

GfÖ Ecological Society of Germany, Austria and Switzerland Basic and Applied Ecology 56 (2021) 322–334 Basic and Applied Ecology

www.elsevier.com/locate/baae

# Scattered woody vegetation promotes European brown hare population

Franz Johann<sup>a,b,\*</sup>, Janosch Arnold<sup>b</sup>

<sup>a</sup>Department of Biometry and Environmental System Analysis, Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, Freiburg im Breisgau D-79106, Germany <sup>b</sup>Wildlife Research Unit, Agricultural Centre of Baden-Württemberg, Atzenberger Weg 99, Aulendorf D-88326, Germany

Received 18 May 2021; accepted 22 August 2021 Available online 26 August 2021

## Abstract

European brown hare populations have declined during the last decades. Agricultural intensification has been identified as a relevant driver of this process and agri-environment schemes have been implemented to foster biodiversity in agricultural land-scapes. Because species-specific outcomes of measures strongly depend on tailored design of the policy framework and the local management, while changing climate may pose additional challenges, policy and management need science-based information of which landscape composition should be promoted to achieve set biodiversity goals.

Here, we used direct observations of European brown hares over 20 years for evaluating the effects of landscape composition and weather conditions on European brown hare density. For the first time, our analysis compared the estimates of machine learning (gradient boosting machine) and linear mixed models in terms of importance of a wide range of explanatory variables for European brown hare densities and effect trends.

Scattered woody vegetation, as represented by the two variables transitional woodland-shrub and small woody features, was on top rankings among the predictors and greater proportions of these elements were accompanied by sharp increases of European brown hare density. Also warmer winter temperature had a positive effect.

We conclude that promoting scattered woody vegetation in agricultural landscapes is a powerful tool for improving European brown hare habitat quality. Particularly with the increasing dynamic in agriculture due to climate change, incentives and regulations that create a long-lasting heterogeneity in the landscape composition through near-natural elements can support the population of this popular mammal.

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*Keywords:* Agricultural intensification; Agri-environment schemes; Climate; Hedges; Heterogeneity; Lagomorpha; Landscape composition; *Lepus europaeus*; Population dynamic; Spotlight count; Subsidies

# Introduction

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Agriculture is a relevant driver of ecosystem changes. The proportion of land used for agriculture was globally 37.1% in 2017 (FAO, 2020), 41.1% in the European Union in 2015 (Eurostat, 2015) and 51.6% in Germany in 2018 (Umweltbundesamt, 2018). The development of agricultural

<sup>\*</sup>Corresponding author at: Department of Biometry and Environmental System Analysis, Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Tennenbacher Str. 4, Freiburg im Breisgau D-79106, Germany.

E-mail address: franz.j.j.johann@web.de (F. Johann).

https://doi.org/10.1016/j.baae.2021.08.012

machinery and of methods and materials to control species composition and plant growth on the field in conjunction with existing policy frameworks and market mechanisms enabled an intensification of agriculture in many parts of the world (Emmerson, Morales, & Oñate, 2016; Stoate, Báldi, & Beja, 2009). Agricultural intensification includes alterations not only on field scale but also on landscape scale. It reduces temporal and spatial heterogeneity (Tscharntke et al., 2005). The increases of yield per unit area were frequently accompanied by deterioration of ecological qualities, losses in biodiversity and reduction of ecosystem services (Billeter et al., 2008; Donald, Green, & Heath, 2001; Emmerson et al., 2016; Flohre et al., 2011; Green et al., 2005; Henle et al., 2008; Kleijn et al., 2009; Landis, 2017; Stoate et al., 2009; Tscharntke et al., 2005).

European brown hare (*Lepus europaeus*) is a commonly known species of European agricultural landscapes and as Easter Bunny an integral part of European culture. However, its real European population is discernibly less firmly established. Populations of this lagomorph have been declining in European countries since the early 1960s (reviewed in Olesen & Asferg, 2006) and the species is listed as vulnerable on the German and Swiss red lists of mammals (Agosti et al., 1994; Meinig, Boye & Hutterer, 2009) and as near-threatened on the red list for Austria (Umweltbundesamt, 2020).

Past efforts to disentangle the interconnected effects of underlying causes suggest that agricultural intensification is the primary driver of the decline (reviewed in Smith, Vaughan, & Harris 2005). The intensified land use reduced the availability of covered resting sites such as hedges or fallows (Pépin & Angibault, 2007; Tscharntke et al., 2005) and altered the availability of food (Jennings, Smith, & Hackländer, 2006; Olesen & Asferg, 2006; Schai-Braun et al., 2015).

