Influence of cereal harvest on adrenocortical activity in European hares (*Lepus europaeus*)

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Abstract

Anthropogenic disturbances, such as habitat modifications and machines, are associated with increased levels of faecal glucocorticoid metabolites (fGCMs) in mammals, an indicator of a stress response. One human-caused process provoking incisive habitat alterations is harvesting arable crops. We investigated the effect of cereal harvest on fGCM concentrations in European hares (*Lepus europaeus*) in arable landscapes in lower Austria during the year 2018 by collecting 591 faecal samples before, during and after cereal harvest. fGCMs were analysed using an enzyme immunoassay, and data were analysed using linear mixed-effects models. We found that neither cereal harvest nor farming practice (organic vs. conventional) caused an overall increase in the hares' stress level. Lower vegetation density and higher proportions of bare ground were negatively correlated with fGCM concentrations, whereas the proportion of stubble fields was significantly positively correlated with fGCM concentrations in European hares. A change to more open landscapes might decrease time spent avoiding predation, and fallen grains may provide a beneficial additional food source for the hares. This indicates that European hares are well adapted to an opening up of the landscape and short-term disturbances such as cereal harvesting. In conclusion, cereal harvest had no large impact on European hares' adrenocortical activity in an arable landscape with small average field size and enough available non-farmed areas.

Keywords Brown hare · Lagomorpha · Non-invasive · Habitat change · Vegetation structure · Agricultural management system

Introduction

Increasing evidence and documented examples suggest that disturbances and habitat alteration as a result of human activity can act as stressors in different mammals (Navarro-Castilla et al. 2013; Rehnus et al. 2014; Lunde et al. 2016; Zbyryt et al. 2018) and birds (Thiel et al. 2008; Casas et al. 2016). The agricultural intensification has caused habitat alterations due to the loss of heterogeneity in agricultural habitats (Benton et al. 2003) and significantly changed harvesting methods by

becoming faster and more efficient (Robinson and Sutherland 2002). Under these circumstances, one might expect that the harvest of arable crops in late summer causes a dramatic change in modern arable landscapes and may act as a stressor in vertebrates inhabiting the agricultural landscape.

One part of the physiological stress response is the activation of the hypothalamic–pituitary–adrenal (HPA) axis and subsequent secretion of glucocorticoids (GCs). The primary role of GCs is basic energy regulation, whereas increased secretion allows animals to mobilize stored energy to cope with stressful situations (Möstl and Palme 2002; Sheriff et al. 2011a). Chronic or long-term increases in GC levels can have detrimental effects on the organism, such as lower immune function, increased energy expenditure and potentially reduced reproduction and survival (Busch and Hayward 2009; Romero and Wingfield 2015). Nowadays, well-validated non-invasive methods are available to measure faecal glucocorticoid metabolites (fGCMs) and thus assess the impact of stressful situations on wildlife (Sheriff et al. 2011a; Palme 2019). Hence, we used fGCMs to evaluate whether harvesting of arable landscapes acts as a stressor

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and shows a negative effect on wildlife. As a typical inhabitant of arable landscapes, which numbers have been declining since the beginning of the twentieth century (Hackländer and Schai-Braun 2018) due to agricultural intensification (Smith et al. 2005), we used the European hare (*Lepus europaeus*) as a model species.

Whether the agricultural management system (conventional vs. organic) plays a part in buffering harvesting effects has not been addressed in studies yet (Marboutin and Aebischer 1996; Cimino and Lovari 2003; Roth et al. 2005; Schai-Braun et al. 2014; Shuford et al. 2015; Conkling et al. 2017). In the case of the study, organic farming was based on the management standards from Agrarmarkt Austria (AMA) implementing the council regulation 834/2007 (European Commission 2009). The associated renunciation of chemically synthetic pesticides and mineral nitrogen fertilizers has to be achieved, among others, by multiannual diverse crop rotation including legumes and other green manure crops and the choice of crop species (European Union 2007). Organic farming results in an increased habitat diversity in agricultural habitats (Norton et al. 2009). However, the increased diversity vary according to factors such as ethical beliefs of the farmer (Shepherd et al. 2003; Hole et al. 2005), respective landscape structures (Bengtsson et al. 2005), organic farming standards and economic realities of the marketplace (Hole et al. 2005). For this reason, the agricultural management system in general is probably unlikely to play a decisive role during harvest for wildlife species.

