erfassungen vorausgewählt. Im Jahr 2020 wurden die aktuellen Wantschaftschrecken-Individuenzahlen durch wiederholte akustische Zählungen entlang vordefinierter Transekte erfasst. Mahdregimes für das Jahr 2018 wurden anhand Befragungen lokaler Landwirte und eigener Beobachtungen im Jahr 2020 rekonstruiert. Die Bodenbedeckung (Offenbodenstellen, verfilzter Boden) wurde für jeden Standort mithilfe eines Holzrahmens mit 40, auf den Wiesenboden auftreffenden Stäben ermittelt. Darüber hinaus werden in dieser Studie abgeleitete Populationsgrößen aus akustischen Transekterfassungen mit einer Fang-Markierung-Wiederfang-Analyse der Wantschaftschrecke verglichen. Es resultierte eine Unterschätzung der Wantschaftschrecken-Populationsgröße mit einem Faktor von 1.36 für akustische Transekterfassungen. *P. denticauda*-Häufigkeiten aus dem Jahr 2020 stiegen nicht signifikant mit einem späteren ersten Mahdzeitpunkt und der Verfügbarkeit von Mahdstreifen an, und zeigten höchste Werte bei intermediären Prozentwerten verfilzten und offenen Bodens. Unabhängig des ersten Mahdzeitpunktes und obgleich diese Studie statistisch limitiert ist, wurde eine hohe Effektstärke auf die Wantschaftschrecken-Populationsgröße bei Flächen mit Mahdstreifen nachgewiesen. Daher schlagen wir jährlich alternierende Mahdstreifen als Haupt-Schutzstrategie für die Wantschaftschrecke vor. Es wird darauf eingegangen, wie Mahd-Effekte durch die natürlichen starken Populationsschwankungen von *P. denticauda* verborgen bleiben. Darüber hinaus diskutieren wir inwiefern sich späterer Mahdzeitpunkte negativ auf die Habitateignung und daher dem Überleben der Wantschaftschrecke auswirken und wie dies durch die Umsetzung von jährlich alternierenden Mahdstreifen und einer Vorweide als alternative Bewirtschaftungsform überwunden werden kann.

**Schlüsselwörter:** Artenschutz, Mahd, Populationsgröße, Verfilzung, Wiesenbewirtschaftung

## Introduction

Species-rich meadows have experienced a massive change in management since the agricultural industrialization in Central Europe, with more uniform and typically earlier and more frequent harvesting schedules leading to a severe insect biodiversity decline in these ecosystems (Hendrickx et al. 2007, Stoate et al. 2009, Habel et al. 2013, Hallmann et al. 2017, Dengler & Tischew 2018, Sánchez-Bayo & Wyckhuys 2019, Fartmann et al. 2021). Orthopterans are particularly sensitive to land-use changes and therefore represent an ideal indicator group to study the effect of habitat management on insect abundance (Poniatowski & Fartmann 2008, Saha & Haldar 2009, Poniatowski & Fartmann 2010, Fartmann et al. 2012).

Earlier work proposed to delay first mowing dates from early to mid-summer to maintain high orthopteran abundances in grasslands (Buri et al. 2013). However, routine late mowing also unfolds negative effects on vegetation structure, favoring grass-dominant plant communities that reduce habitat suitability for orthopterans (Reiter et al. 2004, Briemle & Aulendorf 2007, Löffler & Fartmann 2017). This effect is enhanced by nutrient enrichment from local and atmospheric sources and can result in an increasingly dense grass litter, which suppresses germination of herbaceous plants and precludes orthopterans from accessing bare ground for egg deposition in the upper soil layers (Fartmann & Mattes 1997, Schuhmacher & Fartmann 2003, Reiter et al. 2004, Briemle & Aulendorf 2007, Fartmann et al. 2012). The coverage by organic plant material increases shading, reduces warming and evaporation of the topsoil layer, and thus decreases the chance of successful embryogenesis, leading to lower orthopteran abundance in the subsequent generation (Oppermann 1987, Facelli & Pickett 1991, Van Wingerden et al. 1992, Van Wingerden et al. 1993).

To strike a balance between late harvest times and long-term maintenance of the habitat suitability, compromise suggestions propose leaving uncut refuges for the field fauna (Buri et al. 2013, Kühne et al. 2015, Kaláb et al. 2020). Both management regimes have recently been confirmed to maintain orthopteran functional diversity and to increase orthopteran density and species richness (Buri et al. 2013, Kaláb et al. 2020). Yet, their direct and indirect effects on individual species of particular conservation concern have rarely been explored.

Many studies to date have focused on the impact of management regimes on entire orthopteran communities (Humbert et al. 2012, Buri et al. 2013, Kaláb et al. 2020). However, this approach may fail to reveal species-specific susceptibilities to different management regimes. Such knowledge is crucial, however, when management targets rare and vulnerable species (Chisté et al. 2016). The current work thus focuses on a grasshopper species of particular conservation concern, the Bull Bush Cricket, *Polysarcus denticauda*.