Agri-environment schemes have been implemented in Europe to halt or reverse biodiversity loss by payments to farmers for habitat improvement (Kleijn et al., 2006) and evidence for positive effects of set-asides on leveret survival rate and hare abundance have been reported (Meichtry-Stier et al., 2014; Schai-Braun et al., 2020). However, existing agri-environment prescriptions or direct payments for agricultural cultivation methods may be insufficient, or the measures too imprecise for achieving species-specific targets (Henle et al., 2008; Pe'er et al., 2020; Whittingham, 2011). Therefore, a refinement of the understanding of the mechanisms which affect European brown hare populations is needed for optimizing both the agricultural policy framework and local implementation. To guide policy and management, it is important to understand how properties of landscape mosaics influence biodiversity (Bennett, Radford, & Haslem, 2006). Moreover, for a sustainable development of European brown hare habitats, the effects of the landscape must be related to the proceeding climate change which will bring warmer temperatures and altered precipitation patterns (IPCC, 2007; Lavalle et al., 2009).

Several studies have suggested that climatic factors affect European brown hares. Higher amounts of annual precipita-(Hackländer. Frisch. & Klansek. tion 2001: Van Wieren, Wiersma, & Prins, 2006) or of precipitation during the reproduction period (Nyenhuis, 1995; Rödel & Dekker, 2012) reduced European brown hare sightings or hunting bags; mild winters had been positively correlated with European hare abundance (Schmidt, Asferg, & Forchhammer, 2004) and yearling survival (Marboutin & Hansen, 1998). However, long time series of direct European brown hare observations are rare and existing studies accessing climate effects on hare abundance mostly did not include landscape composition and landscape dynamics (Olesen & Asferg, 2006).

Data from different landscape types over time are highly suitable to gain a better understanding of which factors have the greatest impact on population demographics (Smith et al., 2005). Here we analyze time series of European brown hare counts over 20 years and across a large spatial extent in conjunction with temporally and spatially matching weather information and land cover data. Our goal was to better understand the mechanisms of variation in European brown hare densities. This should help at the development of agriculture policies and land-use planning under climate change scenarios.

#### Materials and methods

#### Study region

The sampling sites were spread throughout the Federal State of Baden-Württemberg (Fig. 1), which covers approximately 35,750 km<sup>2</sup> (Statistisches Landesamt, 2020) in south-west Germany. The vegetation at the sampling sites, was shaped by temperate climate with air-temperatures averaging at 1.6 °C from January to February and 18.7 °C from June to August (DWD, 2020a) on elevations ranging between 100 and 956 m.

In 2018, settlement and transportation covered 14.6% of the federal state at a population density of 310 persons per km<sup>2</sup>. The predominant land uses were agriculture (45.1%) and forest (37.8%). Of the agricultural area, 57.6% were used as arable land, including 2% fallow land and 38.8% were permanent grassland (Statistisches Landesamt, 2020).

#### **Data collection**

The 278 sampling sites were located in separate hunting districts, where the European brown hares had been counted on open land from 2000 to 2019 during two annual count-ing-periods: in spring and in autumn. The counters were usually hunters who counted the hares at night with the help of a standardized spotlight from a car - a widely used method for assessing hare densities (Canova et al., 2020;



**Fig. 1.** Location of the sampling sites in the Federal State of Baden-Württemberg in southwestern Germany (Background map based on BAfG, 2021; EEA, 2021; BKG, 2021; LGL, 2021).

MLR, 2019; Pegel, 1986; Schai-Braun et al., 2020). The reach of the spotlight was 150 m. Tracks and illuminated areas had been set based on orthophotos and site visits and the sizes of illuminated areas were calculated in a geographical information system. Separated sub-areas at the same sampling site were allowed. If the visibility was impaired, non-visible areas were not included in the area sum. The average illuminated count area at a site was 1.51 km<sup>2</sup> (standard deviation  $[SD] = 0.75 \text{ km}^2$ ). At most of the sites counts were conducted over several years. At the same site, European brown hares were counted on average during 7.5 years (SD = 5.3 years). In total we analysed 5564 counts, 2878 of which were conducted in spring and 2686 in autumn. Some counters repeated the count up to four times in the same season of the same year to get more reliable density estimates (Table 1).

