

DANGEROUS MISPERCEPTIONS WITH CONSEQUENCES: SURVIVAL OF EASTERN  
COTTONTAILS ON RESTORED GRASSLANDS SURROUNDED BY AGRICULTURE

BY

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THESIS

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## ABSTRACT

Habitat loss and degradation is a main threat to biodiversity, and the expansion of intensive agricultural practices has negatively affected wildlife populations worldwide. To counteract these effects, large-scale restoration programs have been developed. In the Midwestern United States, where tallgrass prairies have been reduced by >99%, the Conservation Reserve Program has created patches of grassland habitat within a larger matrix dominated by agricultural fields that are temporally dynamic due to planting and harvesting of crops. The effects of the surrounding landscape on restoration success of wildlife species is largely unknown. My main objective was to examine how landscape processes interact with real and perceived predation risk to affect survival of a key herbivore and important prey species, the eastern cottontail (*Sylvilagus floridanus*), in restored grassland habitats and the surrounding agricultural matrix. From June 2014 through June 2016, I radio-collared 95 cottontails and tracked their movements until the transmitter failed or mortality occurred. I then constructed known-fate models in program MARK to identify factors that affected survival rates. I also conducted giving-up density (GUD) experiments in grasslands and adjacent agricultural fields to determine if there were differences in perceived predation risk. As expected, survival of cottontails was higher when they used restored grasslands relative to when they used surrounding habitats. Contrary to my prediction, however, cottontails did not accurately perceive predation risk as they perceived agricultural fields to be safer than grasslands. This mismatch could be due to their emphasis on protecting themselves from avian predation rather than mammalian predation. However, mammals were the main predators in this system, predominately coyotes (*Canis latrans*). My study demonstrates how adjacency of restoration sites to other landscape elements can produce unintended consequences and highlights the complexities of achieving restoration in a highly altered landscape.

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## TABLE OF CONTENTS

<b>Introduction .....</b>	<b>1</b>
<b>Methods .....</b>	<b>5</b>
<b>Results .....</b>	<b>15</b>
<b>Discussion .....</b>	<b>19</b>
<b>Tables and Figures.....</b>	<b>26</b>
<b>Literature Cited .....</b>	<b>35</b>
<b>Appendix: Supplementary Materials.....</b>	<b>42</b>

## INTRODUCTION

Habitat loss and fragmentation is a main threat to biodiversity worldwide (Stuart et al. 2004; Newbold et al. 2015). By the early 20<sup>th</sup> century, the terrestrial biosphere made the transition from being mostly wild to mostly anthropogenic (Ellis et al. 2010). With this large forfeiture of natural habitat, many wildlife populations have declined and species across multiple taxa are facing the threat of extinction (Wilcove et al. 1998; Brooks et al. 2002; Stuart et al. 2004; Schipper et al. 2008). To recover biodiversity and ecosystem services, large-scale restoration projects are needed (Hobbs and Norton 1996; Cosentino et al. 2011; Menz et al. 2013). Landscape restoration is especially relevant to agroecosystems in which restoration outcomes can depend on broader landscape heterogeneity (Tschardt et al. 2005; Concepción et al. 2008; Fahrig et al. 2011) and matrix effects (Donald and Evans 2006; Mulligan et al. 2013).

The Midwestern United States serves as a classic case of these threats to biodiversity and attempted interventions. Temperate grasslands of the Midwest are the most altered biome worldwide and the least protected ecosystem (Hoekstra et al. 2005). Nearly the entire tallgrass prairie has been converted for agricultural purposes (Samson and Knopf 1994). This agricultural intensification is unlikely to stop due to increasing demands to produce biofuel crops (Secchi and Babcock 2007; Fargione et al. 2009; Sayer et al. 2013). The extensive loss of natural habitat combined with effects of fragmentation has led to dramatic population declines of multiple wildlife species (Howe 1994; Samson and Knopf 1994; Sauer et al. 2003; Camill et al. 2004).

The most prominent agri-environment scheme to restore natural habitats in this intensive farming region is the United States Department of Agriculture's (USDA) Conservation Reserve Program (CRP). Since its inception in 1985, this program has encouraged landowners in designated areas through financial incentives to remove their land from agricultural production

and to establish natural habitat. Enrollment for the first few years of the program were slow, but by 1989 there was >12 million ha enrolled (Ferris and Siikamaki 2009). In 2008, an additional initiative—State Acres for Wildlife Enhancement (SAFE)—was added that focuses on restoring habitat to benefit high-priority wildlife species. As of January 2017, approximately 586,815 ha of land was enrolled into the SAFE initiative (USDA Farm Service Agency 2017).

Although simply increasing the amount of grassland habitat can benefit wildlife populations, landscape context and connectivity also can be consequential (Bell et al. 1997; Cosentino et al. 2011; Metzger and Brancalion 2013). Newly created habitat areas may not be large enough to sustain populations alone and become patches highly influenced by the surrounding landscape (Kuussaari et al. 2009; Brudvig 2011). Such effects can be especially likely for programs such as CRP and SAFE that rely on private landowner enrollment and cannot necessarily establish large tracts of land. The result is often multiple, small habitat patches embedded within the larger matrix of agricultural fields. Moreover, the surrounding landscape is temporally dynamic due to crop planting and harvesting so the hostility of the matrix may vary seasonally (Baundry et al. 2003; Vasseur et al. 2013). The adjacency of natural grassland areas and agricultural lands allows for the potential of landscape supplementation, complementation and source-sink dynamics (Dunning et al. 1992). The outcome of these landscape processes depends on both the real and perceived mortality risks for species that cross edges and use both restored patches and adjacent human-dominated habitats. Mismatches in perception and reality can have fitness consequences and in the extreme lead to ecological traps (Robertson and Hutto 2006) producing unintended consequences for restoration programs.

I selected eastern cottontails (*Sylvilagus floridanus*, hereafter cottontails) as a focal species to investigate how landscape processes affect wildlife using restored grasslands in a

dynamic agroecosystem in Illinois. Cottontails can exist in human modified landscapes (Althoff et al. 1997) and will use both restored grasslands and adjacent agricultural fields (Mankin and Warner 1999a). They are also important herbivores that can strongly alter species abundances and community structure of plants through selective foraging (Huntly 1991; Nisi et al. 2015). Additionally, cottontails serve as a main prey item for both mammalian and avian predators (Petersen 1979; Young et al. 2006; Randa et al. 2009), and they are a game species in Illinois valued by the public. Coincident with the intensification of agriculture in the region, cottontails declined dramatically between the 1950s and 1980s (Mankin and Warner 1999b). Despite the initiation of CRP in 1985, population declines of cottontails have continued (Fig. 1).

What could be limiting the recovery of cottontails? In addition to the altered landscape, cottontails have been dealing with a major shift in potential predation risk. Coyotes (*Canis latrans*) were historically uncommon in Illinois, but numbers began to increase in the 1970s and coyotes are now the top predator in the region (Heske and Miller 1995; Gosselink et al. 2003). Mammal prey, particularly lagomorphs and rodents, make up the majority of the coyote's diet (Fichter et al. 1955; Korschgen 1957; Brillhart and Kaufman 1995), and coyotes can be the main predator of cottontails (Cox et al. 1997). Since 1981, coyotes and cottontails have exhibited opposite population trends (Fig. 1;  $r = -0.54$ ,  $p = 0.0007$ ,  $n = 35$ ). The landscape of fear (Laundré et al. 2010) for cottontails should reflect this rise of a top predator.

My main objective was to assess how landscape processes interact with real and perceived predation risk to affect survival of the eastern cottontail in restored grassland habitats and the surrounding agricultural matrix. I specifically wanted to evaluate the influence of the dynamic nature of agricultural systems by comparing habitat use and survival between seasons when crops were present and absent from the landscape. I tested the following hypotheses and

predictions. Survival of cottontails should be higher in habitats that provide dense vegetative cover and concealment from predators, especially coyotes. Therefore, I predicted higher survival rates for cottontails when they used restored grasslands relative to when they used agricultural fields due to grasslands areas having increased amounts of vegetation cover near the ground. This habitat differential should increase when crops are harvested and agricultural fields become barren. Likewise, overall survival should be lower during the non-growing season due to reduced cover on the landscape and constrained movements by cottontails (Mankin and Warner 1999a) that could create a 'pantry effect' for predators. Male cottontails do not generally maintain strict territories; however, they exhibit a dominance hierarchy and compete for breeding opportunities with females (Chapman 1982). Therefore, males may increase their home range size during the mating season, which is March through September in my region (Trent and Rongstad 1974; Bond et al. 2001a; Walker 2003), to gain access to more females. This home range expansion, and the fact that increased movements can lead to higher predation rates (Bond et al. 2001a), leads me to predict that male cottontails will have lower survival than females. If cottontails can correctly assess habitat-specific predation risk, then patterns for perceived risk and survival should align. Hence, I expected cottontails to perceive the restored grasslands as having a lower risk of predation because heterogeneous vegetation should provide better concealment from predators. Finally, I investigated other relevant aspects of predator-prey interactions by determining causes of cottontail mortalities and quantifying associations among daily activity patterns of cottontails, coyote activity, and timing of cottontail mortalities.