*P. denticauda* is the biggest and heaviest bush cricket native to Central Europe (♀: 24-35 mm, ♂: 25-44 mm) and inhabits seminatural meadows with tall and lush vegetation in extensively mown grasslands (mainly belonging to the plant association

Arrhenatheretum elatioris) and non-grazed calcareous grasslands (mainly Mesobrometum). It used to be widely distributed in extensively cultivated grasslands of the Swabian Alb but is now considered “Endangered” in Baden-Württemberg. Today, the main occurrence in Germany lies in Baden-Württemberg in the region of the Swabian Alb (Detzel 1998, Maas et al. 2011, Detzel et al. 2022). Given its large size, inert behavior towards disturbance, and low dispersal ability (Licznier 1999), this flightless cricket is highly susceptible to mowing regime changes in extensively managed grasslands. While postponed mowing dates and uncut refuges are established standards for *P. denticauda* conservation management (Detzel 1998), their effect on local abundance has not yet been examined. Therefore, this study investigated whether variation in *P. denticauda* abundances is associated with differences in first mowing dates and the presence of uncut refuges.

*P. denticauda* lays its eggs in bare ground and therefore requires an accessible soil surface with partially loose soil for a successful reproduction. Thus, it serves as an ideal study species to investigate whether abundance is related to the proportion of open soil versus impenetrable matted vegetation cover.

Given that *P. denticauda*’s reproductive success is dependent on many extrinsic factors like temperature, precipitation, late frost and drought it shows strong annual fluctuations in population size, combined with a largely biennial development cycle (Ingrisch 1986, Detzel 1998, Löderbusch 2015, Köhler 2017, Krech & Köhler 2021), “snapshot” data from single study years provide incomplete information. Thus, we used recent population size data of *P. denticauda* as prior estimates to select study populations in 2020, and reconstructed the management regimes in the year 2018 to get best possible estimates of management effects on *P. denticauda*’s abundance. We then used a correlative approach to link *P. denticauda* abundances in 2020 to mowing regimes in the year 2018 as well as to the proportional coverage of open soil and matted soil cover. Study populations were selected to span from small – and presumed “marginal” – to rather large – and presumed “stable” – local populations, as derived from recent surveys. We predicted that later first mowing and the presence of uncut refuges in 2018 positively affected *P. denticauda* abundance in 2020. Moreover, we hypothesized that increased open soil coverage promoted higher *P. denticauda* abundances, and a reverse pattern for matted vegetation cover. We finally report the results of a complementary survey in a single population to assess consistence of local population size estimates derived from standardized transect surveys to those obtained from a snapshot capture-mark-recapture survey.

## Material and methods

### Study sites

We based our selection of study sites on survey data from a database containing regional *P. denticauda* records and estimated population size categories since 1903. Population size estimates in this dataset were derived from acoustical sur-

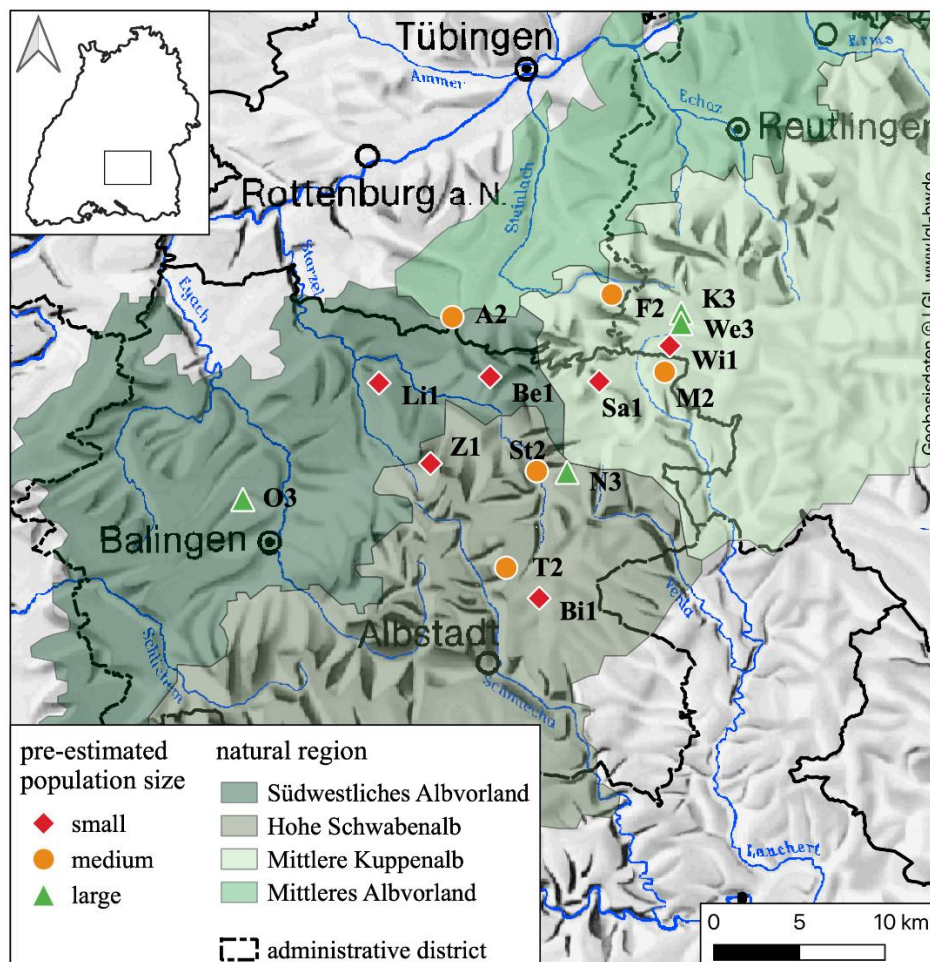
veys in which male individual numbers were counted and then assigned to categories along a semilogarithmic scale (single find = I; 2 - 5 individuals = II; 6 - 10 ind. = III; 11 - 20 ind. = IV; 21 - 50 ind. = V, > 50 ind. = VI). These expert assessments require minimal survey effort, but allow gross judgement of habitat quality or the size and between-year stability populations (Detzel 1992). We grouped these six categories into three populations size classes: small (I, II), medium (III, IV) and large (V, VI), and selected 15 study populations along the northern ridge of the Swabian Alb between Tübingen and Albstadt. For these, most current surveys from 2016, 2018 and 2019 indicated large (n = 4), medium (n = 5) and small (n = 6) population sizes (Table 1).