European brown hares move between daytime resting sites and nocturnal foraging areas (Zaccaroni et al., 2013). As we sought to assess the effect of landscape features on an all-day perspective, we calculated a buffer with 300 m distance for each of the 278 count areas to include distances to potential daytime resting sites, using the findings of

**Table 1.** Frequency of European brown hare counts at the same site during the same season in the same year.

Seasonal onsite count-frequency	Sum of areas sampled in a given year and season	Sum of counts
1	1662	1662
2	1808	3616
3	94	282
4	1	4
Total	3565	5564

Reitz and Léonard (1994) and Rühe and Hohmann (2004) as a guide for the distance. The average buffer size was  $5.75 \text{ km}^2 (\text{SD} = 2.29 \text{ km}^2)$ .

We calculated the percentage of area within these buffers which was overgrown with small woody features (SWFs. EEA 2015a). Thereby, we summed linear (width < 30 m, length  $\geq 50$  m), patchy (200 m<sup>2</sup>  $\leq$  area  $\leq 5000$  m<sup>2</sup>) and special (connective or isolated areas  $\geq 1500 \text{ m}^2$ ) woody structures on open land (for details see EEA 2015a). Further, we assigned temporally matching Corine Land Cover (CLC) types (Copernicus, 2021) to the buffers: for hare counts from 2000 to 2002 CLC-information of the year 2000, for counts from 2003 to 2008 CLC-information of 2006, for counts from 2009 to 2014 CLC-information of 2012 and for counts from 2015 to 2019 CLC-information of 2018. Thereafter, we calculated the proportion of CLC-types within each of the buffers for each count-year. Overall, 26 different CLC-types were present in the buffers. Additionally, we assigned a fragmentation index to the midpoint of the count areas. The indicator measures landscape fragmentation caused by transport infrastructure and sealed areas (EEA, 2015b, 2019a).

To evaluate the effect of weather conditions, we obtained for each year 1 by 1 km climate-grids from DWD Climate Data Centre (DWD, 2020a). Values had been interpolated from measurements of a net of stations and temperatures had been elevation corrected. Seasonal mean air-temperatures were averages over three monthly averages of air-temperature at 2 m above ground (DWD, 2020b). Additionally, we used grids of sums of precipitation over three months (DWD, 2020c) and grids of the annual vegetation begin, which is based on the beginning of flowering of forsythia (Forsythia  $\times$  intermedia, DWD 2020d). For each counting, we extracted temporally explicit climate information from the grids to the midpoints of the count areas. We used mean air-temperature from December to February and precipitation sum from December to February of the winter before each spring count and both precipitation sum from March to May and from June to August before each autumn count. Finally, we calculated the number of days from vegetation begin to the date of spring counts for evaluating possible effects of a more grown up vegetation.

#### Data analysis

We analysed the data focusing on two target variables: hare density at spring counts and hare density at autumn counts. For both responses we firstly fitted gradient boosting machine models (GBM-models, Elith, Leathwick, & Hastie 2008, Hijmans, Phillips, Leathwick, & Elith, 2017) for identifying relevant predictors and to assess nonlinear predictor effects. We hypothesized that besides landscape effects, for spring density air-temperature and precipitation sum during winter were relevant factors, whereas for autumn density precipitation in spring and summer were relevant (Hackländer, Frisch, & Klansek, 2001; Hackländer, Tataruch, & Ruf, 2002; Rödel & Dekker, 2012).

Therefore, the GBM-models based on 2878 spring counts included as predictors the area proportions of each of the 26 CLC-types, the proportion of SWFs and the fragmentation index. Furthermore the weather variables mean air-temperature from December to February and precipitation sum of the same period. Additionally, the spring GBM-models

considered the number of elapsed days from day of vegetation begin to the counting day. The GBM-models based on 2686 autumn counts included as predictors, additionally to proportions of CLC-types, proportions of SWFs and fragmentation index, the weather variables precipitation sum from March to May and precipitation sum from June to August. The GBM-settings were lerning.rate = 0.005, tree. complexity = 7 and n.trees = 15,000. To account for repetitions of counts within the same season of a year at the same site we set site.weight =  $1/N_{seasonal counts}$ . We computed for each season 100 GBM-models and bootstrapped per season the average predictions and 95% confidence intervals (Canty & Ripley, 2021; Davison & Hinkley, 1997).

In our second approach, we fitted parametric linear mixed models (LME-models) using maximum likelihood estimates (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2020). For each seasonal full LME-model we included the 12 most important predictors, which had a relative influence of at least 2.5% as evaluated by the corresponding GBM-model (Fig. 2). Multiple counts at the same site during the same



Fig. 2. Relative influence of predictors in the GBM-models; only predictors that reached an influence level indicated on the right side of the vertical dashed line (relative influence > 2.5%) were included in the LME-models.



