

Ecological correlates of stress for a habitat generalist in a biofuels landscape

S.L. Fredebaugh-Siller, C.D. Suski, Z.C. Zuckerman, and R.L. Schooley

Abstract: Understanding the success of habitat generalist species requires knowledge of how individuals respond to stressors that vary across habitats within landscapes. Habitat structure can affect stress by altering predation risk, conspecific densities, and densities of heterospecific competitors. Increased demand for biofuels will alter habitat structure for species in agroecosystems worldwide. We measured stress responses of deer mice (*Peromyscus maniculatus* (Wagner, 1845)), a widespread habitat generalist, in a biofuels landscape. We quantified fecal corticosterone concentrations for individuals in four biofuel crops: switchgrass (*Panicum virgatum* L.), miscanthus (*Miscanthus × giganteus* Greef & Deuter ex Hodkinson & Renvoize), mixed prairie, and corn (*Zea mays* L.). We also evaluated stress responses of deer mice to the annual harvesting of corn. Deer mice inhabiting switchgrass and mixed prairie had higher fecal corticosterone concentrations compared with mice in corn and miscanthus. Fecal corticosterone concentrations correlated positively with abundances of conspecifics and behaviorally dominant voles (prairie vole, *Microtus ochrogaster* (Wagner, 1842); meadow vole, *Microtus pennsylvanicus* (Ord, 1815)) across habitats. Stress levels of deer mice depended on how habitat structure modified the competitive environment. Deer mice did not exhibit increased fecal corticosterone concentrations in response to corn harvest, a rapid and extensive habitat disturbance common to agroecosystems. Our research is the first to investigate how landscape change due to biofuels expansion can affect stress levels of individuals.

Key words: bioenergy, competition, deer mouse, corticosterone, habitat disturbance, *Microtus*, miscanthus, *Peromyscus maniculatus*, predation risk, switchgrass, voles.

Résumé : Pour comprendre le succès d'espèces généralistes en ce qui concerne l'habitat, il est nécessaire de connaître la réaction des individus aux différents facteurs de stress dans divers habitats au sein du paysage. La structure de l'habitat peut avoir une incidence sur le stress en modifiant le risque de prédation, la densité d'individus conspécifiques et la densité de concurrents hétérospécifiques. La demande accrue de biocarburants modifiera la structure des habitats d'espèces d'agroécosystèmes à l'échelle mondiale. Nous avons mesuré la réaction de stress de souris sylvestres (*Peromyscus maniculatus* (Wagner, 1845)), une espèce répandue et généraliste en ce qui concerne l'habitat, dans un paysage de biocarburants. Nous avons quantifié les concentrations de corticostérone fécale d'individus dans des zones à biocarburants de quatre types, à savoir, le panic raide (*Panicum virgatum* L.), le miscanthus (*Miscanthus × giganteus* Greef & Deuter ex Hodkinson & Renvoize), la prairie mixte et le maïs (*Zea mays* L.). Nous avons également évalué les réactions de stress de souris sylvestres à la récolte annuelle du maïs. Les souris sylvestres habitant dans le panic raide et la prairie mixte présentaient des concentrations de corticostérone fécale plus élevées que celles des souris habitant dans le maïs ou le miscanthus. Dans tous les habitats, les concentrations de corticostérone fécale étaient positivement corrélées à l'abondance d'individus conspécifiques et de campagnols (campagnol des prairies, *Microtus ochrogaster* (Wagner, 1842); campagnol des champs, *Microtus pennsylvanicus* (Ord, 1815)) au comportement dominant. Les niveaux de stress des souris sylvestres dépendaient de l'effet de la structure de l'habitat sur la concurrence environnante. Les souris sylvestres ne présentaient pas d'augmentation des concentrations de corticostérone fécale en réaction à la récolte du maïs, une perturbation rapide et importante de l'habitat répandue dans les agroécosystèmes. Nos travaux sont les premiers à examiner l'effet des modifications du paysage découlant de l'expansion des biocarburants sur les niveaux de stress d'individus. [Traduit par la Rédaction]

Mots-clés : bioénergie, concurrence, souris sylvestre, corticostérone, perturbation de l'habitat, *Microtus*, miscanthus, *Peromyscus maniculatus*, risque de prédation, panic raide, campagnol.