European hares use open ground with short vegetation as feeding areas within home ranges (Tapper and Barnes 1986; Mayer et al. 2018), whereas resting areas are chosen in landscapes providing shelter (Tapper and Barnes 1986; Neumann et al. 2011). During summer, arable crops provide mainly cover (Tapper and Barnes 1986; Rühle and Hohmann 2004; Neumann et al. 2011) and only seldom both forage and shelter (Reitz and Léonard 1994; Mayer et al. 2018). European hares feed selectively on different plant species (Reichlin et al. 2006) and select especially a diet rich in fat (Schai-Braun et al. 2015). Accordingly, harvest may alter the availability of habitats providing shelter, as well as the arrangement of required habitats within home ranges. Remaining habitats might be further away from each other leading to an increased energy expenditure (Swihart 1986) and predation risk. Moreover, suitable habitats could act as hot spots for European hares, resulting in potential risks of social stress (Lindlöf et al. 1978; Monaghan and Metcalfe 1985). As harvest neither influenced the home range size during resting periods nor the resting position in an arable landscape with enough non-farmed features (< 10%), such habitat types may buffer harvest effects (Schai-Braun et al. 2014).

The aim of this study was to investigate the influence of cereal harvest in an arable landscape on the stress level (measured by fGCMs) of European hares. Our hypotheses were

that (1) cereal harvest increases fGCM levels in European hares; (2) the harvest-induced increase in fGCM levels results irrespective of the agricultural management system; (3) the reduction of shelter, measured by the change in vegetation density and height, increases fGCM levels; and (4) the availability of non-farmed features buffers the effect of cereal harvest on fGCM concentrations. We tested these hypotheses by collecting faecal pellets of European hares in an arable landscape over three periods—before, during and after harvest—allowing for a comparison of fGCM concentrations.

Materials and methods

Study area

The study was conducted in two adjacent hunting grounds (Kronberg 48° 25' N, 16° 31' E and Traunfeld 48° 27' N, 16° 31' E) of 842 ha (Kronberg 390 ha, Traunfeld 452 ha) in Lower Austria during the year 2018. In the study area, arable land dominated (88%), of which 24% was used for growing cereals. Stubble fields were covered by stubble from a previous crop, whereas bare ground was free from vegetation after tillage. For an overview of the habitat types in the study area, see Table 1. The average field size was 1.85 ha (± 0.1 SE). The field edge index, describing the length of the border between two different habitat types and therefore the diversity within an area, was 23.77 km per 100 ha (Pegel 1986). Organic farming was practised on 39% of the study area.

Predators such as corvids (e.g. Eurasian magpie *Pica pica*, carrion crow *Corvus corone*) or predatory mammals (e.g. stoat *Mustela erminea*, weasel *Mustela nivalis*, pine marten *Martes martes*, beech marten *Martes foina*, red fox *Vulpes vulpes*, badger *Meles meles*) were similarly controlled in both hunting grounds based on the legal foundation. Other birds of prey (e.g. common buzzard *Buteo buteo*, kestrel *Falco tinnunculus*, marsh harrier *Circus aeruginosus*), and storklike birds (order Ciconiiformes; e.g. grey heron *Ardea cinerea*, white stork *Ciconia ciconia*, great egret *Ardea alba*) were fully protected by law. The hunting season for hares started in both study areas on 1 October and ended 31 December in the year 2018.

Hare density was estimated each year in autumn and spring by spotlight counts (Langbein et al. 1999) from the local hunting association. Thereby, the complete agricultural land of the study area was illuminated with spotlights and hares counted during each spotlight count. On average 132 European hares per 100 ha (± 33.9 SE) in Kronberg and 109 individuals per 100 ha (± 0.7 SE) in Traunfeld were counted in the year 2018.