Fig. 3. AICs of LME-models; the named predictor was omitted in each case; 'none' = full model; horizontal lines show AIC-differences to the full model; models for spring counts (A) and models for autumn counts (B).

season in a year were weighted inverse to their frequency. As the GBM-effect plots showed nonlinear relations between predictor and response, we configured each fixed effect predictor as a polynomial of degree 2 to allow for non-straight relations also in the LME-models. To account for repeated measurements, we included year nested in site as random effect and additionally included an autocorrelation structure of the same form (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2020). We evaluated the importance of predictors in the LME-models by comparing the AIC of the full models with the AICs of models which omitted in each case one predictor of the full model. LME-predictions for a predictor effect were calculated with other predictors set to the mean; 95% prediction intervals include random effect variance (Johnson & O'Hara, 2014; Lüdecke, 2018). All calculations were performed in R (R Core Team, 2020).

# Results

The GBM-models for both European brown hare density in spring and in autumn (Fig. 2), showed strong influence of arable land, transitional woodland-shrub (TWS) and small woody features (SWFs). The weather variables had relevant influence, whereby precipitation in spring and summer were more decisive than precipitation or mean air-temperature in winter. Fragmentation was not among the most relevant factors, whereas the time interval between vegetation-begin and day of count was identified as a relevant predictor.

At the second approach, in both the LME-model for spring-density (Fig. 3A) and for autumn-density (Fig. 3B) the variable TWS improved the AIC most, followed by SWFs. In the LME-model for spring counts, all included land cover types except pastures and water bodies led to

significant effects (p < 0.05). The effect of mean air-temperature December to February was significant. In contrast, precipitation sum had no significant effect. In the LME-model for autumn counts, all land cover terms except water bodies had significant effects whereas both precipitation variables had only non-significant impacts. For model coefficients, see Appendix A: Tables A1 and A2.

The mean proportion of TWS in the buffers was 0.21% and TWS was present at 30 of the 278 sites. TWS area proportions above 2% were accompanied by a substantial increase of European brown hare density, with a trend of increasing hare numbers at increasing percentages of TWS (Fig. 4A and B). Similarly, greater proportions of SWFs led to higher densities at proportions above 5% (Fig. 5A and B); the average proportion was 4.51% and SWFs were present at all sites. Higher mean winter air-temperatures were accompanied by very variable responses in the GBM-model (Fig. 6A) and higher European brown hare densities in the LME-model (Fig. 6B).

#### Discussion

The two model types showed consistent trends but a different ranking of the evaluated explanatory variables. In the GBM-models (Fig. 2) climate variables had stronger effects than in the LME-models (Fig. 3). The GBM-models considered repeated counting during the same season in different years at the same site as independent observations (only repetitions in the same season of the same year had been weighted), whereas the LME-models evaluated year as a random effect nested in site. Moreover, the nonparametric GBM-models allowed more flexibility along the predictor gradients — that is along the features of the



Proportion transitional woodland-shrub [%]



Proportion transitional woodland-shrub [%]

**Fig. 4.** Change in brown hare density relative to the mean value of the predictions (dashed line) depending on area proportion of transitional woodland-shrub in GBM-models (A); LME-models for brown hare density depending on area proportion of transitional woodland-shrub (B); shades indicate 95% confidence intervals (A & B).

sites – compared to the LME-models (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2020). Therefore, the lower ranks of the climate variables in the AIC-rankings of the LME-models suggest that precipitation and winter mean air-temperature were less strong drivers on a large spatial scale, whereas these variables had noticeable impact on hare densities on the site scale. And, on a large spatial scale, the differences of the land cover compositions were a more crucial criterion for European brown

hare density than the varying weather conditions (compare Gabriel et al. 2010, Tschumi et al. 2020).