## METHODS

### *Study areas*

I conducted all fieldwork at the Sibley and Saybrook Habitat Areas located in east-central Illinois (Ford and McLean County, respectively). Both sites lie within the Grand Prairie Region that was historically covered by tallgrass prairie but has since been converted to agricultural land. Sibley Habitat Area is a single 259-ha parcel with little relief (elevation ranged from 238 m to 252 m ASL). Saybrook Habitat Area includes multiple parcels ranging in size from 8 to 129 ha. However, I focused on two specific parcels: Saybrook Main site was 129 ha and Saybrook Anchor site was 65 ha (elevation ranged from 252 m to 273 m ASL). These restored grassland sites included a mix of warm season grasses (e.g., big bluestem, *Andropogon gerardi*; little bluestem, *Schizachyrium scoparium*; switchgrass, *Panicum virgatum*; Indian grass, *Sorghastrum nutans*), cool season grasses (e.g., smooth brome, *Bromus inermis*; wild rye, *Elymus virginicus* and *E. canadensis*), forbs, and invasive plants such as Canada thistle (*Cirsium arvense*) and green and giant foxtail (*Setaria spp.*). The Illinois Department of Natural Resources (IDNR) managed both restoration sites with the main purpose of providing high-quality grassland habitat for ring-necked pheasants (*Phasianus colchicus*) and increasing regional hunting opportunities. Land management techniques implemented by IDNR included prescribed burning, mowing, and herbicide application targeting invasives.

The surrounding landscape was dominated by corn and soybean crop fields (Fig. 2), which is characteristic of intensively farmed portions of the Midwest region. Ford County consists of 96.7% cropland and McLean County consists of 94.5% cropland (USDA NASS 2012). Herbicides are used to control weeds during the growing season so agricultural fields, especially corn, do not provide dense ground cover (Mankin and Warner 1999a).

Climatic conditions during this study were typical with average winter (December to March) temperatures of 0°C, and average summer (June to September) temperatures of 22°C. The annual precipitation was slightly above normal for all three years, with 2015 being the wettest year of the study, but averaged 110.5 cm across 2014-2016 compared to the 91.7 cm (mean from 1901 to 2000). Annual snowfall was variable with 104.1 cm in 2014, 54.8 cm in 2015, and 36.6 cm in 2016 (mean for 1981 to 2010 is 52.0 cm; NOAA 2017).

### *Capture and Radiotracking*

Eastern cottontails were captured on grassland study sites from June 2014 to November 2015 using a combination of Tomahawk live traps (Model 207, Tomahawk Live Trap Co., Tomahawk, Wisconsin) and wooden box traps. I baited traps with fresh apple slices and a rabbit urine scent lure (Wildlife Control Supplies, East Granby, Connecticut; WCS Rabbit Urine). Traps were set in the late afternoon and checked the following day by 12:00. For all captured individuals, I recorded their sex, body mass, and capture location. I uniquely marked all individuals with a passive integrated transponder (PIT) tag, and cottontails weighing  $\geq 800$  g were fitted with a 20-g radio transmitter with a mortality sensor (Model M1555, Advanced Telemetry Systems, Isanti, Minnesota) attached to a cable-tie collar. Handling time was limited to  $\leq 30$  min and individuals were released at their capture site.

I located radiomarked individuals using a three-element yagi antenna via triangulation or homing techniques a minimum of once per week until the mortality sensor activated or the transmitter failed. To increase the accuracy of triangulation calculations, I acquired bearings from locations with a minimum separation of 15°. Additionally, if an individual was active, all bearings were taken within 20 min. To account for temporal variation in movements, I

conducted radiotelemetry at varied times that included diurnal, crepuscular, and nocturnal sampling.

Mortality sensors activated when a transmitter remained stationary for 8 h. When this sensor was triggered, I recovered individuals to determine the location, habitat, and presumed cause of the mortality. I categorized the cause of mortality as mammalian predation, avian predation, unknown predation, vehicular, or other. I assigned categories by examining the site for predator sign (e.g., scat, tracks, feathers) and inspecting cottontail remains when present for indicators (e.g., bite marks on collar or base of neck, chest cavity eaten, buried carcass, bone fragments, and blood or fur trail; Trent and Rongstad 1974; Cox et al. 1997).

#### *Home Range and Grassland Use*

I divided the study period into two seasons for analysis based on the harvest and growth of crops to reflect major changes in landscape context of the grasslands. The majority of crops were harvested by mid-October (19 to 25 October, 2015 and 17 to 23 October, 2016) and growth of crops sufficient to provide cover for cottontails occurs by June (Mankin and Warner 1999a). Therefore, the ‘crop-up season’ was defined as 1 June through mid-October, and the ‘crop-down season’ was defined as mid-October to 31 May.

I calculated locations of cottontails from the telemetry data with LOAS 4.0 (Ecological Software Solutions, LLC, Hegymagas, Hungary). Using  $\geq 3$  bearings, I employed the maximum likelihood estimator and calculated error ellipses using the 95% chi-square distribution. Any triangulations with error ellipses  $\geq 4$  ha were discarded (Fritsky 2006), and most estimated locations had much smaller error ellipses. Individuals that were located far into agricultural

areas had larger error ellipses, but even for these individuals, I was confident in my habitat classification of the location due to the large size of agricultural fields.

I used the calculated locations to estimate annual and seasonal 95% home ranges with kernel utilization distributions (KUD) using  $h_{REF}$  smoothing parameters in the ADEHABITAT package in R (Calenge 2006). I estimated home ranges for individuals with  $\geq 15$  relocations within the respective season. This cut-off included individuals with fewer locations than what is typically recommended ( $>30$ ; Seaman et al. 1999; Wauters et al. 2007), but allowed me to retain 49 individuals (52% of the sample) that would have been discarded while still providing reliable information on areas used by cottontails.

To determine factors that influenced size of home ranges (95% KUD), I constructed linear mixed models with a normal error distribution and an identity link in program R (package lme4). Sex, site, body mass at time of collaring, and season were included as fixed effects, and individual was treated as a random effect. I used mass at capture as a proxy for age because it is difficult to determine the age of rabbits past 100 days (Lord 1963), and due to the weight requirement for radiocollaring ( $\geq 800$  g), all collared cottontails were considered older than 100 days. All singular and additive combinations of covariates and a sex x season interaction were modeled, as well as a null model for comparison. I used  $AIC_c$  (Akaike Information Criterion adjusted for small sample size; Burnham and Anderson 2002) to rank models.

I digitized habitats as grassland, cropland (noting corn or soybean for different years), and developed (roads, mowed roadsides, farmsteads, and gravel parking areas) in ArcMap 10.4 (ESRI, Redlands, California) based on 2012 Illinois NAIP digital orthophoto quadrangles (Illinois State Geological Survey 2015) and field reconnaissance. Using ArcMap, I then

identified the habitat composition (grassland, cropland, and developed) of each core area and home range.

Although all cottontails were captured initially on grasslands, most individuals used surrounding agricultural fields and developed areas to varying extents. To assess potential predictors for the proportion of grassland habitat within a cottontail's home range, the inverse of their propensity to use surrounding habitats, I constructed generalized linear mixed models (GLMMs) in program R using package nlme. Models were fitted with a binomial error structure and the logit link function. Sex, site, body mass at time of collaring, and season were included as fixed effects, and the GLMMs accounted for repeated measures on each individual cottontail (random effect). All singular and additive combinations of covariates were modeled, plus a sex x season interaction, and a null model for comparison. I used  $AIC_c$  (Burnham and Anderson 2002) to rank models. Models within 2  $\Delta AIC_c$  units were considered competitive models, and final parameter estimates and 95% CIs were calculated using model averaging (Burnham and Anderson 2002).

### *Survival Analysis*

I used known-fate modeling in program MARK (White and Burnham 1999) to evaluate survival of radiomarked cottontails based on weekly encounter histories from 28 June 2014 to 17 September 2016 (114 weekly intervals). I used a staggered entry design in which cottontails were added to the data set on the date that they were collared. Individuals whose signal was lost due to transmitter failure or movement outside the study area were right censored. I used a two-stage approach to identify variables related to survival while preventing overparameterization of models. The initial model set contained all single effects and additive combinations of season (crop-down = 0, crop-up = 1), mass at capture, sex (female = 0, male = 1), and site as covariates,

plus a sex x season interaction due to the expectation of males moving more during the breeding season (Trent and Rongstad 1974) and having lower survival. The important covariates were then incorporated with additional covariates of habitat use to build a second model set. I calculated the habitat covariates by assuming the observed telemetry locations during each week were representative of the proportion of time the individual spent in each habitat (Griffin and Mills 2009). For example, an individual that had four locations within the weekly time interval with two being in grassland, one in developed, and one in corn would have a proportional habitat use of 0.50, 0.25, and 0.25, respectively. I incorporated this proportion as a time-varying individual covariate for survival (Griffin and Mills 2009). All singular and additive combinations of covariates were modeled, plus combinations including the interaction of sex x season and four interactions for sex x habitat use (e.g., sex x grassland use). I used  $AIC_c$  to rank models, and  $AIC_c$  and model deviance to evaluate covariate importance during both stages.