Introduction

Animals face many potential stressors that can include factors such as high population densities (Boonstra and Boag 1992; Bian et al. 2011; Sheriff et al. 2012), interspecific competition (Van Zwol et al. 2012), predation risk (Sheriff et al. 2012), habitat loss and fragmentation (Janin et al. 2011), and environmental stochasticity and climate change (Brown and Fuller 2006; Kiesecker 2011). Persistent elevated stress levels arising from these stressors can lower immune system function and increase disease risk (Ellis et al.

2012; Owen et al. 2012; Thomason et al. 2013). Chronic stress can also negatively impact fitness of individuals by lowering reproductive success (Cyr and Romero 2007) or survival (Goutte et al. 2010), which in turn can influence population dynamics (Sheriff et al. 2011).

Habitat structure is an additional factor that can affect stress levels of individuals by influencing perceived predation risk (Hik et al. 2001; Mateo 2007; Sheriff et al. 2012) and the social environment including conspecific densities (Pride 2005; Sheriff et al. 2012; Creel et al. 2013). Relatively less attention has been paid,

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however, to how habitat structure could affect stress levels via interspecific interactions other than predation, especially interactions with behaviorally dominant competitors (Grant 1970; Van Zwool et al. 2012). Additionally, stress of individuals could be influenced by habitat disturbances such as vegetation removal (Kuznetsov et al. 2004; Jaimez et al. 2012) if these landscape modifications change perceived predation risk or other stressors.

The growing demand for production of sustainable bioenergy crops is expected to greatly alter habitat structure in agricultural landscapes (Dale et al. 2011; Wiens et al. 2011). Conventional row crops such as corn (*Zea mays* L.) are currently used for biofuels production in the United States. However, second generation biofuels such as switchgrass (*Panicum virgatum* L.), miscanthus (*Miscanthus × giganteus* Greef & Deuter ex Hodkinson & Renvoize), and mixed prairies are possible replacements that could benefit wildlife (Fletcher et al. 2011). Most biofuels–biodiversity research has emphasized how species abundances respond to biofuel crops (Semere and Slater 2007; Bellamy et al. 2009; Robertson et al. 2011), and the impacts that biofuel production could have on wildlife at the individual level have not been quantified. The proposed integration of physiological assessments and landscape ecology (Ellis et al. 2012) has not been attempted for biofuels landscapes.

Deer mice (*Peromyscus maniculatus* (Wagner, 1845)) are an ideal study species for asking how habitat structure contributes to stress levels of a successful habitat generalist. Deer mice are the most widespread native species of small mammal in North America (Hofmann 2008). In agricultural landscapes of the midwestern United States, deer mice are the only native small mammal occurring in corn–soybean rotations (Getz and Brighty 1986; Whitaker 1996), where they are exposed to annual crop harvests that should represent habitat disturbances. In other habitats, deer mice are components of more diverse communities of small mammals. In grasslands, deer mice occur with meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) and prairie voles (*Microtus ochrogaster* (Wagner, 1842)). Deer mice and meadow voles are aggressive toward each other (Grant 1970), and deer mice avoid space occupied by the larger voles (Grant 1971). Hence, biofuel habitats that support voles could impose stress on deer mice through competitive interactions.

Here, we ask how stress levels of deer mice respond to habitat structure and disturbance that could influence perceived predation risk, conspecific abundances, and encounter rates with competitors. We hypothesized that stress levels of deer mice, as measured by fecal corticosterone concentrations, would differ among biofuel crops due to differences in habitat structure. Corn and miscanthus represent relatively open habitats with little undergrowth to provide concealment cover, which could result in greater perceived predation risk (Kotler 1984; Mateo 2007; Sheriff et al. 2012). Hence, we predicted that fecal corticosterone concentrations of deer mice would be higher in corn and miscanthus habitats compared with those for switchgrass and mixed prairie. However, this prediction might not be supported if stress levels of deer mice respond mostly to competitive interactions with conspecifics and heterospecifics, which could be stronger in switchgrass and mixed-prairie habitats. Finally, we predicted that deer mice living in corn fields would have elevated levels of fecal corticosterone following crop harvest due to the rapid and extreme habitat alteration.