European brown hare density can differ widely depending on the region (Canova et al., 2020). For our data, both model algorithms identified proportion of transitional woodlandshrub (TWS), proportion of small woody features (SWFs) and proportion of arable land as the most relevant causes of varying hare density. Our findings underpin results of earlier studies which showed that arable land is favorable habitat



**Fig. 5.** Change in brown hare density relative to the mean value of the predictions (dashed line) depending on area proportion of small woody features in GBM-models (A); LME-models for brown hare density depending on area proportion of small woody features (B); shades indicate 95% confidence intervals (A & B).

for European brown hares in temperate cultural landscapes (Ala-Hulkko et al., 2016; Smith et al., 2005). However, a homogenous agricultural characteristic implies risks in terms of cover and food availability (Frylestam, 1980; Smith et al., 2004; Tapper & Barnes, 1986). This theory is supported by our data and the depicted effects of the two explanatory variables representing scattered woody vegetation: TWS (Fig. 4A and B) and SWFs (Fig. 5A and B) were accompanied by sharp increases of European brown hare densities at higher proportions of the woody elements but lowest

densities if the woody elements were absent or covered very small proportions of the buffer area. Within-habitat heterogeneity is a crucial factor for European brown hare habitat suitability (Benton, Vickery, & Wilson, 2003; Canova et al., 2020; Smith et al., 2004; Tapper & Barnes, 1986).

Scattered woody vegetation, such as tree groups, hedgerows, bushes or large-scale progressive vegetative succession on fallow land, increase the temporal and spatial heterogeneity in agricultural landscapes. Our results revealed that these elements noticeably contributed to



Mean air temperature December to February [°C]

**Fig. 6.** Change in brown hare density relative to the mean value of the predictions (dashed line) depending on mean air temperature December to February in the GBM-model (A); LME-model for brown hare density depending on mean air temperature December to February (B); shades indicate 95% confidence intervals (A & B).

support European hare populations. Thereby, two mechanisms come into action: Their function as shelter and their function as feeding sites.

Scattered woody vegetation improves the year-round availability of shelter from predation and from unfavorable weather. Particularly predation by foxes is considered a relevant factor of European brown hare mortality. Domestic cats and dogs can also predate on leverets (Hummel, Meyer, & Hackländer, 2017; Panek, 2009). Voigt and Siebert (2020) observed significantly longer survival of adults and leverets in covered habitat compared to open habitat; particularly in the first days after birth leverets gained from shelter. For adults, covered resting sites at short distance reduce the risk of being detected while moving from resting sites to feeding grounds or while moving to nurse offspring; and facilitate to escape from predation when they are detected (Hummel, Meyer, & Hackländer, 2017; Panek, 2009; Vaughan et al., 2003; Voigt & Siebert, 2020). Avian predators can also jeopardize European brown hare survival (Hummel, Meyer, & Hackländer, 2017) and trees often serve as their outlook. However, our results clearly show a positive effect of SWFs and TWS. In terms of weather, woody vegetation may provide shelter from wind and offer areas which are dryer and less covered with snow than the surrounding. Smith et al. (2004) found that in winter, tall habitat was preferred to short/medium habitat. Furthermore, non-cultivated areas are not affected by supplying slurry and provide shelter from cultivation machinery (Olesen & Asferg, 2006). The positive impact of scattered woody vegetation in terms of shelter comes along with improvement of nutrition.

Hares utilise small home ranges, therefore they need a variety of food resources in short distance (Katona et al., 2010). Heterogeneity is particularly important in times of food shortage. In agricultural landscapes, woody elements increase the spatial and temporal heterogeneity of available food resources in several respects: (1) by being food themselves (reviewed in Katona et al. 2010, Olesen & Asferg, 2006). Gidenne (1997) pointed out that lignocellulose has a favorable effect on the digestive process and health of lagomorphs. (2) Furthermore, hedges and shrubs are a stronghold against light machinery. Because they hamper cultivation, a variety of weeds may thrive in their immediate vicinity. Weeds are a crucial part of hare nutrition, especially in spring and summer (Brüll, Pielowski, & Pucek, 1976; Frylestam, 1980; Hackländer, Arnold and Ruf, 2002; Katona et al., 2010; Reichlin, Klansek, & Hackländer, 2006; Schai-Braun et al., 2015). However, they are rare in intensively managed agriculture, not least because of the application of herbicides (Emmerson et al., 2016; Olesen & Asferg, 2006). The high proportion of winter cereals in present agriculture may have shifted the nutritional bottleneck to the period of reproduction (Olesen & Asferg, 2006; Schmidt et al., 2004), because grown up crops and harvested fields are unfavorable feeding grounds (Reichlin et al., 2006). Non-cultivated areas can serve as relevant food resource in this period. However, hedges and other smallscale woody vegetation have been widely removed during recent decades for intensifying agriculture (Emmerson et al., 2016; Robinson & Sutherland, 2002; Tscharntke et al., 2005) entailing a reduction of the related plant diversity (Bunce et al., 1994; McCollin, Moore, & Sparks, 2000; Schai-Braun et al., 2015). (3) Furthermore, woody vegetation influences the microclimate of the surrounding for instance by shadowing or by being windshield (Sánchez & McCollin, 2015). Therefore, plant composition and the temporal development of vegetation neighboring trees and bushes may differ from other places, increasing the heterogeneity of food resources. (4) Additionally, greater proportions of hedgerows may indicate more field margins and smaller field sizes and potential greater variation of crops in a mosaic of fields. High European brown hare density has been found to be associated with high crop diversity (Canova et al., 2020; Olesen & Asferg, 2006; Smith et al., 2005).