**Table 1:** The 15 selected study populations and their allocation to their acronym, altitude [m a.s.l.], earlier survey date, initial population size category and size class.

Study population			Recent population size estimates		
Acronym	Site name	altitude [m a.s.l.]	survey date	size category	size class
Be1	Beuren	670	25.06.19	II	
Li1	Lindichstraße, Hechingen	505	30.05.19	I	
Sa1	Salmendingen	815	28.06.19	I	
Wi1	Wilmandingen	827	21.06.19	I	small
Bi1	Bitz	885	25.06.19	II	
Z1	NSG Zellerhorn	838-909	16.07.19	II	
A2	NSG Altwiesen	494	25.06.19	IV	
St2	Starzeln	639-644	25.06.19	III	
F2	NSG Filsenberg	797	26.06.18	III	medium
M2	Melchingen	823	02.07.19	III	
T2	Albstadt-Tailfingen	886	25.06.19	III	
N3	NSG Nähberg	824	23.06.16	VI	
O3	Ostdorf	562	25.06.19	V	
K3	Kirchberg, Sonnenbühl- Undingen	816	25.06.19	VI	large
We3	Weinstein, Sonnenbühl- Undingen	823	23.06.16	VI	

The 15 study sites are situated in the administrative districts Reutlingen, Tübingen and Zollernalbkreis, and cover a gradient from the lower foothills of the Swabian Alb (< 600 m a.s.l.) across the ascending escarpment zones up to the Swabian Alb plateau (~ 900 m a.s.l.) (Table 1, Fig. 1). The area covers four natural regions of the Swabian-Keuper-Lias Plains and the Swabian Alb in the Southwest German Scarpland: “Südwestliches Albvorland”, “Mittleres Albvorland”, “Mittlere Kuppenalb” and “Hohe Schwabenalb” (LUBW 2010). These natural regions reflect local topography that is determined by the northeastern-southwestern oriented escarpment of the Swabian Alb, a Jurassic limestone mountain ridge (Fig. 1).

Given the biennial development of *P. denticauda* (Köhler 2017) we expected individual abundances in 2020 to be most directly affected by mowing regimes (first mowing date and mowing pattern) in 2018. These were reconstructed from on-site mowing surveys in 2020, combined with judgments obtained from local farmers for each site and prescribed management routines for the two nature reserves (NSG Altwiesen, NSG Filsenberg).



**Fig. 1:** Location of the 15 study populations in Baden-Württemberg, Germany. Diamond, dot and triangle symbols indicate initially assumed small, medium and large population size classes respectively (see Tab. 1), background shading the natural regions (LGL, 2017). For further detail link each population by its acronym to Table 1.

## Abundance estimates

### Acoustical transects

In 2020, the population sizes of *P. denticauda* were determined via repeated acoustic surveys along predefined transects in each study site. Because *P. denticauda* inhabits meadows with rather tall vegetation and hides when disturbed, acoustical detection is considered the most accurate survey technique (Detzel 1988, Gardiner et al. 2005, Köhler et al. 2010).

Transects of approximately 300 m length were placed *a priori* to cover all meadow habitat types per site in QGIS (version 3.16.3, QGIS Development Team 2020). Transects were surveyed during the phenological maximum of *P. denticauda* between mid-June (18/06/20) and end-July (30/07/20). For maximum singing activity, surveys were restricted to favorable weather conditions (sunshine, >18°C, low wind speeds). Given that singing activity of *P. denticauda* can substantially vary between days (Schlumprecht & Waeber 2003, Köhler et al. 2010), we surveyed each site on three to seven days and localized each singing male on aerial photographs. For analysis, we only considered the maximum count per study site because acoustic surveys are known to rather underestimate population sizes (Gardiner & Hill 2006, this study).