Materials and methods

Site description

The University of Illinois Energy Farm is a 130 ha experimental farm located in central Illinois (40°3′49.864″N, 88°11′36.060″W) used for research on production of second generation and traditional biofuel crops. We sampled small mammals in plots of mixed tallgrass prairie, switchgrass, miscanthus, and corn. Plots were arranged in two spatial blocks: block 1 included two 0.69 ha

plots of each of the four biofuel crops and block 2 included one 3.53 ha plot of each crop. All plots were planted in 2008, with portions of miscanthus plots replanted in 2009 and 2010. All crops were monocultures except for mixed prairie that contained 28 species of prairie grasses and forbs (Feng and Dietze 2011). Mixed-prairie plots reached a mean height of 1 m before harvest. Switchgrass is a native, perennial prairie grass (Robertson et al. 2011) that was planted densely and grew to ~1.5 m tall before harvest. Miscanthus is an exotic, cold-tolerant, perennial species from Asia that is used as a second generation biofuel (Heaton et al. 2004; Semere and Slater 2007) and has a similar structure to bamboo (Fargione 2010). Miscanthus plants were spaced ~84 cm apart at planting and can grow to a height of 3 m before harvest. Corn plots were rotated to soybean every third year (next in soybean in 2013) and grow to ~2.5 m tall at maturity.

Sample collection

We selected fecal samples as a way to evaluate corticosterone concentrations because the method is noninvasive (Sheriff et al. 2010) and has been biochemically validated for deer mice (Harper and Austad 2000). Increased glucocorticoid production is not always indicative of chronic stress in wild animals (Dickens and Romero 2013). For deer mice, however, there is experimental evidence that increased fecal corticosterone concentration is an appropriate physiological marker for chronic stress in natural populations (Pedersen and Greives 2008).

Deer mice were captured using Sherman live traps spaced 6 m apart along one transect in each plot (16 traps in each 0.69 ha plot, 36 traps in each 3.53 ha plot). For the four biofuels, trapping occurred on one to four nights in September 2011, when crops were mature and prior to the annual corn harvest. Additional trapping occurred in corn and mixed-prairie plots after the corn harvest (two nights in October 2011 and three nights in November 2011). Traps remained open for ≤6 h to minimize holding time of individual deer mice, thus avoiding trap-related stress that could potentially influence corticosterone levels in fecal samples (Harper and Austad 2000). Captured animals were ear-tagged for individual identification, weighed, and their sex and age (adult or juvenile) were determined. Additionally, the reproductive status of each animal was classified as reproductive (females = pregnant or lactating; males = scrotal) or not reproductive. Fecal samples were collected from traps and immediately placed in labeled microcentrifuge tubes and frozen in liquid nitrogen. Samples were stored at –80 °C until extraction. For analysis, we used only the first fecal sample from adult mice; juveniles were excluded. We also used only samples from mice considered residents of a specific plot (i.e., not trapped in another plot during subsequent sampling). Of all mice captured, 63% were classified as residents and 37% were classified as nonresidents. Traps were cleaned of all debris and fecal material after each trap-night.

Conspecific and heterospecific abundances

We measured abundances of deer mice and voles (prairie vole + meadow vole) on plots with a catch-per-unit-effort (CPUE) index based on number of individuals captured per trap, adjusted for sprung traps (Beauvais and Buskirk 1999). Correlations between counts of captured individuals (i.e., CPUE) and density estimates from mark-recapture models are high for deer mice ($r^2 = 0.93–0.97$) and for prairie voles ($r^2 = 0.81–0.98$) (Slade and Blair 2000). We used the previously described number of traps and trap spacing. Trapping was conducted for four consecutive nights in August 2011 (abundance estimates before harvest of corn) and for four consecutive nights in October 2011 (abundance estimates after harvest of corn). This project was conducted under the approved University of Illinois Institutional Animal Care and Use Committee protocol No. 12100.

Fecal corticosterone measurement

Fecal corticosterone concentration was quantified based on extraction methods outlined in Keeley et al. (2012) and Metrione and Harder (2011). Briefly, samples were thawed and approximately 0.05 g of feces was weighed, mixed with 1 mL of 80% ethanol, and homogenized using a hand-held tissue homogenizer. Samples were then vortexed and placed horizontally on a plate shaker. After 14–18 h of shaking overnight, samples were centrifuged and used at a 1:10 dilution in the corticosterone enzyme immunoassay (EIA) kit (kit # ADI-900-097; Enzo Life Sciences, Inc., New York, USA; Rothschild et al. 2008) as per manufacturer instructions. Samples were run in duplicate. Reported levels were within assay detection range. There were six plates run, with the first plate being used only to determine an acceptable dilution level, and each plate contained samples from the four different crops. Our inter-assay CV was 9%. Our intended intra-assay CV cutoff was 10% as per manufacturer recommendations. However, 27 out of 105 samples fell outside this range but had a CV < 15%, which is still within an acceptable range based on our experience with this technique.