Our study not only supported earlier results of utilization (Bresiński, 1983; Petrovan, Ward, & Wheeler, 2013; Tapper & Barnes, 1986) and positive abundance effects (Vaughan et al., 2003; Zellweger-Fischer, Kéry, & Pasinelli, 2011) of woody vegetation but also stressed its great importance for habitat improvement: Both modeling approaches identified TWS and SWFs as highly ranking factors with the potential for a sharp increase of European brown hare abundance.

Both agricultural intensification and weather conditions have been suggested as factors with impact on European brown hare abundance. However, whereas many previous studies were consistent with regard to the effect of agricultural intensification, their results in terms of weather effect were often contradictory. In their review of 77 European studies, Smith et al. (2005) found no significant effect of annual precipitation and mean January temperature on spring density. Our results suggest that the effect of weather conditions is strongly linked to the local habitat quality. In the LME-models, which evaluated effects of explanatory variables by considering year nested in site as a random effect, weather variables had lesser impact than in the GBMmodels with repeated observations in different years at the same site considered as independent, and densities varying freely along the predictor gradients. In the LME-models, only air-temperature from December to February had significant impact in regard to weather variables, with a trend to higher density at warmer temperatures. Cold winters may increase hare mortality because of higher energetic costs of thermoregulation (Hackländer et al., 2002) and reduce pregnancy rates and litter size (Hewson & Taylor, 1975).

Climate studies predicted warmer winters and observed a lengthening of the period between the last spring frost and the first occurrence of autumn frost (EEA, 2019b; Lavalle et al., 2009). Our results suggest that milder winter and longer vegetation period per se, will not improve European brown hare energy balance and habitat, but the availability of shelter and food is widely determined by actions of the farmers in the form of management calendar and the spatial pattern and quality of cultivated and non-cultivated plants.

Our results support the theory that agricultural intensification was the main driver of declining European hare densities. This is also underpinned by agricultural data of the region: The average agricultural area of a farm in the Federal State of Baden-Württemberg increased from 10.4 ha in 1980 to 35.8 ha in 2019. The yield of crops increased from  $5710 \text{ kg}^{*}\text{ha}^{-1}$  in 1988 to 7570 kg $^{*}\text{ha}^{-1}$  in 2019. In contrast, the number of workers per 100 ha decreased from 10.4 in 1981 to 4.5 in 2016 (Statistisches Landesamt, 2020). The obvious polarity between the increased yield at increased area cultivated per farm and the reduction of labor force suggests a sharp increase of the importance of machinery application. Accordingly, the utilized land had been consolidated and reshaped suitable for efficient machine use, resulting in a decline of non-cultivated areas, such as TWS and SWFs. However, agricultural landscapes are of minor habitat

quality for many species including European brown hare, if spatial and temporal land cover heterogeneity is missing (e.g. Tscharntke et al. 2005).

## Conclusions

The sustainable production of food and plant resources for human needs is a challenge (Emmerson et al., 2016; Landis, 2017; Whittingham, 2011). Our data showed that scattered woody vegetation is a relevant element for sustaining European brown hare populations in agricultural landscapes. Farmland management policies that target to halt the loss of biodiversity must include the reestablishment of temporal and spatial heterogeneity of land cover. Promoting small woody features and transitional woodland-shrub is a powerful tool on this trajectory.

## Funding

This study was funded by the Ministry of Rural Affairs and Consumer Protection of the Federal State of Baden-Württemberg.

#### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgments

We thank Dr. Manfred Pegel who initiated the European brown hare count project at the Wildlife Research Institute of the Federal State of Baden-Württemberg, Dr. Johanna Arnold for the current project coordination and Guido Dalüge for managing the counts and setting the count areas during recent years on behalf of the Wildlife Research Institute. Many thanks to all counters for long-lasting cooperation and the fieldwork during darkness.

## **Supplementary materials**

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j. baae.2021.08.012.

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