Habitat mapping

We digitized all habitat types in the study area using plot maps and ArcGIS 14.4.1 (ESRI). Each plot was visited to determine

Table 1 The 31 habitat types used to classify the study area's land use, a classification into seven categories and their area covered in percent before, during and after harvest in Lower Austria in the year 2018

Classification	Habitat type	Scientific name	Area (%)		
			Before harvest	During harvest	After harvest
Cereals	Winter wheat	<i>Triticum aestivum</i> L.	22.26	4.87	—
	Barley	<i>Hordeum vulgare</i> L.	5.77	3.76	—
	Triticale	<i>x Triticosecale</i>	4.61	0.11	—
	Rye	<i>Secale cereale</i> L.	0.77	0.32	—
	Spelt	<i>Triticum spelta</i> L.	0.45	0.45	—
Field crops	Corn	<i>Zea mays</i> L.	7.64	7.64	7.64
	Mustard	<i>Sinapis alba</i> L.	4.23	4.23	4.23
	Soybean	<i>Glycine max</i> M.	3.44	3.44	3.44
	Sunflowers	<i>Helianthus annuus</i> L.	3.38	3.38	3.38
	Oil pumpkins	<i>Cucurbita pepo</i> L.	3.10	3.10	3.10
	Sugar beet	<i>Beta vulgaris</i> L.	2.94	2.94	2.94
	Flax	<i>Linum usitatissimum</i> L.	2.89	2.89	2.89
	Rape	<i>Brassica napus</i> L.	2.89	—	—
	Poppy	<i>Papaver somniferum</i> L.	1.73	0.44	—
	Broad bean	<i>Vicia faba</i> L.	1.23	1.23	1.23
	Fennel	<i>Foeniculum vulgare</i> L.	0.78	0.78	0.78
	Buckwheat	<i>Fagopyrum esculentum</i>	0.62	0.62	0.62
	Peas	<i>Pisum sativum</i> L.	0.47	0.24	—
	Safflower	<i>Carthamus tinctorius</i> L.	0.20	0.20	—
	Millet	<i>Panicum miliaceum</i> L.	0.15	0.15	0.15
Grassland	Fallow land	—	7.78	7.78	7.78
	Lucerne	<i>Medicago sativa</i> L.	4.92	4.92	4.92
	Red clover	<i>Trifolium pratense</i> L.	0.76	0.76	0.76
	Field edge	—	0.38	0.38	0.38
Tree-covered habitat	Forest	—	7.56	7.56	7.56
	Hedge	—	2.96	2.96	2.96
	Copses	—	1.33	1.33	1.33
Specialty crops	Vine	<i>Vitis vinifera</i>	3.99	3.99	3.99
	Pasture	—	0.71	0.71	0.71
Bare ground	All bare ground	—	—	5.30	26.61
Stubble fields	All stubble fields	—	—	22.88	12.54

the habitat type based on the main vegetation/usage type. Two adjacent plots with the same habitat type were considered to be one, while plots with different habitat types were considered to be separate. Habitat changes caused by harvest or subsequent tillage were noted daily during sampling periods.

We mapped the vegetation density as well as the vegetation height for each plot at three random points before each faecal pellet sampling period. The mean values of a given plot were used for the entire plot. The vegetation density was determined by the amount of soil that remained visible through the vegetation in a frame (1 m × 1 m) (Gehlker 1977). The mean values were categorized as open (< 25%), sparse (25–49%), medium (50–70%) and dense (> 75%) (Schai-Braun et al. 2014). The vegetation height was measured at the same

points with a meter stick and classified as short (< 70 mm), medium (70–220 mm) and tall (> 220 mm) according to Smith et al. (2004).