Statistical analysis

We tested for differences in fecal corticosterone concentrations of deer mice using mixed linear models and restricted maximum-likelihood estimation (PROC MIXED, SAS Institute Inc. 2009). We \log_{10} -transformed corticosterone measures so that model residuals passed normality tests (Kolmogorov–Smirnov test, all $P > 0.05$; PROC UNIVARIATE, SAS Institute Inc. 2009). We modeled block as a random effect, using variance components as the covariance structure, and tested significance of the blocking using the Wald Z test. Other independent variables were treated as fixed effects and we report results of type III tests.

First, we tested for differences in corticosterone levels of deer mice among the four biofuel crops to ask if stress levels differed among habitats. Each corticosterone sample was from a different individual (15–17 individuals per crop, total $n = 64$). Then, we expanded the model to include covariates that might explain observed differences in corticosterone concentrations among crops including sex, reproductive status, conspecific abundance, and vole abundance. Because voles were only captured in switchgrass and mixed-prairie plots, we also evaluated the expanded model using the subset of deer mice from these two habitats ($n = 32$).

To evaluate whether deer mice responded to the disturbance caused by the annual harvest of corn, we compared corticosterone levels of mice in corn and mixed prairie (control habitat with no harvesting) both before (September 2011) and after (October–November 2011) the corn harvest. Again, each corticosterone sample was from a different individual (16–24 individuals per crop each time period, total $n = 74$). We tested for effects of crop (corn vs. mixed prairie), time (before harvest vs. after harvest of corn), and a crop \times time interaction. Our prediction would be supported by a significant interaction in which fecal corticosterone concentrations of deer mice increase between time periods in corn plots but not in prairie plots.

Results

Fecal corticosterone concentrations in deer mice differed among biofuel crops ($F_{[3,59]} = 3.27$, $P = 0.027$). Mice had elevated fecal corticosterone concentrations in switchgrass and mixed prairie relative to corn and miscanthus (Fig. 1). Block was not an important source of variation ($Z = 0.52$, $P = 0.301$).

The expanded model with covariates indicated that fecal corticosterone concentrations in deer mice were influenced by crop type, conspecific abundance, and vole abundance (Table 1, Fig. 2).

Fig. 1. Fecal corticosterone concentrations (ng/g) for deer mice (*Peromyscus maniculatus*) in four biofuel crop plantings ($n = 15$ –17 individuals per crop). Crops with the same letters do not differ statistically ($P > 0.05$). Horizontal lines are medians, boxes indicate 25th and 75th percentiles, and whiskers indicate 5th and 95th percentiles.

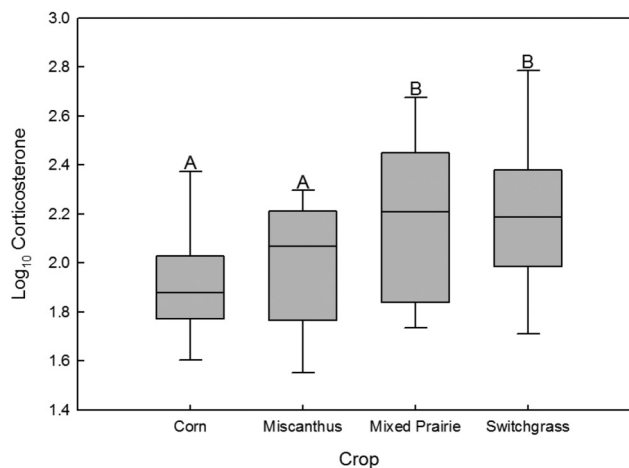


Table 1. Mixed linear model for fecal corticosterone concentrations in deer mice (*Peromyscus maniculatus*) inhabiting biofuel plantings.

Fixed effect	df	F	P
Crop	3, 55	3.26	0.028
Sex	1, 55	0.00	0.974
Reproductive status	1, 55	0.06	0.815
Conspecific abundance	1, 55	4.92	0.031
Vole abundance	1, 55	5.30	0.025

Note: Crop consists of mixed prairie, switchgrass, miscanthus, and corn. Sex represents samples from 26 males and 38 females. Spatial block was a random effect (not shown).