### Capture-mark-recapture analysis at the study site NSG Zellerhornwiese

The precision of the acoustic transect method was assessed through a capture-mark-recapture analysis at NSG Zellerhorn during the phenological maximum of *P. denticauda* on two consecutive days (27/07/2020 and 28/07/2020). Population size was calculated using the Lincoln-Petersen point-estimation method given that the assumption of a closed population should be near-perfectly fulfilled during that short survey period. We assumed equal trapability of all individuals before and after their first capture (Mares et al. 1981).

The entire study area was extensively scanned for *P. denticauda* during both days. On the first day, all detected bush crickets were marked on the pronotum with a colored pen (Edding 780 creative) and released. On the following day, the procedure was repeated and the number of marked and unmarked individuals recorded. Population size  $N$  and its approximate 95% confidence interval were calculated using the following equations (Mares et al. 1981):

$$N = \frac{(M * C)}{r} \quad (1)$$

$$Var(N) = \frac{(M+1)*(C+1)*(M-r)*(C-r)}{(r+1)^2+(r+2)} \quad (2)$$

$$\text{Upper and lower 95\% CI} = N \pm 1.96 * \sqrt{Var(N)} \quad (3)$$

with  $M$  the number of marked individuals on day 1,  $C$  the number of captured individuals on day 2,  $r$  the number of recaptured individuals on day 2, and  $\text{Var}(N)$  the estimated variance of population size.

### Comparison of abundance estimates

We restricted the comparison of population size estimates derived from the capture-mark-recapture analysis with those derived from acoustic transect surveys on males, given the small female samples from both approaches. For transect counts, we assumed a reliable detection distance of 15 m, and extrapolated the recorded number of males in this corridor to total potential habitat size in the study area as derived from aerial photographs in QGIS. Potential habitats for *P. denticauda* excluded non-habitat areas like forest margins and frequently used pathways.

### **Soil surface measurement**

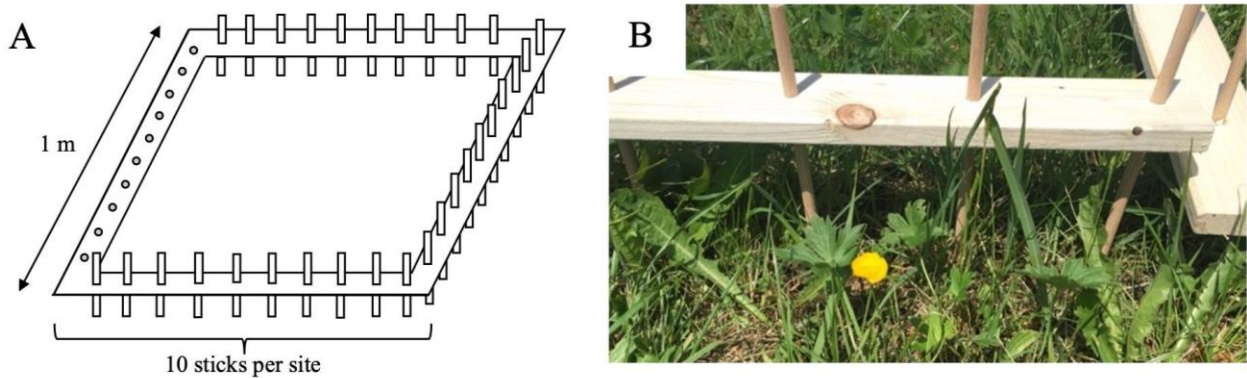
Soil surface coverage was estimated in early June 2020 on each site (except for Ostdorf) within randomly placed 1 m<sup>2</sup> wooden frames. To obtain unbiased cover estimates, frames had 10 sticks mounted on each side, and we counted the number of sticks that touched either the bare soil surface (open soil), or a layer of dead, not mineralized plant and grass matter (matted vegetation) (Fig. 2). This measurement was repeated six to ten times per study site at haphazardly chosen distances perpendicular to a directional transect line across each surveyed meadow. Mean proportional coverages of open soil and matted soil per study site were integrated in the further analysis.

### **Statistical analysis**

To explain variation in 2020 *P. denticauda* abundances from the 2018 mowing regimes, we conducted generalized linear models (GLM) with the glmmTMB package (Brooks et al. 2017) in R, version 4.0.4 (R Development Core Team 2021). Maximum counts of *P. denticauda* per transect were implemented as the response variable. Given substantial over- or underdispersion in some of these models, we consistently used a negative binomial response distribution and a log-link scale. The first model included the estimated mowing dates in 2018 as a continuous predictor, and the presence or absence of uncut refuge patches as a factor predictor. We further included their interaction to check whether the association between *P. denticauda* numbers and mowing dates varied with the presence of uncut refuges.