### *Predator-Prey Activity Patterns*

To estimate daily activity patterns for cottontails and coyotes in my region, I used data from camera traps deployed on 30 grassland restoration sites (median = 29 ha), including the Sibley and Saybrook sites, in central Illinois (Berry et al. 2017). Each site was sampled with four cameras (Bushnell Trophy Cam, Model 119436c) for four consecutive weeks during the crop-up season (2014) and again during the crop-down season (2014-2015) for a total of 4,638 camera nights. See Berry et al. (2017) for additional sampling details. For both species, I tallied the number of independent photographs (>60 min apart) for 1-h intervals. I tested for seasonal differences in daily activity patterns for cottontails using a Chi-squared test for grouped data (Kovach 2009). Data for coyotes were too sparse to examine seasonal patterns. Other

mammalian carnivores that might prey on cottontails were rare including red fox (*Vulpes vulpes*, 0 photographs) and American mink (*Neovison vison*, 2 photographs).

### *Timing of Cottontail Mortalities*

At each study site, automated radio telemetry systems (ARTS) were used to monitor the radiomarked cottontails. ARTS were comprised of a tower (10.7 – 13.7 m tall), six 3-element yagi antennas, and an automated receiving unit (ARU; Alessi et al. 2010; Ward et al. 2013; Celis-Murillo et al. 2016). Between 1 and 6 ARUs were active on a given site at a time. Each ARU records the signal strength, noise, and pulse width for each of the frequencies on a programmed list for each of the 6 antennas attached to each ARU. Changes in distance and transmitter antenna orientation relative to the ART antennas result in fluctuations of signal strength that can be used to infer activity and animal movement (see Alessi et al. 2010; Ward et al. 2013 for details).

To determine when a cottontail died, I reviewed ARU data from the interval preceding the date when I had determined that mortality had occurred in the field. I identified the hour of day when movement ceased (i.e., signal strength was constant) as the time of death. Often there was an extreme increase in signal strength or a rapid shift in animal bearing immediately prior to the estimated time of death. Such rapid increases likely were the result of a mammalian predator or raptor moving the transmitter >1 m above the ground (Deppe et al. 2015; Celis-Murillo et al. 2016), or a predator moving a dead cottontail a large distance. Therefore, I used the initial change in signal strength to estimate the time of death. I tested for differences in time of death for cottontails between the crop-up and crop-down seasons using the nonparametric Mardia-Watson-Wheeler Test (Kovach 2009).

## *Measuring the Landscape of Fear*

To determine if perceived predation risk by cottontails differed between restored grasslands and surrounding crop fields of corn and soybeans, I attempted to measure the giving-up density (GUD; Brown 1988; Bedoya-Perez et al. 2013) in each habitat during the crop-up season (September 2015) and the crop-down season (April 2016). Despite running the GUD experiment three times during the crop-down season, most trials resulted in no foraging by cottontails, providing insufficient data. Therefore, I only analyzed GUDs for the crop-up season.

GUD is the amount of resources remaining in a depletable resource patch after a set period that includes foraging by the focal species (Brown 1988; Duggan et al. 2012). GUD provides an estimate of the quitting harvest rate (H) that can be expressed as

$$H = C + P + \text{MOC}$$

where C is the energetic cost of metabolism and activity, P is the cost of predation, and MOC is the missed opportunity cost (i.e., cost of not foraging elsewhere.) My design included spatial blocking in which I conducted GUD trials for the habitats being compared on the same day under identical climatic conditions (see below). Thus, the energetic costs of foraging (C) were equal across habitats. Likewise, because each cottontail had the opportunity to forage in all habitats, simply by moving a short distance across the ecotone, missed opportunity costs of foraging (MOC) should have been integrated across habitats (Brown and Alkon 1990). Therefore, any differences in GUDs among habitats should reflect differences in perceived predation risk (P; (Brown 1988; Brown and Alkon 1990; Stephens et al. 2007). A lower GUD would indicate that a habitat is perceived as safer. GUD experiments have been successfully applied to assess foraging costs for cottontails (Abu Baker and Brown 2009; Abu Baker et al. 2015).

The GUD experimental setup consisted of 15 transects, of four tray stations each, running perpendicular across grassland-agricultural field (either corn or soybean) edges. Each of the two habitats within a transect had two foraging trays, one near the edge (25 m away) and one closer to the interior (100 m from edge, see Fig. A1). Each station consisted of a plastic nursery tray (37.3 cm diameter) filled with 25 g of dried alfalfa pellets designed for pet rabbits (Oxbow Essentials Young Rabbit Food, Oxbow Animal Health, Murdock, Nebraska) and 4 cups of a sand substrate. I monitored a random subset of trays with a trail camera to verify that cottontails were the predominant foragers at trays. Prior to the experiment, trays with alfalfa pellets and sand were set out for two days to acclimate cottontails to the trays. Following acclimation, trays were set out for 24 h, after which the tray was revisited and deemed disturbed or undisturbed. If a tray was disturbed, I collected the contents, replenished the tray and left it out for another 24 h. If a tray was undisturbed, I assumed no foraging had occurred and left the tray out for an additional 24 h. After the second 24-h period, I collected the contents of all trays. Farming activities and weather limited the length of the experiment. Additionally, if precipitation occurred during the experimental period resulting in disintegration of alfalfa pellets, I repeated the trials. After a completed trial, I sifted tray contents to separate the alfalfa pellets from the sand. The alfalfa was then dried to reduce it to a stable dry mass for analysis.

At all GUD stations, I measured vegetation cover that could have affected concealment or predator surveillance, and thus perceived risk. Within a 5-m radius plot, I measured the amount of ground, low (<1 m), and high (1-2 m) cover. Horizontal ground cover was visually estimated as the percent of plot covered by any type of vegetation. I measured low and high cover (foliage volume) by placing a density board (200 by 50 cm) at the center of the plot, where the GUD tray was located, and walking 5 m away and recording the percentage of squares obscured by

vegetation (design modified from Noon 1981; Elbroch et al. 2015). Measurements were taken in all four cardinal directions and then averaged. I measured low cover from a kneeling position and high cover a standing position to prevent parallax problems (Noon 1981).

I analyzed GUDs by constructing a linear mixed effects model (lme4 package in R) that incorporated habitat (grassland, cornfield, soybean field), tray location (edge or interior), and day of experiment (1 or 2) as fixed effects, transect as a random effect to account for spatial blocking, and tray station as a repeated measure. Because trays with an ending GUD of 25 g meant either that it was too risky to forage or simply that a tray was never encountered, I also ran the same mixed model including only data from foraged trays (GUD <25 g). I did not include my vegetation cover variables into the mixed models for GUD because two were highly correlated with habitat type. Instead, as an aid in interpreting the GUD results, I constructed separate linear mixed effects models and conducted post-hoc Tukey test to examine whether ground, low, and high cover varied among habitats.

## RESULTS

I captured 143 cottontail rabbits and 95 individuals (44 males, 51 females) that weighed  $\geq 800$  g were fitted with radio collars (Sibley: 52 individuals, Saybrook-Main: 32 individuals, Saybrook-Anchor: 11 individuals). Individuals were radiocollared for an average of 105 days (range 1-395 days) and relocated an average of 42 times (range 1-168) for 4,016 relocations across all individuals. Seventy-four of the 95 (77.9%) individuals were associated with known mortality events.

### *Home Range Size and Grassland Use*

The top model for predicting home range size included sex ( $\beta_{\text{sex}} = 3.43$ , SE = 4.07), season ( $\beta_{\text{season}} = 3.62$ , SE = 3.56) and their interaction ( $\beta_{\text{sex} \times \text{season}} = 12.76$ , SE = 5.62; Table A1). Males generally had larger home ranges than females and home ranges were smaller during the crop-down season [male: crop-up 27.6 ha (SE = 7.1), crop-down 10.2 ha (SE = 2.4); female: crop-up 10.5 ha (SE = 3.8), crop-down 6.0 ha (SE = 1.1)]. However, the difference between male and female home range sizes was much greater during the crop-up season.

The proportion of home ranges composed of grassland habitat ranged from 0.125 to 1.00 but averaged 0.638 (SE = 0.031, n = 70). There were six competitive models for predicting the proportion of grassland in home ranges of cottontails (Table 1). All competitive models contained season, site, or both (see Table A2 for model-averaged parameter estimates). Use of grasslands increased for both sexes during the crop-down season when cover in surrounding habitats was limited (Fig. 3). Site was most likely identified as an important predictor of grassland use due to patch size and edge effects. Sites at the Saybrook Habitat Area were smaller and therefore had more grassland-agricultural interfaces, so cottontails would be more

likely to use non-grassland habitats. Although not strongly supported (Table 1), home ranges of females tended to contain more grassland habitat than those of males (Fig. 3).

### *Predictors of Cottontail Survival*

My assessment of the initial model set for explaining survival of cottontails indicated that body mass, sex, season, and a sex x season interaction were potentially important covariates (Table A3). Thus, I carried these covariates over to my full analysis that included habitat covariates. There was no support for site as a covariate in that none of the competitive models ranked higher than the null model included site (Table A3), so site was not retained.

The assessment of known-fate models incorporating habitat variables identified a single top model for explaining cottontail survival (Table 2; see Table A4 for results for the entire candidate set). The top model included effects of season ( $\beta_{\text{season}}=1.05$ , SE = 0.27), sex ( $\beta_{\text{sex}} = -0.52$ , SE = 0.38), and grassland use ( $\beta_{\text{grass}} = 0.56$ , SE = 0.35), but also interactions between sex and grassland use ( $\beta_{\text{sex} \times \text{grass}} = 1.23$ , SE = 0.58) and sex and season ( $\beta_{\text{sex} \times \text{season}} = -0.89$ , SE = 0.61). Survival probability for both sexes was related positively to use of grasslands, but this effect was stronger for males (Fig. 4). Weekly survival of females was much higher during the crop-up season (0.984, SE = 0.007) compared to the crop-down season (0.956, SE = 0.008), whereas survival rates of males were similar between seasons (Fig. 5; crop-up = 0.957, SE = 0.013, crop-down = 0.960, SE = 0.009). Hence, females had higher survival rates than did males during the crop-up season but not during the crop-down season (Fig. 5). The estimate of mean annual survival, expanded from weekly survival rates across both sexes, was 0.168 (SE = 0.048, n = 95).