Specifically, corticosterone concentrations correlated positively with abundances of both conspecifics ($\beta = 2.895$, $SE = 1.305$) and voles ($\beta = 9.870$, $SE = 4.287$). After controlling for variation associated with the abundance of both conspecifics and voles, fecal corticosterone concentration in deer mice was lower in corn ($P = 0.010$), miscanthus ($P = 0.040$), and switchgrass ($P = 0.042$) relative to mixed prairie. Fecal corticosterone concentrations were not related to sex or reproductive status (Table 1). As before, the random block effect was not significant ($Z = 0.64$, $P = 0.260$). Our results from the mixed linear model using only deer mice from switchgrass and mixed-prairie habitats were consistent with results from the full data set (supplementary Table S1).¹

Our analysis of stress in deer mice in relation to corn harvesting indicated that fecal corticosterone concentrations depended on crop type ($F_{[1,69]} = 12.73$, $P < 0.001$) but not on sampling time ($F_{[1,69]} = 0.62$, $P = 0.435$) or a crop \times time interaction ($F_{[1,69]} = 1.41$, $P = 0.240$). Fecal corticosterone concentrations were higher in prairie than in corn during both the before and after harvest periods (Fig. 3). Block was not a significant random effect ($Z = 0.58$, $P = 0.282$).

Discussion

Our investigation of stress levels of deer mice provided insights into what factors affect stress for a successful habitat generalist. Contrary to our prediction, deer mice had lower fecal cortico-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0157>.

Fig. 2. Surface plot of fitted values for fecal corticosterone concentrations (ng/g) in deer mice (*Peromyscus maniculatus*) from a mixed model with a random block effect and biofuel crop, conspecific abundance, vole abundance, sex, and reproductive status as fixed effects. Conspecific and vole abundances are number of individuals captured per trap-night on plots where corticosterone levels were measured.

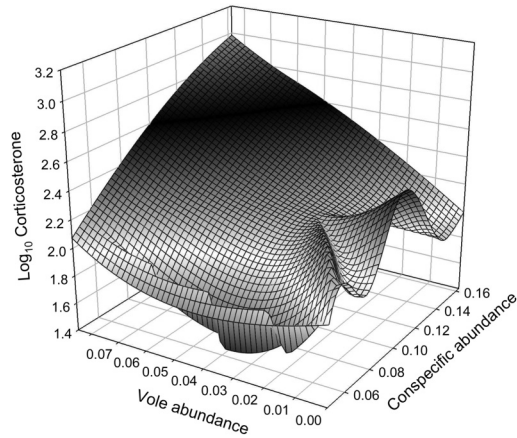
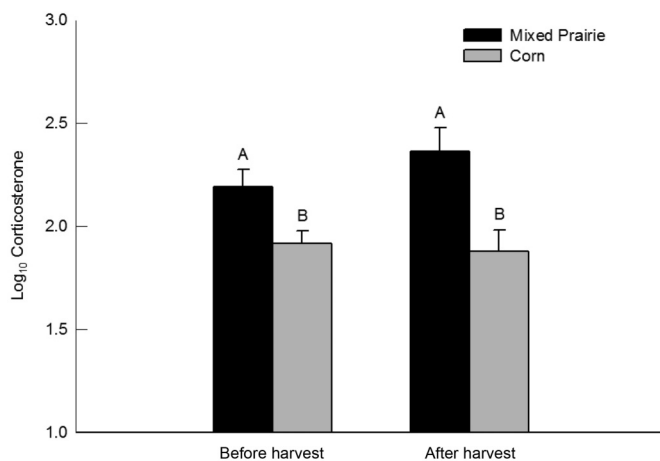


Fig. 3. Fecal corticosterone concentrations (ng/g) mean + 1 SE of deer mice (*Peromyscus maniculatus*) on mixed prairie and corn plots before and after the fall harvest of corn. Bars with the same letters do not differ statistically ($P > 0.05$). Stress levels of deer mice in corn fields did not respond to habitat disturbance associated with harvest.



sterone concentrations in corn and miscanthus habitats, which are more open at ground level, compared with the densely vegetated switchgrass and mixed prairie. Predation risk may have played a role in this pattern of habitat-specific stress. Possible trade-offs exist between hiding cover and obstructive cover that can affect perceived predation risk. In some instances, vegetation may increase predation risk for species that require visual detection to avoid predation (e.g., Schooley et al. 1996). However, deer mice generally avoid open microhabitats if cover is available (Kotler 1984; Travers et al. 1988; Stapp and Van Horne 1997), and deer mice are at greater risk of capture when attacked by owls in open areas (Longland and Price 1991). Moreover, when we compared stress levels for deer mice in switchgrass and mixed prairie only (supplementary Table S1),¹ which have similar vegetation cover, we still found fecal corticosterone concentrations were influenced by conspecific and heterospecific abundances. These results suggest perceived predation risk due to vegetation structure is unlikely to be the key driver of stress in deer mice. However, we

acknowledge that a definitive test would require experimental manipulation of predation risk (e.g., Sheriff et al. 2009).