To provide a standardized indicator for the difference in mean cricket abundance between study sites with and without uncut refuge patches we calculated Hedges'  $d$  with the R package *esc* (Lüdecke 2019). Effect sizes beyond 0.2, 0.5 and 0.8 are typically considered as small, medium or large effects, respectively (Lenhard & Lenhard 2016, Glen 2021).





**Fig. 2:** A: Illustration of the 1 m<sup>2</sup>-wooden frame with 10 wooden sticks mounted on each site for determining the degree of open soil area and matted soil cover. B: Measurement in the field. The wooden sticks contact the soil surface.

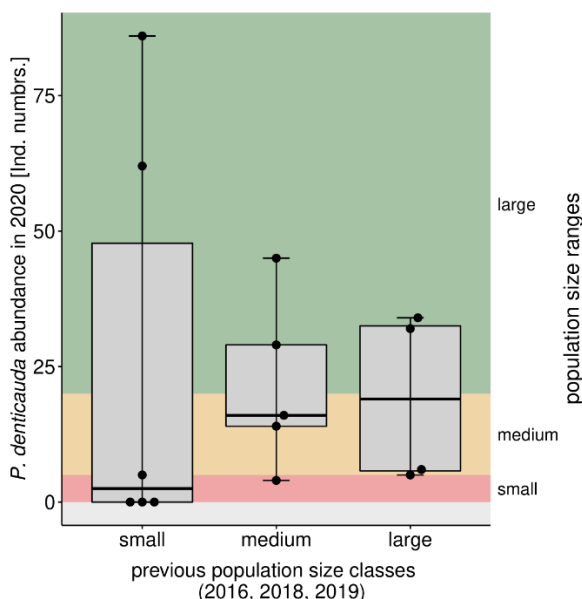
Model two and three included the mean percentage of open soil areas and matted soil cover as predictors, respectively. Because visual inspection of the raw data implied non-linear relationship, the predictors were also added as quadratic terms. Study site ID was added as a random factor to correct for unexplained variance due to site-specific non-measured environmental differences across study sites.

The AIC value of the open soil model did not significantly improve by implementing the predictor as a polynomial term. Yet, for comparison purpose, we decided to maintain the polynomial term also in this model.

## Results

### Consistency of *P. denticauda* population sizes

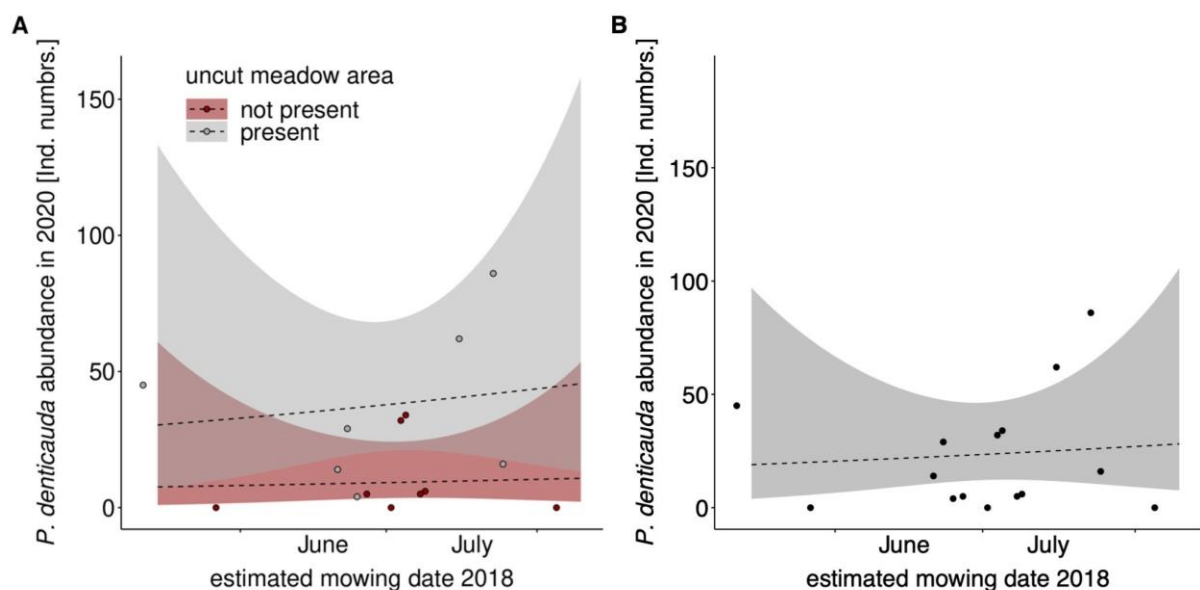
In 2020, adult *P. denticauda* could be confirmed in 12 out of 15 surveyed populations, with maximum counts ranging between 5 and 86 individuals. Yet, these counts only poorly reflected previous expert assessments of – presumed stable – population size classes (Table 1, Fig. 3) with no directional trend in the difference between current and earlier population size classes (Fig. 3).