### *Predator-Prey Activity Patterns*

I obtained 614 independent photographs of cottontail rabbits (170 during crop-up season, 444 during crop-down season). Daily activity patterns did not differ between seasons ( $\chi^2_{23} = 15.58, P = 0.872$ ). Cottontails were mainly active between 18:00 and 7:00 with crepuscular peaks (Fig. 6; mean time = 00:01). Coyotes were also mainly active between 18:00 and 7:00 based on 33 independent photographs (Fig. 6; mean time = 00:21).

### *Timing of Cottontail Mortalities*

I estimated the time of death for 48 cottontail rabbits (20 males, 28 females). Of these mortalities, 12 occurred during the crop-up season and 36 during the crop-down season. The time of death did not differ between seasons ( $W = 3.27, P = 0.195$ ). The majority of mortalities occurred at night when cottontails were active (Fig. 6, mean time = 00:13). Forty-two of the 48 (87.5%) mortalities occurred during the active period for coyotes (Fig. 5).

Prior to determining time of death, I independently classified the probable cause of mortality based on field sign (mammalian predation = 21, avian predation = 3, vehicle = 3, unknown predation = 21). Nineteen of the 21 (90.5%) mortalities classified as mammalian predation occurred during the active period for coyotes.

### *Perceived Risk and the Landscape of Fear*

When data from all trays were analyzed for the crop-up season (Fig. 7), GUDs for cottontails differed among habitats ( $F = 3.83, p = 0.029, df = 2, 42$ ) and between days ( $F = 13.63, p < 0.001, df = 1, 53$ ). Whether the tray was located on the interior or exterior of the site did not matter ( $F = 0.26, p = 0.615, df = 1, 37$ ). GUDs did not differ between the two crop types ( $p = 0.870$ ). However, GUDs were lower in cornfields compared to grasslands ( $p = 0.046$ ), and lower

in soybean fields than in grasslands ( $p = 0.008$ ; Fig. 7). The mean GUD was 18.8 g (SE = 1.48) in corn, 20.0 g (SE = 1.31) in soy, and 22.9 g (SE = 0.59) in grassland. When data from only foraged trays were analyzed (Fig. A2), habitat remained a predictor of GUDs ( $F = 4.62$ ,  $p = 0.009$ ,  $df = 2, 42$ ), however neither day ( $F = 0.10$ ,  $p = 0.752$ ,  $df = 1, 17$ ) nor interior-exterior location ( $F = 0.01$ ,  $p = 0.937$ ,  $df = 1, 34$ ) was important.

Ground cover was less in both corn and soybean fields when compared to grasslands ( $p < 0.001$ ). Mean ground cover was 58.1% (SE = 2.34) in cornfields, 66.5% (SE = 4.98) in soybean fields, and 91.8% (SE = 2.77) in grasslands. Low cover (<1 m) did not vary among habitats ( $p = 0.56$ ). However, high cover (1-2 m) was greater in cornfields (69.7%, SE = 3.99) than in grasslands (18.4%, SE = 4.69;  $p < 0.001$ ) and less in soybean fields (1.15%, SE = 0.59) compared to grasslands ( $p = 0.003$ ).

## DISCUSSION

My results indicate that large-scale restoration programs in agroecosystems can have complex and unexpected outcomes for species intended to benefit from the created habitats. My prediction that cottontails would have higher survival when using restored grasslands than when using adjacent agricultural fields was supported, however the relationship was stronger for males than for females. My prediction that females would have higher survival than males was also supported, but only during the crop-up season. Both sexes constrained their movements and increased their use of grasslands during the crop-down season. Contrary to expectations, however, the benefit of using grasslands was not greater during the crop-down season. Movements in agricultural fields were always relatively risky. Surprisingly, my GUD experiments indicated that perceived predation risk by cottontails did not align with real risk. During the crop-up season, cottontails perceived agricultural fields to be safer despite the elevated mortality risks in those habitats.

Survival of cottontails was affected by an interaction between sex and season. I can suggest two explanations that are not mutually exclusive and difficult to disentangle because temporal changes in the agricultural matrix (crop planting and harvesting) are confounded by seasonal changes in weather. First, the lower survival of females during the crop-down season could reflect reduced cover on the overall landscape and increased predation pressure on the grassland patches where cottontails restrict their movements. Second, the lower survival of females during the crop-down season could reflect winter weather. Survival rates of cottontails residing in the northern part of their geographic range can be lower during winter due to lower temperatures, snowy conditions, and lower abundance or quality of food resources (Keith and Bloomer 1993; Villafuerte et al. 1997; Bond et al. 2001a; Boland and Litvaitis 2008). In

particular, predation by coyotes can be higher during winter when cottontails are less cryptic, have greater difficulty moving through snow, and have higher energy needs (Keith and Bloomer 1993; Boland and Litvaitis 2008). Males most likely encounter the same pressures. However, male survival remains consistent between seasons, and males have lower survival compared to females during the crop-up season, probably due to their larger home ranges and increased movements associated with the breeding season. Male home ranges drastically expand during the breeding season and reach their peak in mid-May to mid-July (Trent and Rongstad 1974), which aligns with the height of the crop-up season. Bond et al. (2001b) also observed that females had lower movement rates during the breeding season than did males but similar rates during the nonbreeding season. Moreover, cottontails that were killed by predators had greater movement rates the week before death than individuals that survived (Bond et al. 2001a).

Overall, the annual survival rate of 0.168 for cottontails in my study was lower than survival rates from many other studies (0.20-0.40; Trent and Rongstad 1974, Medve 1987, Bond et al. 2001a, Boland and Litvaitis 2008, Crawford 2014). Home range sizes were also much larger in this region (annual averages were 24.2 ha for males and 14.6 ha for females) as compared to other regions with less disturbed and fragmented habitats (see Mankin and Warner 1999a). The lower survival rate combined with greater home range sizes suggests that although cottontails can persist in this highly altered environment with small patches of natural habitat, it may be a low-quality landscape due to high predation pressure and limited food resources. Most of the documented mortalities were due to predation, although body condition could have been a predisposing factor for some individuals.

Both sexes have higher survival when moving in restored grasslands instead of agricultural fields and developed areas. However, males benefit more than females from staying

in the grassland habitat (Fig. 4). This differential again might be driven by the movement behavior of males, especially during the breeding season, which puts them at greater risk when traversing areas with suboptimal concealment. Females also use non-grassland habitats, but they were not undergoing large movements and thus were staying closer to grassland-agricultural edges (commonly observed during telemetry) potentially allowing them to benefit from increased hiding cover nearby.

If the agricultural matrix is negatively affecting survival, why use it at all? Foremost, there may simply not be enough grassland habitat. This region has undergone dramatic changes and while most land conversion occurred in the mid-1900s, the intensification of row-crop agriculture continues to impact the area further reducing the amount of suitable habitat (Warner 1994). Even with efforts such as CRP and SAFE, wildlife species are forced to seek out alternative habitats to supplement or complement native habitat patches (Dunning et al. 1992). When selecting between adjacent habitats, cottontails must balance the needs of mating opportunities (discussed above), food resources, microclimate, and predation risk. Cottontails are generalist herbivores and consume a wide variety of plants including grasses, legumes, and broad-leaved forbs (Dusi 1952; Korschgan 1980). Cornfields treated with herbicides offer little vegetation to provide food resources (Mankin and Warner 1999a) and current agricultural practices leave little residue in the fields after harvest. Although cottontails have been observed eating soybeans (Washburn 2000), it is unknown what percent of their diet this crop could compose. Humberg et al. (2007) reported cottontails, combined with small rodents, were responsible for <2% of the damage to soybean fields and a negligible amount of damage to cornfields in Indiana. It is therefore likely that most cottontails rely on grassland areas for food resources. Selecting a desirable microclimate may be achieved through use of multiple habitats.

Althoff et al. (1997) found that cottontails selected microenvironments that had dense cover that provided insulating effects, which allowed individuals to conserve metabolic energy or to reduce heat load. In Illinois during the crop-up season, soybean fields have similar microclimatic conditions to grasslands, whereas cornfields have higher temperatures but less humidity (Cosentino et al. 2011). Thus, cottontails could be seeking out soybean fields as supplemental habitat for favorable temperatures, or they could use cornfields for the lower humidity levels.