Faecal pellet collection

Faecal pellets of European hares were collected in three periods from 12 June until 24 July 2018. “Before harvest” was defined as the time period immediately before cereal harvest started (12 June–17 June 2018). The second period “harvest” was during the winter wheat harvest (04 July–11 July 2018), whereas the “after harvest” period started 2 weeks later (18 July–24 July 2018). We collected all faecal pellets over a total transect length of 72 km along field boundaries and on tractor

Table 2 Model 1 averaged coefficients of the covariates farming practice, collecting period, vegetation density and vegetation height for the response variable fGCM ($n = 591$)

		Estimate	Std. error	z value	P value
Collecting period	Intercept	16.741	1.050	15,923	< 0.001
	Farming practice	− 1.786	1.349	1322	0.186
	Before harvest	− 0.091	1.718	0,053	0.958
	After harvest	0.274	1.916	0,143	0.887
	Vegetation density	Dense/open	1.678	0,827	0.408
		Medium	− 2.755	0,968	0.333
		Medium/dense	− 0.591	0,251	0.802
	Vegetation height	Open	− 4.105	3,010	0.003
		Medium/tall	− 0.227	0,091	0.927
		Short	− 3.998	1,474	0.140
		Short/medium	− 1.842	0,479	0.632
		Short/tall	0.345	0,123	0.902
		Tall	− 0.702	0,352	0.725

lines in the crops. No hare movement due to discomfort caused by faecal pellet collection was noticed. Additionally, we examined areas with sparse vegetation and resting places of walked up hares near the transects for faecal pellets. Due to the increased locomotor activity of European hares during night and dawn (Schai-Braun et al. 2012), we started early in the morning (04:45 am) collecting fresh faecal pellets and stopped when identification of freshness was no longer possible (10:30 am) to avoid further bacterial degradation of fGCMs (Möstl et al. 1999; Thiel et al. 2005). All samples were transported in a styrofoam cooler box with six ice packs during field collection and later stored frozen at -20°C following the procedure of Rehnus et al. (2010). We stopped collecting during rainy weather conditions to prevent misidentification of freshness and washing out effects (Rehnus et al. 2009).

Each sample location was recorded with a GPS device (Garmin GPSMAP 60Cx) and consisted of a minimum of three pellets. The positional data were mapped in ArcGIS, and around each sample location, a circle with the size of 10 ha was drawn. We chose a 10-ha circle because 24-h home range sizes of European hares in comparable agricultural

landscapes were recorded to be around 10 ha (Schai-Braun and Hackländer 2014). Subsequently, the habitat composition within the circle was evaluated on the assumption that it was used by the individual hare during the last 24 h.

Sample analysis

To determine fGCM concentrations, we used a group-specific 11-oxoandrosterone enzyme immunoassay (EIA), which measures 11,17-dioxoandrostanes (a group of cortisol metabolites). This EIA has proven suited for European hares (Teskey-Gerstl et al. 2000). Faecal pellets were dried at 75°C for 5 h. Afterwards, each sample was homogenized and 0.20 g (± 0.005 g) mixed with 4.0 ml methanol (100%) and 1.0 ml distilled water. Subsequently, the mixture was shaken for 30 min and centrifuged ($2500 \times g$, GS-6KR, Beckman Coulter) for 10 min to determine the amount of fGCMs in the supernatant after a 1:10 dilution with assay buffer (Palme and Möstl 1997; Palme et al. 2013). Samples below the detection limit (2.1 ng/g faeces) were set at 2.1 ng/g faeces for the statistical analyses.

Table 3 Model 2 averaged coefficients of the covariates farming practice, collecting period and habitat types for the response variable fGCM ($n = 591$)

		Estimate	Std. error	z value	P value
Collecting period	Intercept	15.593	2.237	6.965	< 0.001
	Farming practice	− 2.575	1.491	1.724	0.085
	Before harvest	0.186	2.487	0.075	0.941
	During harvest	− 1.162	1.967	0.590	0.555
Habitat type	Bare ground	− 6.876	3.103	2.212	0.027
	Stubble fields	7.285	3.493	2.083	0.037
	Specialty crops	4.550	3.946	1.151	0.250
	Grassland	3.845	3.802	1.010	0.312
	Cereals	2.789	3.684	0.756	0.450
	Field crops	1.974	3.366	0.586	0.558
	Tree covered	1.715	4.101	0.417	0.676