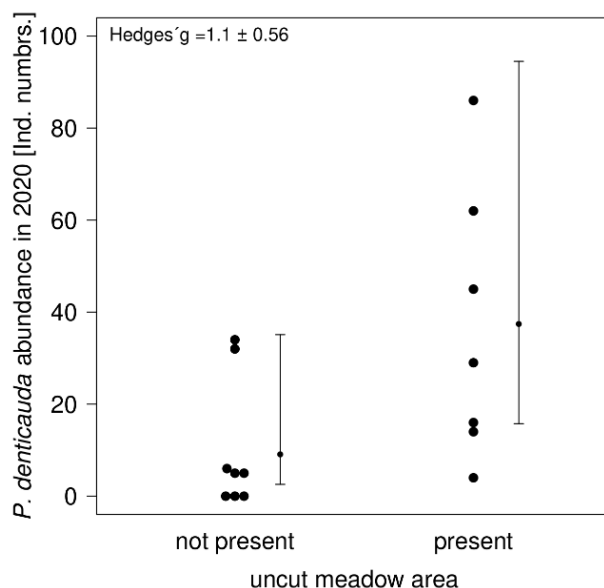
**Fig. 3:** *P. denticauda* individual numbers counted in the study year 2020 in relation to the previous and presumed stable population size classes from the survey years 2016, 2018 and 2019. Population size ranges are displayed as background colours (large = green, medium = orange, small = red).

## *P. denticauda* abundance and mowing regimes

We found no indication that the association of 2018 mowing dates with *P. denticauda* abundance in 2020 varied with the availability of uncut refuges (GLM interaction term,  $z = 0.028$ ,  $df = 10$ ,  $p = 0.98$ , Fig. 4A), so we continued to separately interpret both main effects. Contrary to our expectation, and possibly mediated by the large between-site variation in population sizes, mowing dates could not predict local abundance of *P. denticauda* (GLM  $z = 0.22$ ,  $df = 10$ ,  $p = 0.83$ , Fig. 4B). Likewise, *P. denticauda* abundance in 2020 did not differ significantly between meadows with uncut refuges and entirely mown meadows (GLM  $z = 0.3$ ,  $df = 10$ ,  $p = 0.77$ ). Yet, the estimated mean effect size between the availability and absence of uncut refuges in association with *P. denticauda* numbers was high (mean Hedges'  $d = 1.1$ ,  $SE = 0.56$ , Fig. 5).



**Fig. 4:** Maximum *P. denticauda* individual numbers in 2020 in relation to the estimated first mowing dates in 2018. A: split by meadows with an uncut grass area versus meadows mown entirely. B: without grouping into present and not present uncut meadow area. Lines show model predictions, shading their 95 % confidence intervals.



**Fig. 5:** Relation between meadows with an uncut refuge patch versus meadows mown entirely in 2019 and the abundance of *P. denticauda* in 2020  $\pm$  95% confidence intervals.

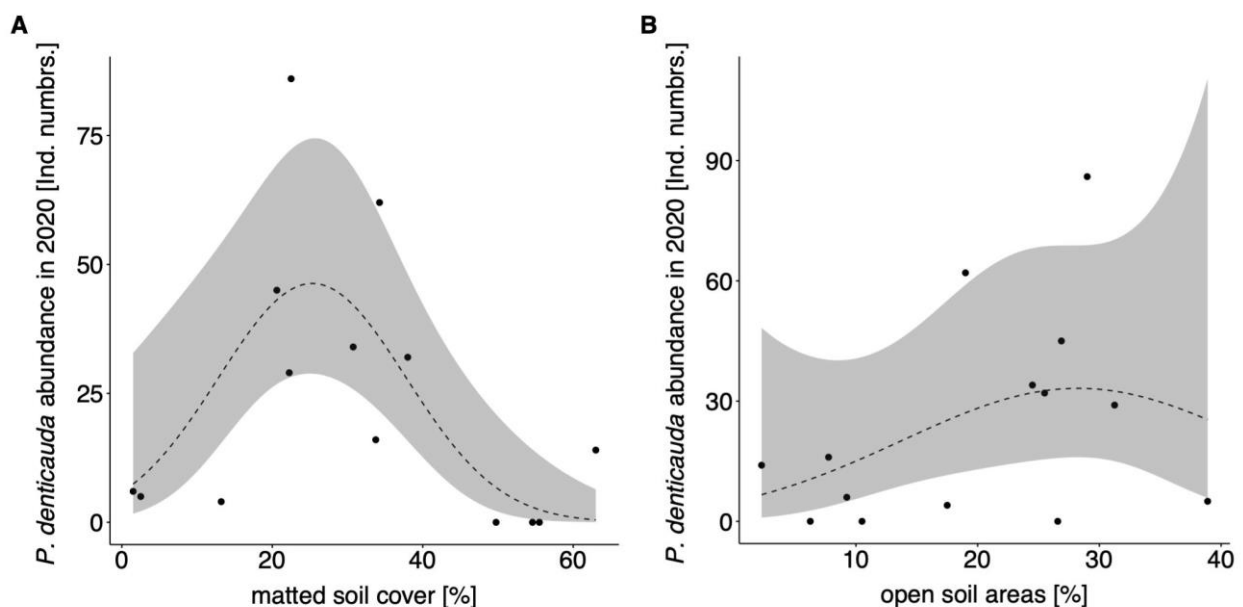
## Consistency between capture-mark-recapture and acoustical transect estimates