The last main component of habitat selection is predation risk. Cottontails prefer areas with dense vegetation; vegetation structure rather than plant species composition is a driving factor in habitat selection (Althoff 1983). Previous GUD experiments have shown that lagomorphs (cottontails and jackrabbits, *Lepus californicus*) forage more at stations that are located under or closer to cover (Longland 1991; Abu Baker et al. 2015). Grasslands provided the greatest amount of ground cover when compared to corn and soybean fields, and all habitats had similar low cover. Hence, grasslands provided concealment from ground predators, such as mammals, that was equal to or better than agricultural fields. Cornfields provided the greatest amount of high cover followed by grasslands and then soybean fields. Hence, cornfields during the growing season provided the best hiding cover from avian predators. My GUD results indicate cottontails perceived agricultural fields to be safer than grassland areas and thus may be using these habitats as predator refuges. Even if the assumption of the GUDs experiment that missed opportunity costs were equal across habitats was incorrect, cottontails still spend a substantial amount of time in agricultural fields that provide few resources and at a minimum, there was no evidence that cottontails recognized these adjacent habitats as riskier than grasslands.

This disjunction between perceived and real predation risk is imperative to understand because it may be limiting the benefits of the grassland restoration efforts. Agricultural fields have been identified as ecological traps for other species (Hiron et al. 2012; Northrup et al. 2012; Hale and Swearer 2016) and it is important for conservation to identify such traps (Battin 2004). For cottontails, it may be difficult for them to assess risk in a dynamic landscape due to a large suite of predators that use different hunting strategies. Predators of cottontails in this region include coyotes, red fox (*Vulpes vulpes*), weasels (*Mustela spp.*), raptors, owls, as well as domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*; Trent and Rongstad 1974; Crawford 2014). Avian predators hunt primarily by sight, whereas most mammalian predators use both sight and scent to detect prey items (Bond et al. 2001a; Thibault and Ouellet 2005). Bond et al. (2001a) suggested that spatial use by cottontails was explained better by avian predation than by mammalian predation. This notion is consistent with patterns from my study and it offers a possible explanation for the use of mature cornfields—to provide substantial overhead cover to avoid avian predation. The problem for cottontails is that most mortalities recorded in this study were not due to avian predators but to mammalian, predominately coyotes.

There are several reasons why cottontails may be suffering high mortality from coyotes. First, coyotes were originally rare in Illinois, but numbers have dramatically risen making them the dominant predator of the region (Heske and Miller 1995). Secondly, although coyotes are plastic in behavior and considered to be opportunistic, generalist predators, they select lagomorphs as their main prey in many areas (Korschgen 1957; MacCracken and Hansen 1987; Windberg and Mitchell 1990; Young et al. 2006; Landré et al. 2009). Coyote activity patterns also align with those of cottontails (Fig. 6; see also Arias-Del Razo et al. 2011). These factors suggest coyotes may be specifically targeting cottontails putting increased predation pressure on

the population. Rising abundances of coyotes have caused declines in other lagomorph populations (Wagner and Stoddart 1972). Moreover, because coyotes were not previously prevalent in the region and coyote densities have rapidly increased, cottontails may not be recognizing coyotes as their main predators and may be more concerned with protecting themselves against avian predators. This hypothesis would indicate that their landscape of fear has not been updated yet. Lastly, certain habitats may be hindering the effectiveness of evasive maneuvers. The two predatory responses of cottontails are to either crouch low to the ground to avoid detection, or to run in a zig-zag pattern as fast as possible until they can get to sufficient cover (Marsden and Holler 1964). Although Mankin and Warner (1999b) suggested that the uniform spacing of row crops would be perfect for evasive movements, the optimization of row spacing and plant densities (Duvick and Cassman 1999; Wibbicombe and Thelen 2002) could make evasive movements more difficult. My observations in the field suggest the current crop spacing is tight with little space for a full-sized cottontail to squeeze between rows. If cottontails are unable to employ their favored zig-zag movement behavior, escape would be difficult once they are spotted by a coyote in a cornfield. Therefore, the rapid increase in numbers of coyotes combined with agricultural intensification practices that inhibit escape patterns could be contributing to the decline of eastern cottontails.

Extensive land conversion for agriculture purposes has prompted the need for landscape-scale restoration programs. However, scaling up restoration from local sites to landscapes has been challenging (Menz et al. 2013), and assessments of agri-environment schemes have often been inadequate for determining outcomes (Kleijn and Sutherland 2003). My study demonstrated how adjacency of restoration sites to other landscape elements affects their functioning and produces unintended consequences. Creating larger habitat patches could reduce

edge effects and possible negative impacts of neighboring habitats. However, increasing patch size is not always an option. In fact, my grasslands were large in comparison to other restoration sites in the SAFE program (Mulligan et al. 2013, Berry et al. 2017). Effects of landscape context on restoration outcomes may be inevitable in most agroecosystems. Nevertheless, the created habitat provided by programs such as CRP and SAFE likely benefit biodiversity, especially in regions in which natural habitat is scarce. However, these benefits may be reduced for focal species that practice landscape supplementation with negative fitness consequences.

## TABLES AND FIGURES

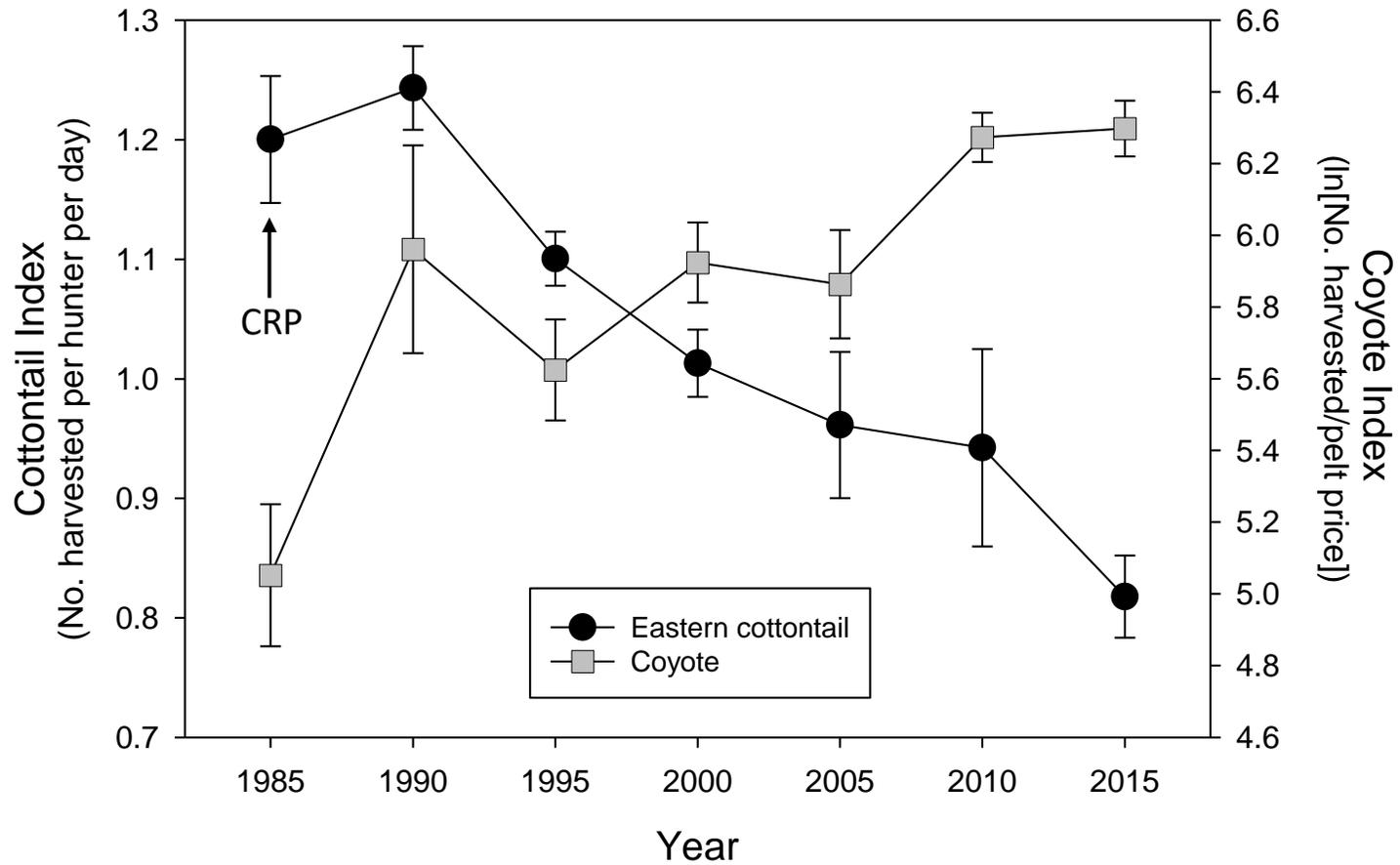
**Table 1.** Ranking of generalized linear mixed models used to predict the amount of restored grassland habitat within home ranges of eastern cottontails (*Sylvilagus floridanus*; n = 70) in Illinois, USA, 2014-2016. Model covariates include sex, season (crop-up or crop-down), site (Sibley Habitat Area or Saybrook Habitat Area), and mass (kg) when collared.