Statistical analysis

All statistical analyses were done with R 3.5.2 (R Development Core Team 2018). First, we grouped faecal samples according to the collecting period (before, during and after harvest). The Games-Howell test for post hoc testing was used to reveal differences between seasons (Peters 2018). Further analyses were conducted using linear mixed-effects models using the package lme4 (Bates et al. 2015). We tested the effects of the covariate vegetation height and density (model 1) as well as the covariate habitat types (model 2) on the response variable fGCM concentrations in two separate full models. This was because our sample size did not allow us to include all predictor variables together in one model. Thus, two models we computed to avoid overfitting. Both models included the collecting day as random factor in order to account for the different days of faecal sample collection within the three periods. Furthermore, the models included the explanatory variable collecting period (before harvest, harvest, after harvest) and type of farming practice (organic vs. conventional farming). Since there were never any significant interaction effects in our linear mixed-effects models ($p > 0.1$), we did not include interactions in our models. The full models were used to create a set of models with all combinations of the independent variables using the package MuMIn (Bartoń 2019). P values and estimates (β) were extracted by model averaging (including all models with delta AIC <

10). P values less than 0.05 were considered as significant. The residuals of the full models were checked for normal distribution by viewing QQ plots and histograms. Additionally, residuals were plotted against fitted values to analyse homogeneity, censored data problems (Fox 2015) and goodness of fit of the models. Post hoc tests were computed with significant categorical variables using the Tukey's all-pair comparisons method in the package multcomp (Hothorn et al. 2008).

Results

We collected 591 faecal pellet samples on an overall transect length of 72 km. Two hundred twelve samples were collected before, 212 during and 167 after harvest. Twenty-five faecal pellet samples were below the detection limit of fGCMs (before, 21; during, 2; after harvest, 2), but model diagnostics indicated no substantial censored data problems.

The influence of cereal harvest and farming practice on faecal fGCM concentrations

We found no significant differences in fGCM concentrations between collecting periods (Fig. 1, each $P > 0.1$, Tables 2 and 3) or farming practice (Fig. 2, each $P > 0.1$, Tables 2 and 3).

Fig. 1 fGCM concentrations of European hare faecal pellets collected before, during and after harvest in Lower Austria in the year 2018 ($n = 591$). Data are shown as medians with 25th/75th and 10th/90th percentiles. Same letters indicate no significant differences between groups (post hoc: $P > 0.1$). See text for details on statistics

Fig. 2 fGCM concentrations of European hare faecal pellets according to organic vs. conventional farming collected in Lower Austria in the year 2018 ($n = 591$). Data are shown as medians with 25th/75th and 10th/90th percentiles. Same letters indicate no significant differences between groups (post hoc: $p > 0.1$). See text for details on statistics

The influence of vegetation density and height on faecal fGCM concentrations

Vegetation density as well as vegetation height changed during the study period (Table 4). Vegetation height had no effect on fGCM concentrations (each $P > 0.1$, Table 3), whereas vegetation density had a significant influence on fGCM concentrations. The post hoc test revealed a significant difference between the categories open and dense (Table 5). Hence, faecal pellets found in plots with more than 50% of “open” vegetation density had significantly lower fGCM concentrations than faecal pellets found in plots with more than 50% of “dense” vegetation density (Fig. 3; $\beta = -4.014$, $p = 0.021$).

The influence of habitat types on faecal fGCM concentrations

The habitat-type stubble fields positively affected fGCM concentrations (Fig. 4; $\beta = 6.494$, $P = 0.031$), whereas bare ground had a significant negative effect on fGCM concentrations in European hares (Fig. 5; $\beta = -7.153$, $P = 0.013$). Thus, an increased proportion of stubble fields in the plots augmented fGCM concentrations, while an increased proportion of bare ground in the plots lowered fGCM concentrations. All other habitat types had no significant impact on the adrenocortical activity in European hares (each $P > 0.1$, Table 3).