The capture-mark-recapture analysis revealed a population size of  $185 \pm 15$  male (estimator  $\pm$  95% CI) individuals at NSG Zellerhornwiese, based on 106 marked individuals on day 1, and recaptures of 71 marked versus 66 unmarked individuals on day 2. We further marked 11 females but recaptured none. The acoustical transect estimation at the same site produced a maximum of 62 individuals, extrapolated to 136 males for the entire meadow area. This confirms the expected underestimation of the population size when surveying acoustically, here by a factor of approx. 1.36.

### *P. denticauda* abundance and soil cover

*P. denticauda* abundance and the percentage of matted soil cover exhibited a quadratic relationship (GLM  $z = -3.1$ ,  $df = 9$ ,  $p < 0.001$ ), with an increase up to 30 % coverage and a decrease for even higher percentage cover (Fig. 6A).

The relationship between *P. denticauda* abundance and the percentage of open soil areas showed a similar non-linear pattern, but with large variation in the model coefficient estimates (GLM estimated of the quadratic term:  $z = -0.9$ ,  $df = 10$ ,  $p = 0.4$ ). Still, the illustrated model predictions are consistent with a slight increase for low percentages of open soil areas up to approximately 30 % and a decreasing tendency for higher percentages of open soil areas (Fig. 6B).



**Fig. 6:** *P. denticauda* abundances in 2020 in relation to A: the percentage of matted soil cover  $\pm$  95 confidence intervals. B: the percentage of open soil areas  $\pm$  95 confidence intervals.

## Discussion

### Consistency of *P. denticauda* population sizes

*P. denticauda* population size estimates in 2020 diverged strongly from population size classes in previous surveys. This could be due to (i) different survey methods used in previous years and this study, but also to (ii) natural inter-annual population fluctuations of *P. denticauda*.

The first reason associates with different study aims. Most earlier population surveys aimed to judge *P. denticauda* presence to establish large-scale distribution maps, whereas this study aimed for precise population size estimates to compare sites. This implies a systematic bias towards higher population size estimates in the current study compared to previous estimates. Nevertheless, the acoustic counts in 2020 still underestimated the true male population size as revealed by our capture-mark-recapture analysis at the NSG Zellerhornwiese. Such underestimation of orthopteran population sizes has already been confirmed by other studies for several sampling techniques compared to the more objective determination of population size by the mark-release recapture method (Gardiner & Hill 2006). Whether our observed ‘underestimation factor’ of 1.36 could serve as an appropriate correction factor for acoustically estimated population sizes of *P. denticauda* requires confirmation by comparable quantitative studies.

The second reason may be particularly relevant of *P. denticauda*, which is known for exceptionally strong fluctuations in population size (Engel 1951, Detzel 1998, Löderbusch 2015, Krech & Köhler 2021). Its temperature-driven embryonic and larval development and thus reproductive success can vary strongly on the landscape level with overall climate and short-term variation in weather conditions, and on the habitat level with microclimate and vegetation structure (Dempster 1963, Lockwood & Lockwood 1991, Köhler 1996, Fischer et al. 2016, Didham et al. 2020). In addition, *P. denticauda* exhibits a primarily biennial life cycle (Ingrisch 1986, Köhler et al. 2010, Widmer & Pfändler 2013, Köhler 2017), which can generate additional biennial population fluctuations (Krech and Köhler (2021).

### *P. denticauda* abundance and mowing regimes

Earlier studies reported positive effects of postponed mowing on orthopteran density, with a five-fold increase two years after mowing had been postponed by one month (Buri et al. 2013). This short-term benefit likely results from a prolonged reproductive period (Grant et al. 1993) and thus higher deposited egg numbers (Buri et al. 2013). *P. denticauda* reaches its phenological maximum – depending on in situ altitude and thermal energy accumulation (populations of the foreland of the Swabian Alb vs. high-level Alb-plateau) – around end-June to end-July (Detzel 1998), implying optimal mowing no earlier than mid-July or early-August on sites with core populations of this species. Especially in years with cooler springs, where temperature-dependent egg and larval development can postpone *P. denticauda* phenology into late-summer (Remmert 1985, Ingrisch 1986, Löderbusch 2015), mid-June mowing as established standard on species-rich hay meadows in Baden-

Württemberg (EU-Code 6510) is considered too early for safe reproduction (Löderbusch 2015, RPTü 2018, UM 2018, Vogt et al. 2019, MRL 2022). *P. denticauda* abundances in our study varied substantially and revealed only a mild positive association with later mowing dates in preceding years, at best. At the same time, and independent of local first mowing, we found a high positive mean effect size on abundance for meadows with uncut refuges compared to meadows without such refuges, with mean population sizes on average about 3-times larger (note that this estimate associates with broad confidence intervals given small sample size). Consistent with earlier studies, we therefore propose uncut refuges as a core conservation strategy for the Bull Bush Cricket (Buri et al. 2013).