Model	Δ AICc	AICc Weight	K	Deviance
season + site	0.000	0.179	4	193.830
season	0.407	0.146	3	196.352
sex + season + site	1.500	0.084	5	193.186
sex + season	1.676	0.077	4	195.506
season + mass + site	1.811	0.072	5	193.496
site	1.845	0.071	3	197.790
season + mass	2.111	0.062	4	195.941
null	3.025	0.039	2	201.054
sex + season + (sex x season) + site	3.356	0.033	6	192.865
sex + site	3.359	0.033	4	197.189
sex + season + mass + site	3.444	0.032	6	192.953
sex + season + mass	3.539	0.030	5	195.224
sex + season + (sex x season)	3.541	0.030	5	195.226
mass + site	3.737	0.028	4	197.567
sex	4.290	0.021	3	200.235
mass	4.821	0.016	3	200.766
sex + season + (sex x season) + mass + site	5.291	0.013	7	192.593
sex + mass + site	5.362	0.012	5	197.047
sex + season + (sex x season) + mass	5.390	0.012	6	194.900
sex + mass	6.221	0.008	4	200.051

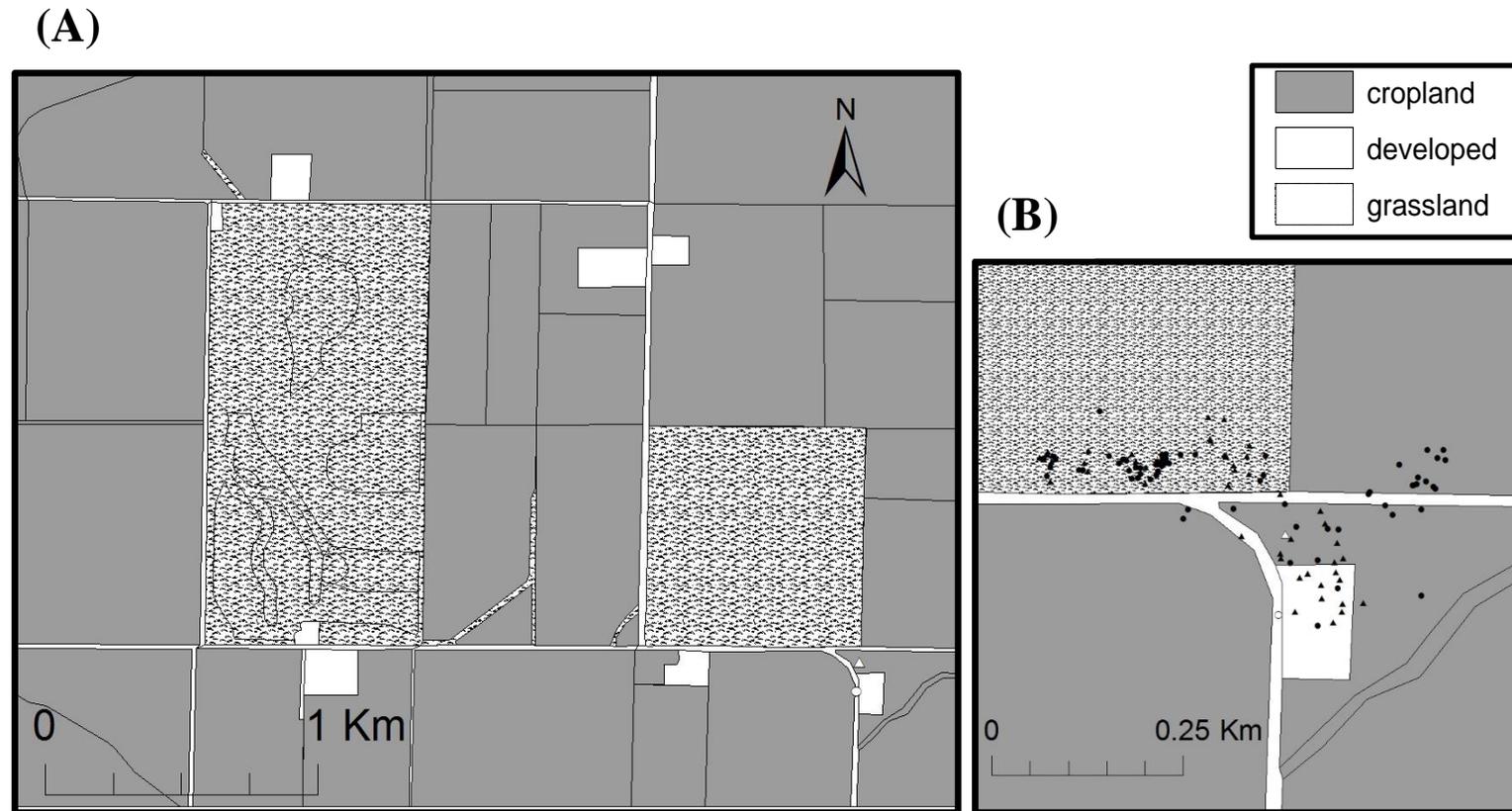
**Table 2.** Ranking of known-fate models of survival for 95 eastern cottontails (*Sylvilagus floridanus*) in Illinois, USA, 2014-2016.

Model covariates include sex, season (crop-up or crop-down), proportional use of habitats (grass, corn, soybean, developed), and mass (kg) when collared. Presented are all models within the 95% confidence set and the null model.

Model	$\Delta$ AICc	AICc Weights	K	Deviance
season + sex + grass + (sex x season) + (sex x grass)	0	0.324	6	582.105
season + sex + grass + (sex x season)	2.776	0.081	5	586.894
season + grass	2.912	0.076	3	591.051
season + sex + corn + soy + dev + (season x corn) + (season x soy) + (season x dev) + (sex x season)	3.264	0.063	10	577.293
season + sex + mass + grass + (sex x season)	3.555	0.055	6	585.660
mass(kg) + grass	3.689	0.051	3	591.828
season + corn + soy + dev	3.894	0.046	5	588.013
season + sex + corn + soy + dev + (sex x season)	3.926	0.045	7	584.015
season + sex + mass + corn + soy + dev + (sex x season)	4.039	0.043	8	582.110
season + sex + corn + soy + dev + (sex x corn) + (sex x soy) + (sex x dev) + (sex x season)	4.169	0.040	10	578.198
season + sex + grass + (sex x season) + (season x grass)	4.600	0.032	6	586.704
season + grass + (season x grass)	4.921	0.028	4	591.051
season + corn + soy + dev + (season x corn) + (season x soy) + (season x dev)	5.106	0.025	8	583.177
season + sex + corn + soy + (sex x season) + (season x corn) + (season x soy)	5.163	0.025	8	583.234
season+ corn + soy + (season x corn) + (season x soy)	6.759	0.011	6	588.864
{.}	18.127	<0.001	1	610.277

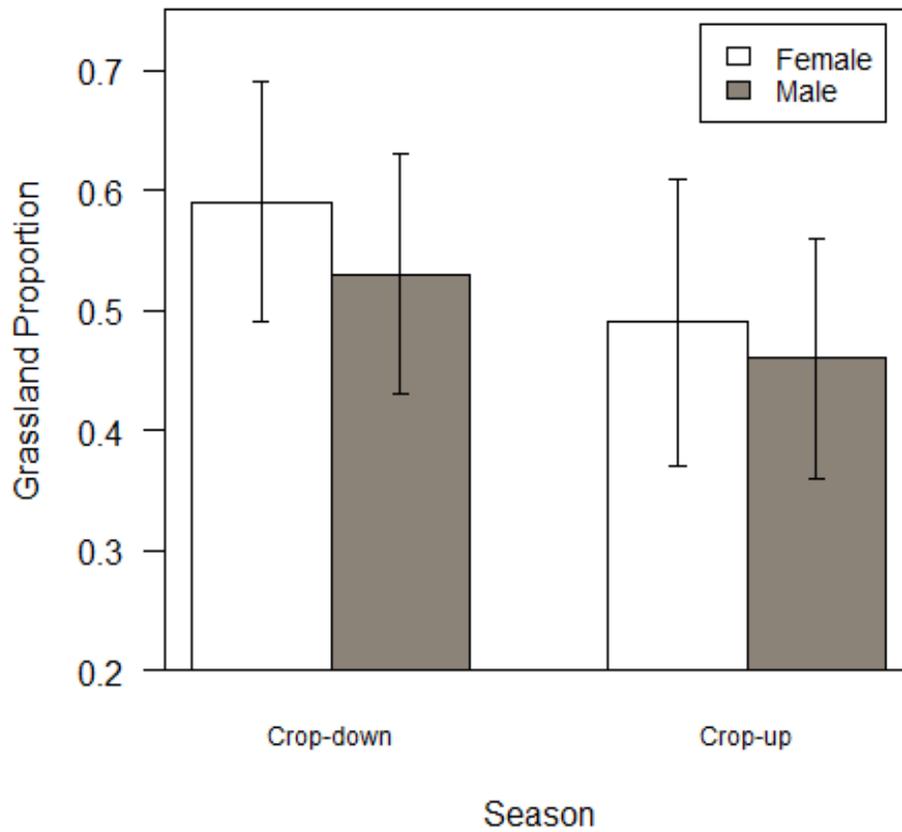


**Figure 1.** Trends for eastern cottontails and coyotes in Illinois (1981-2015) based on harvest data adjusted for effort (see Mankin and Warner 1999b, Gosselink et al. 2003). Each symbol is the mean ( $\pm 1$  SE) for the preceding five years (e.g., 1985 = 1981 to 1985). The Conservation Reserve Program (CRP) was initiated in 1985.