Discussion

In our study, we used the non-invasive approach of measuring fGCM concentrations in order to detect an influence of anthropogenic-induced habitat changes. Faecal GCMs appear to be a reliable indicator of the physiological stress response, as well as the most practical and least invasive (Sheriff et al. 2011b). However, there are a number of potential confounding factors. Season, diurnal rhythm, changes in diet, reproductive state, individual and sex can all influence concentrations of fGCMs (Dantzer et al. 2014; Palme 2019). These possible

Table 5 Post hoc test results (estimates β and p -values) of the grouped vegetation densities for the covariate fGCM concentrations using the Tukey's all-pair comparisons method

	Estimate	Std. error	<i>P</i> value
Open vs. dense	− 4.014	1.344	0.021
Open vs. dense/open	− 5.837	2.245	0.063
Open vs. medium	− 1.475	3.020	0.987
Open vs. medium/dense	− 3.494	2.590	0.635
Medium vs. dense	− 2.539	2.823	0.886
Medium vs. dense/open	− 4.362	3.386	0.674
Medium/dense vs. dense	− 0.520	2.347	0.999
Medium/dense vs. dense/open	− 2.343	2.988	0.927
Medium/dense vs. medium	2.019	3.601	0.978
Dense/open vs. dense	1.823	2.016	0.884

risks were minimized as all faecal pellets were collected during one season, within a short time period and at nearly the same time of the day (Palme 2019). Possible confounding effects might have resulted from the individual and sex since we collected “anonymously” (Rehnus and Palme 2017). Hence, we cautiously interpret the result as a first indication of the impact that harvest may have on the stress level. Further studies should show whether the individual and sex play a crucial role in this context. The proportion of non-detects was higher before (9.9%) than during (0.9%) or after harvest (1.2%). Our maximum fGCM concentrations was 65.6 ng/g faeces, and we interpret that values of ≤ 2.1 ng/g faeces (lower than the detection limit of the EIA) indicate no stress. Hence, we assume no mayor influence of the unequal distribution of non-detects between the different periods on our results.

Influence of cereal harvest on fGCM concentrations

A meta-analysis, including mammals, birds, reptiles and amphibians, has shown that anthropogenic-induced disturbances including habitat modifications and machines were associated

Table 4 Relative frequency of vegetation height and density in the study area before, during and after harvest in Lower Austria in the year 2018

	Category	Classification	Area (%)		
			Before harvest	During harvest	After harvest
Vegetation height	Short	< 70 mm	2.81	7.72	29.03
	Medium	70–220 mm	2.87	23.96	14.82
	Tall	> 220 mm	94.31	68.32	56.16
Vegetation density	Open	< 25%	5.27	33.08	46.50
	Sparse	25–49%	9.00	1.76	0.27
	Medium	50–75%	21.64	16.83	14.38
	Dense	> 75%	64.09	48.32	38.85

Fig. 3 fGCM concentrations of European hare faecal pellets according to vegetation density collected in Lower Austria in the year 2018 ($n = 591$). Only the dense ($> 75\%$) and open ($< 25\%$) categories are shown. Data are shown as medians with 25th/75th and 10th/90th percentiles. Different letters indicate significant differences between groups. See text for details on statistics

consistently with increased fGCM concentrations (Dantzer et al. 2014). In contrast, we found no significant differences

in fGCM concentrations between three faeces collecting periods, including cereal harvest.

An effect of harvesting arable crops on fGCM concentrations is assumed when required habitat requisites disappear, and such a change leads to a lack of suitable habitats. In 2018, cereal harvest started early but was repeatedly interrupted by unsuitable weather conditions. Therefore, only 28% of the study area was affected by habitat changes during the “harvest” sampling period. The average field size, or even better the field edge index, determines the habitat diversity within a home range (Pegel 1986). As the average field size was low (1.84 ha) and the field edge index was large (23.77 km per 100 ha), we suggest that European hares could use plenty of different habitats unaffected by harvest within their home range. Non-farmed features, such as hedges, fallow land, and set-asides preferred by European hares (Smith et al. 2004; Pépin and Angibault 2007; Cardarelli et al. 2011; Vidus-Rosin et al. 2011; Schai-Braun et al. 2013), accounted for 11% of the agricultural landscape. Additionally, positively selected food plants such as lucerne (*Medicago sativa* L.), red clover (*Trifolium pratense* L.) and soybean (*Glycine max* M.) (Reichlin et al. 2006) accounted for 9% of the study area. This assumption is in line with the findings of Hunnink et al. (2020) that human disturbance including agriculture and farming practices were only found to be a secondary stressor compared to forage availability in impala (*Aepyceros melampus*). Furthermore, habitat complexity seems to be an important factor by explaining differences in fGCM levels in another