Under this regime, only parts of the local population are exposed to harvesting mortality, and survivors can immediately find foraging habitat and shelter from predators or desiccation in the adjacent uncut areas (Bräu & Nunner 2003, Gardner & Hassall 2009, Humbert et al. 2012, Van de Poel & Zehm 2014). Large and flightless orthopterans like *P. denticauda* likely face a substantial risk for avian predation when crossing cut meadow patches, calling for rather short distances between uncut refuge strips (Evans et al. 1997, Guido & Gianelle 2001, Sladkowska 2011). Van de Poel and Zehm (2014) recommend maximum distances of 50 m. Further, uncut refuges should follow local habitat gradients (e.g. with respect to moisture, exposition, or slope inclination), and alternate yearly to maintain vegetation and habitat quality.

To counteract the negative effects of long-term postponed very late mowing on the vegetation and thus habitat suitability for *P. denticauda*, we propose to combine current mowing dates with uncut refuges on 10 % of *P. denticauda* habitat (Van de Poel & Zehm 2014). In particular permanent late mowing can favor semi-natural grasslands to develop into rather monotonous and grass-dominated stands that accumulate a thick layer of grass litter, reduce insolation of the soil surface, and suppress germination of less competitive herbaceous plants (Briemle & Aulendorf 2007, Partzsch 2016). Such processes occur even more pronounced with the increasing eutrophication from local and atmospheric sources (Bobbink 1991). This grass-enrichment and matted vegetation effect, in turn may compromise habitat suitability for *P. denticauda* (Reiter et al. 2004, Briemle & Aulendorf 2007), which requires herbaceous food, access to open soil for egg deposition, and insolation for larval development (Ingrisch 1986, Detzel 1998, Köhler 2017, Detzel et al. 2022).

The association between *P. denticauda* abundance and matted vegetation cover found in this study was consistent with previous studies suggesting that grass litter accumulation has negative thermal effects on embryogenesis and egg hatching, and thus orthopteran abundance, due to enhanced shading (Facelli & Pickett 1991, Van Wingerden et al. 1993, Fartmann & Mattes 1997). Soil surface coverage in our study revealed a peak abundance of *Polysarcus* at intermediate availability of matted vegetation and open soil coverage (approx. 30 %, with broad confidence intervals). This agrees with previous studies emphasizing the importance of accessible

bare soil as habitat requirement for orthopterans as oviposition, basking and courtship ground (Van Wingerden et al. 1992, Schulz 2003, Fartmann et al. 2012, Weiss et al. 2013).

Consequently, and to guarantee the availability of open soil patches, we suggest early pasture as an alternative management practice for *P. denticauda* conservation. As extensive grazing of meadows in the beginning and end of the growing season was an integral part of the grassland management until the 19<sup>th</sup> century (Kapfer 2010, 2019), this management practice has contributed essentially to the formation of the species-rich meadow community and is of underestimated importance. Particularly previous grazing withdraws many nutrients from the meadows since grasses are hit in the most productive period. Further, the side effect of ungulates creating open soil patches can ensure the needed bare soil requirement for *P. denticauda* oviposition.

Where pasture management seems unfeasible, its effects can at least partially be imitated by optional early mowing regimes (“Schröpfungsschnitt”) (Hely et al. 2018). If early mowing occurs at small-scale patches within larger grasslands, orthopterans initially avoid, but quickly repopulate those patches with increasing vegetation height without having negative impacts for the population (Detzel 1984, Bamann 2018, this study). This procedure is a potential solution in particular for more productive grassland sites, where the increasing biomass of dominant grass species compromises habitat quality under permanent mid- or late-summer mowing.

### **Suggestions for conservation practice**

Since the found pattern in our study hint at a potentially strong benefit for uncut refuges we propose to implement uncut refuges as a core conservation strategy for the Bull Bush Cricket. Further, the fact that permanently late first mowing is not a feasible option to maintain the needed habitat quality for this species in long term and additional stays in contrast to *Polysarcus*’ phenology, alternating mown meadow stripes seem to be a good standard to preserve this species.

Uncut refuges should be implemented on 10 % of the meadow area, in a reachable distance of maximum 50 m between mowing stripes and should be located along characterizing habitat gradients like moisture gradients and slope inclination. Anyhow, important is an annual alternating location of these unmown refuges to counteract an excessive grass litter cover and consequently ensure habitat quality and thus a successful embryogenesis and egg hatching of the thermophilic development of *P. denticauda* on the whole habitat area. To guarantee the availability of open soil patches for oviposition we suggest reintroducing the traditionally implemented pre-grazing on meadows as alternative management practice for the conservation of *P. denticauda*. On grass-dominant sites with an emerging grass litter layer and in more productive grasslands in the foreland of the Swabian Alb an annual alternating partly early mowing can be an expedient solution approach to remove nutrients and hence maintain long-term habitat suitability for *P. denticauda*.

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