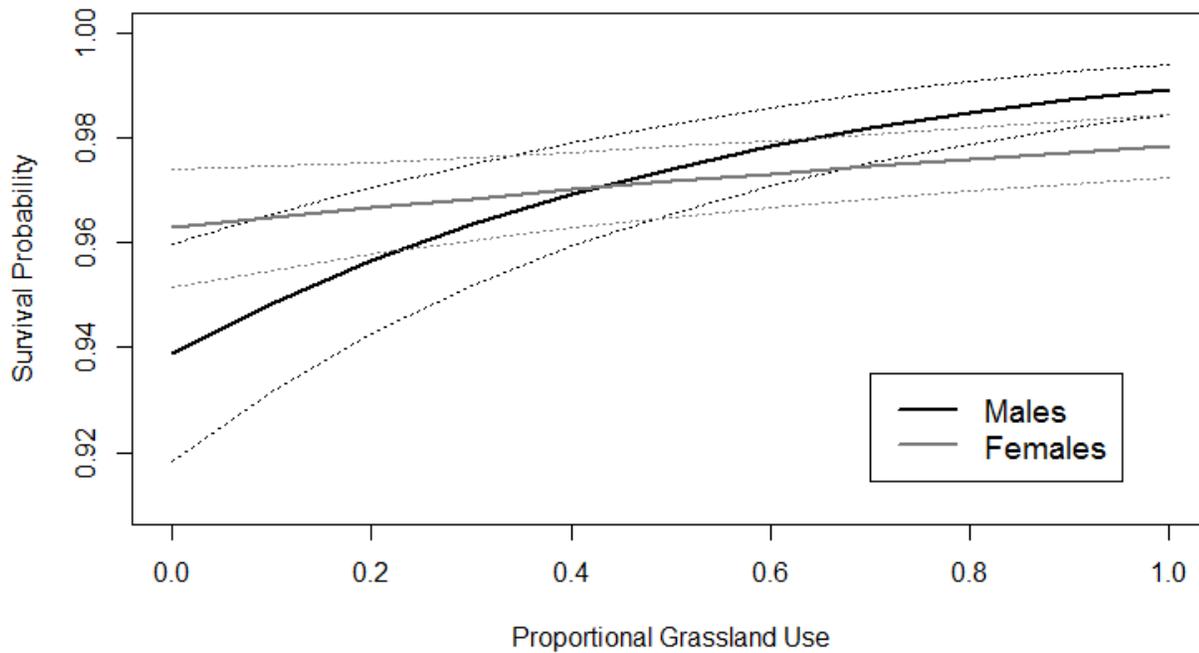


**Figure 2.** (A) Map of the Saybrook study site located in central Illinois. Note the two grasslands are completely surrounded by agricultural fields; 95% of the surrounding county is cropland used to grow corn and soybeans.

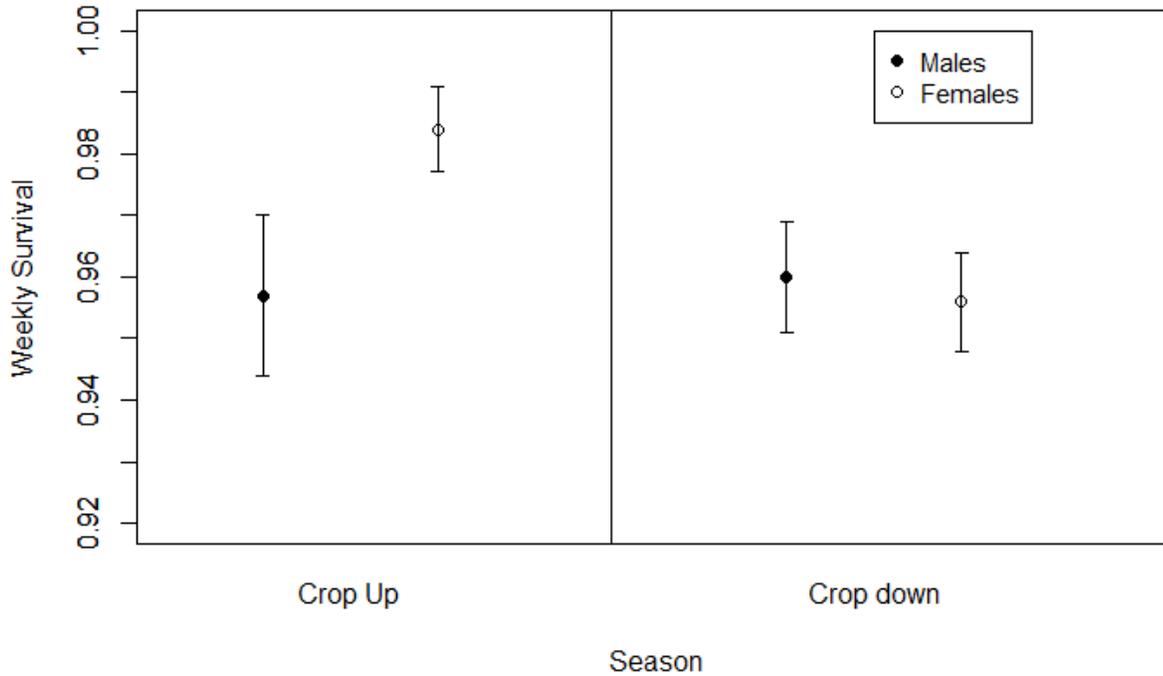
(B) Map of an enlarged portion of lower right hand corner of the eastern grassland with movements of two radio collared eastern cottontails represented. Triangles are locations for one female, circles are locations for one male, and hollow icons represent their mortality locations.



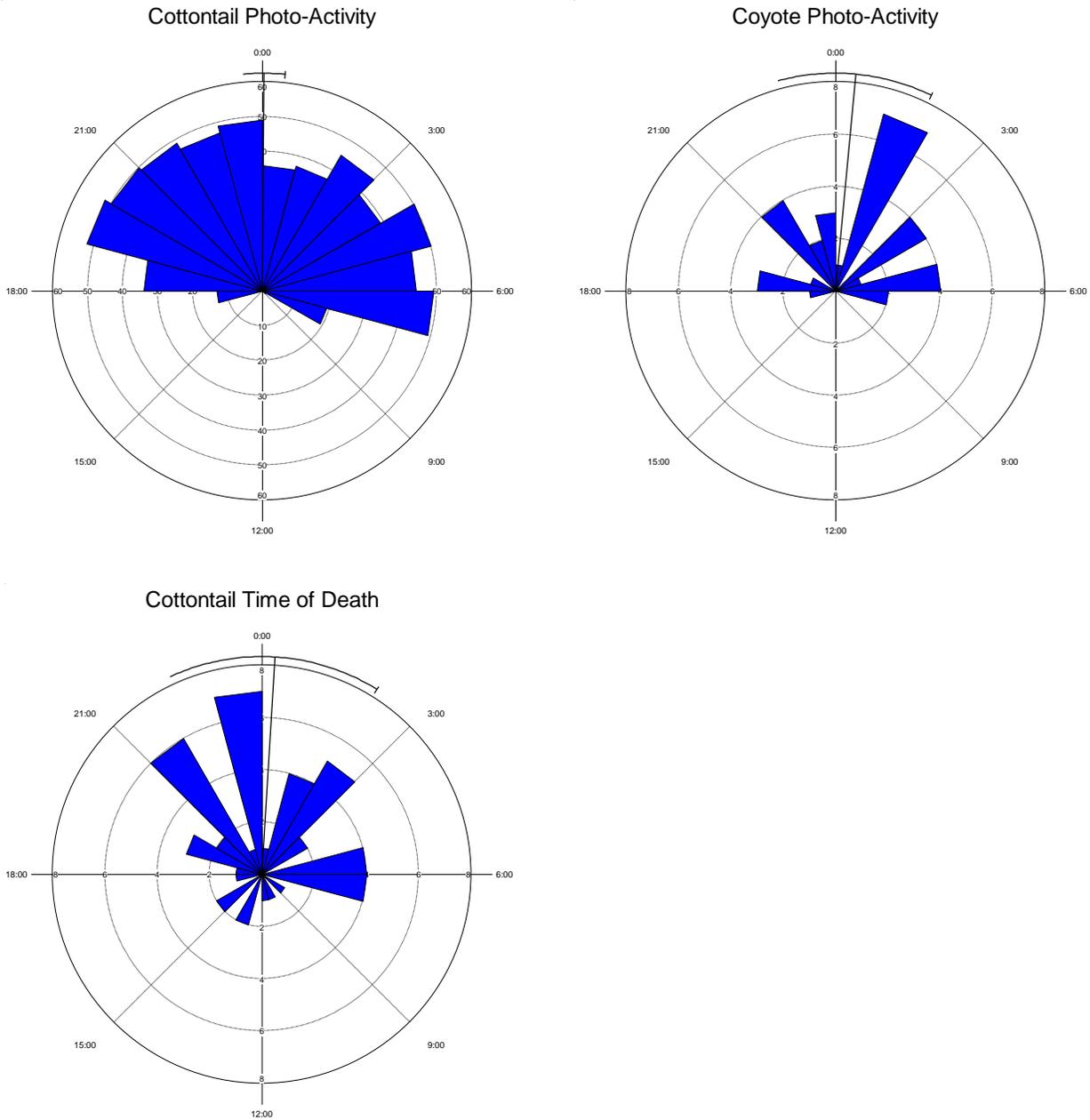
**Figure 3.** Mean ( $\pm 1$  SE) proportion of grassland habitat within eastern cottontail (*Sylvilagus floridanus*) home ranges (n = 70) in Illinois, USA, 2014-2016. Other habitats within home ranges included agricultural fields (corn and soybean) and developed areas.