Fig. 4 The influence of the proportion of stubble fields within the 10-ha circular plots on fGCM concentrations of European hare faecal pellets collected in Lower Austria in the year 2018 ($n = 591$). The regression line is statistically significant. See text for details on statistics

Fig. 5 The influence of the proportion of bare ground within the 10-ha circular plots on fGCM concentrations of European hare faecal pellets collected in Lower Austria in the year 2018 ($n = 591$). The regression line is statistically significant. See text for details on statistics

small mammal the common vole (*Microtus arvalis*, Navarro-Castilla et al. 2013). Hence, we suggest that the providing of unaffected habitats could buffer an effect of agricultural practices due to harvesting in the European hare.

Influence of farming practice on fGCM concentrations

As predicted, the agricultural management system had no significant effect on fGCM concentrations of European hares during harvest. The conventionally managed land of the study area had a high proportion of non-farmed features, such as set-asides (organic 8.3%, conventional 7%) and hedges (organic 1.7%, conventional 3.2%), as well as small average field size (organic 1.62, conventional 1.8 ha) and a high field edge index (organic 25.12 km, conventional 24.65 km per 100 ha), and was, thus, comparable to the organically farmed study area. This suggests that a diverse small-scale landscape is more likely to limit the effect of cereal harvest on fGCM concentrations of European hares than the farming system. This is in line with the expectation of Bengtsson et al. (2005) that organic farming has a positive effect in intensively managed agricultural landscapes, but not in diverse small-scale landscapes.

Influence of vegetation density and height on fGCM concentrations

Changes in predation risk were associated with impacts on the stress levels within the genus *Lepus* (*Lepus americanus*; Sheriff et al. 2011b). In contrary to this, harvest-induced reduction of vegetation density led to lower fGCM concentrations in our study. This might be explained by Marboutin and Aebischer (1996) reporting that active European hares decreased time spent scanning after harvest because the landscape was easier to overview. Furthermore, European hares are morphologically well adapted to open landscapes due to their origin in the Eurasian steppe (Hackländer and Schai-Braun 2018). Cereal harvest increased the amount of open vegetation densities from 5 up to 47% in the study area but dense and medium vegetation densities still account for 53%. We assume that in a small-scale landscape, enough suitable habitats for shelter are provided after harvest for resting hares and rather more areas become accessible again for hares during activity (Rühe 1999; Mayer et al. 2018).

Vegetation height is often used to determine habitat utilization in European hares (Rühe 1999; Smith et al. 2004; Mayer et al. 2018). However, we found no influence of vegetation height on fGCM concentrations. This suggests that vegetation density should be considered more closely as an essential factor for active and resting European hares in future hare studies. This is in line with Neumann et al. (2011) reporting that cover value is especially important for shelter selection in resting European hares.

Influence of habitat types on fGCM concentrations

Higher fGCM concentrations due to stubble fields are difficult to interpret. Habitat degradation is associated with increased adrenocortical activity in a variety of wildlife species (Marra and Holberton 1998; Homan et al. 2003; Martínez-Mota et al. 2007; Jachowski et al. 2012; Johnstone et al. 2012; Rimbach et al. 2013; Balestri et al. 2014). However, previous studies on European hares indicated a positive habitat selection of stubble fields (Ahrens 1990; Lewandowski and Nowakowski 1993; Reitz and Léonard 1994) and an increased use of already cut cereal fields (Schai-Braun et al. 2014). Since stubble fields only occur through harvesting processes, increased fGCM level associated with stubble fields is not congruent with the findings that harvest did not alter the fGCM levels. Future studies have to show in which context this result should be seen.

Lower fGCM concentrations due to bare ground can be explained by the preference of such habitats by European hares (Schai-Braun et al. 2013). The dug-over fallen grains started to shoot and provided an additional food source due to rainy weather conditions (Pfister 1984; Späth 1989; Chapuis 1990).

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