As predicted, stress levels of deer mice were associated positively with conspecific densities. Our results are consistent with studies of other species that have found a positive relationship between corticosterone levels and densities of conspecifics (Boonstra and Boag 1992; Rogovin et al. 2003; Harper and Austad 2004; Bian et al. 2011; Sheriff et al. 2012). Intraspecific competition for resources, and food in particular, may be occurring in this agricultural landscape (Davidson and Morris 2001), and restricted food availability can increase stress levels (Harper and Austad 2000). Additionally, the higher stress levels could reflect mice competing for nesting areas or having aggressive interactions to establish dominance (Grant 1970).

We also found that deer mice inhabiting crops with higher abundances of voles had increased corticosterone levels. Voles are behaviorally dominant to deer mice (Grant 1970), and only co-occurred with deer mice in switchgrass and mixed prairie. Elevated fecal corticosterone concentrations of deer mice in switchgrass and mixed prairie reflected the presence of the larger, dominant voles (Grant 1970; Hallett et al. 1983) in those habitats. Deer mice and voles do not have high overlap in diet (Abramsky et al. 1979); voles are herbivores that mainly consume grasses and forbs, whereas deer mice are omnivores (Hofmann 2008). Nevertheless, evidence suggests interference competition occurs between deer mice and voles. In field experiments, removal of voles from grassland plots results in expanded space use and higher abundances of deer mice (Grant 1971; Abramsky et al. 1979). Aggressive interactions with competing heterospecifics can result in elevated stress hormone levels, which have the possibility to impact offspring (McCormick 2009).

We cannot completely rule out differences in diet of deer mice among habitats as a factor contributing to observed patterns for fecal corticosterone concentrations (Goymann 2012). Diets with high fiber content could result in greater fecal output rates, which could decrease fecal corticosterone concentrations for a given production of corticosterone (Hayssen et al. 2002; Goymann 2012). However, this scenario is likely an oversimplification because increased fiber consumption can increase, decrease, or have no effect on fecal corticosterone concentration (Dantzer et al. 2011; Goymann 2012). Moreover, because deer mice are highly omnivorous (Hofmann 2008), we would not expect their diets to vary substantially among habitats during the same season, which would be more likely for a strict herbivore that might feed on a particular plant species in a given habitat.

Most species exposed to anthropogenic disturbances and habitat alterations experience some degree of stress following such events (Kuznetsov et al. 2004; Jaimez et al. 2012). Surprisingly, stress levels for deer mice were unaffected by the extensive habitat disturbance related to corn harvest. Individuals displayed higher concentrations of fecal corticosterone in mixed-prairie plantings designed to mimic native tallgrass prairie than in barren cornfields after harvest. Deer mice occur over a large geographic range and may be physiologically adjusted to the disturbance regimes of different ecosystems. Their ability to tolerate disturbances and occupy open environments (Hofmann 2008; Brehme et al. 2011) likely contributes greatly to their generalist lifestyle. For instance, abundances of deer mice are not negatively affected by other landscape alterations that rapidly remove cover such as mowing (Slade and Crain 2006; Kaufman and Kaufman 2008) and fire (Brehme et al. 2011; Zwolak et al. 2012). An intriguing hypothesis to explain our observed pattern for fecal corticosterone is that deer mice may have experienced an annual disturbance of crop harvests for a sufficient number of generations to have evolved a physiological tolerance to such perturbations.

Expansion of biofuel crops across landscapes throughout the world is projected to affect species diversity and community composition (Robertson et al. 2011; Wiens et al. 2011). We have demon-

strated that biofuel crops could have more subtle effects at the individual level by influencing stress levels, even for habitat generalist species. Our results also indicate that habitat structure can have its strongest effect on stress by modifying the competitive environment through changes in the distribution and abundance of conspecifics (Creel et al. 2013) and heterospecifics. Our research represents the first use of fecal glucocorticoids to noninvasively monitor stress in animals in relation to production and harvesting of biofuels. Future research might benefit from use of other physiological measures, such as free glucocorticoids and corticosteroid-binding globulin (Breuner et al. 2013), to understand the stress ecology in dynamic agroecosystems.

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