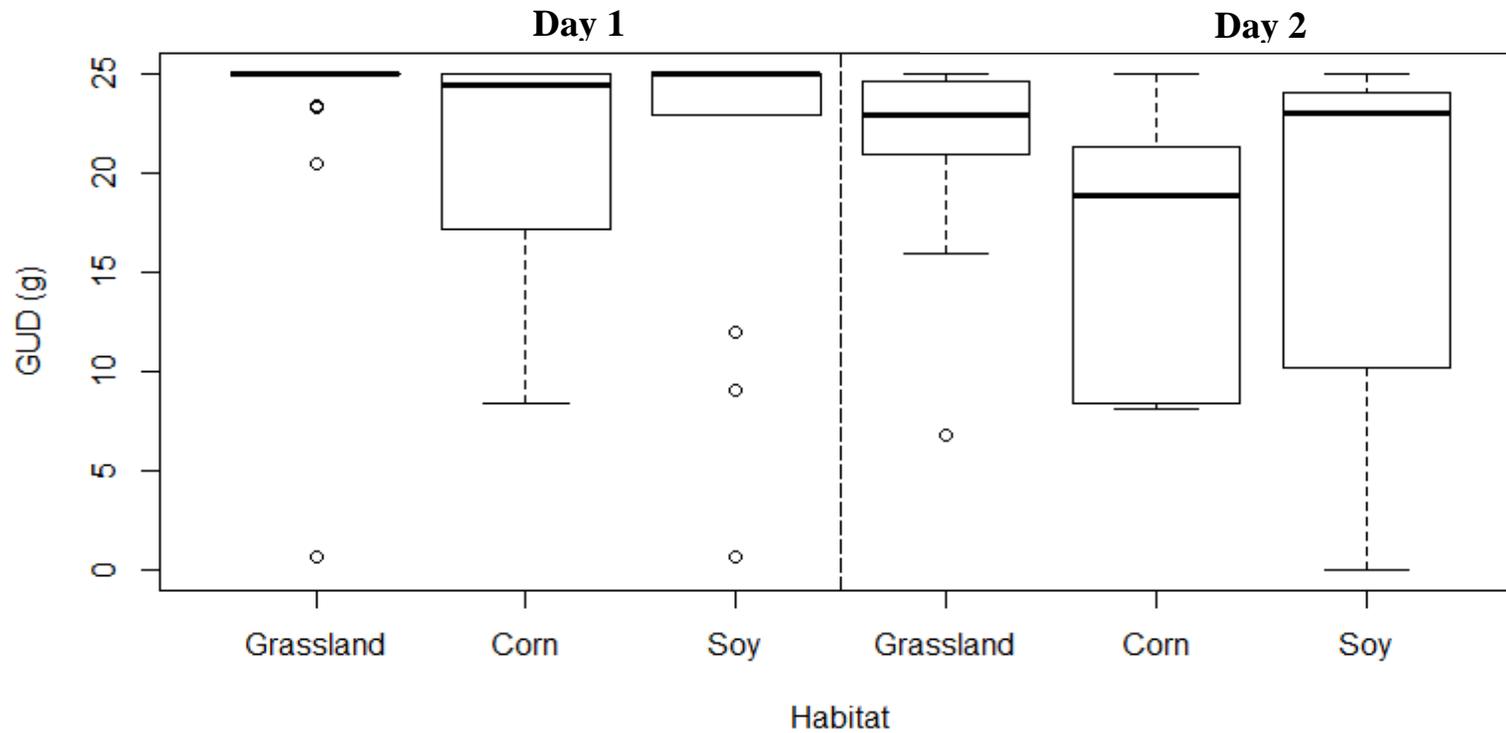
**Figure 4.** Estimates of weekly survival rates for male and female eastern cottontails related to use of restored grassland habitat. Dotted lines represent  $\pm 1$ SE. Estimates are derived from the top ranking known-fate model [season + sex + grass + (season x sex) + (sex x grass)] using data from 95 eastern cottontails (44 males, 51 females) radiotracked in Illinois, USA, 2014-2016. Mortality risk was higher for individuals that left grasslands more often to use other habitats (agricultural fields and developed).



**Figure 5.** Weekly survival estimates with 95% CI for two harvest seasons (crop-up = 19 weeks; crop-down = 33 weeks). Estimates are derived from the top ranked known-fate model [season + sex + grass + (season x sex) + (sex x grass)] using data from 95 radio-collared eastern cottontails (44 males, 51 females) tracked in Illinois, USA, 2014-2016. Use of grasslands was held to its mean value for each sex-season combination.



**Figure 6.** Daily activity patterns of cottontail rabbits and coyotes based on the number of independent photographs (>60 min apart) from camera traps on 30 grassland restoration sites in central Illinois (top). Estimated time of death for 48 cottontail rabbits tracked with an automated radio telemetry system on our main study sites in eastern Illinois (bottom). For all figures, the mean and 95% CI are shown.



**Figure 7.** Giving-up density (GUD) of eastern cottontails in restored grasslands and adjacent agricultural fields. GUDs are from experiments conducted at Sibley and Saybrook Habitat Areas in Illinois during September 2015 when crops were present in the agricultural fields. The thick horizontal lines represent medians, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers indicate minimums and maximums (excluding outliers.)

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## APPENDIX: SUPPLEMENTARY MATERIALS

**Table A1.** Ranking of linear mixed models used to predict home range sizes of eastern cottontails (*Sylvilagus floridanus*; n = 70) in Illinois, USA, 2014-2016. Model covariates include sex, season (crop-up or crop-down), site (Sibley Habitat Area or Saybrook Habitat Area), and mass (kg) when collared.

<b>Model</b>	<b>Δ AICc</b>	<b>AICc Weight</b>	<b>K</b>	<b>Deviance</b>
sex + season + (sex x season)	0	0.369	6	701.0
sex + season + (sex x season) + mass	1.534	0.172	7	700.2
sex + season + (sex x season) + site	2.059	0.132	7	700.7
sex + season	2.574	0.102	5	705.9
sex + season + (sex x season) + mass + site	3.564	0.062	8	699.8
sex + season + mass	4.153	0.046	6	705.1
sex + season + site	4.466	0.040	6	705.5
season	5.429	0.024	4	711.0
sex + season + mass + site	6.009	0.018	7	704.6
season + site	7.077	0.011	5	710.4
season + mass	7.550	0.008	5	710.9
season + mass + site	9.193	0.004	6	710.2
sex	9.233	0.004	4	714.8
sex + site	10.686	0.002	5	714.0
sex + mass	10.824	0.0016	5	714.1
null	10.977	0.0015	3	718.7
site	12.183	0.0008	4	717.7
sex + mass + site	12.208	0.0008	6	713.2
mass	13.030	0.0005	4	718.6
mass + site	14.208	0.0003	5	717.5

**Table A2.** Calculated parameter estimates from top competing models (within 2  $\Delta$ AICc) explaining variation in proportion of grassland used by eastern cottontails (*Sylvilagus floridanus*) in Illinois, USA, 2014-2016. Model averaged estimates of parameters ( $\beta$ ), unconditional standard errors (SE), and 95% CIs are included. Covariates included site (Sibley Habitat Area or Saybrook Habitat Area), season (crop-up or crop-down), sex, and mass (kg) at time of collaring.

<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>
Intercept	0.623	0.369	-0.097	1.343
Site	-0.552	0.343	-1.221	0.118
Season	-0.708	0.345	-1.380	-0.036
Sex	-0.293	0.342	-0.960	0.373
Mass	0.558	0.577	-0.567	1.683

**Table A3.** Ranking of the initial known-fate models of survival based on weekly survival rates of 95 eastern cottontails (*Sylvilagus floridanus*) in Illinois, USA, 2014-2016. Model covariates include sex, season (crop-up or crop-down), and mass (kg) when collared.

<b>Model</b>	<b><math>\Delta</math> AICc</b>	<b>AICc Weights</b>	<b>K</b>	<b>Deviance</b>
sex + season + (sex x season)	0	0.135	4	602.755
sex + season + (sex x season) + mass(kg)	0.288	0.117	5	601.032
mass(kg)	0.598	0.100	2	607.369
{.}	1.501	0.064	1	610.277
mass(kg)+sex	1.605	0.061	3	606.369
mass(kg) + season	1.618	0.060	3	606.383
sex + season + (sex x season) + site	1.635	0.060	5	602.379
sex + season + (sex x season) + mass(kg) + site	1.944	0.051	6	600.675
sex	1.966	0.051	2	608.737
season	2.337	0.042	2	609.108
mass(kg) + site	2.434	0.040	3	607.198
mass(kg) + season + sex	2.519	0.038	4	605.274
season + sex	2.712	0.035	3	607.477
mass(kg) + site + sex	3.225	0.027	4	605.980
site	3.323	0.026	2	610.094
mass(kg) + season + site	3.525	0.023	4	606.280
site + sex	3.565	0.023	3	608.329
season + site	4.232	0.016	3	608.996
mass(kg) + season + site + sex	4.249	0.016	5	604.993
season + site + sex	4.429	0.015	4	607.184

**Table A4.** Ranking of known-fate models of survival for 95 eastern cottontails (*Sylvilagus floridanus*) in Illinois, USA, 2014-2016.

Model covariates include sex, season (crop-up or crop-down), proportional use of habitats (grass, corn, soybean, developed), and mass (kg) when collared.

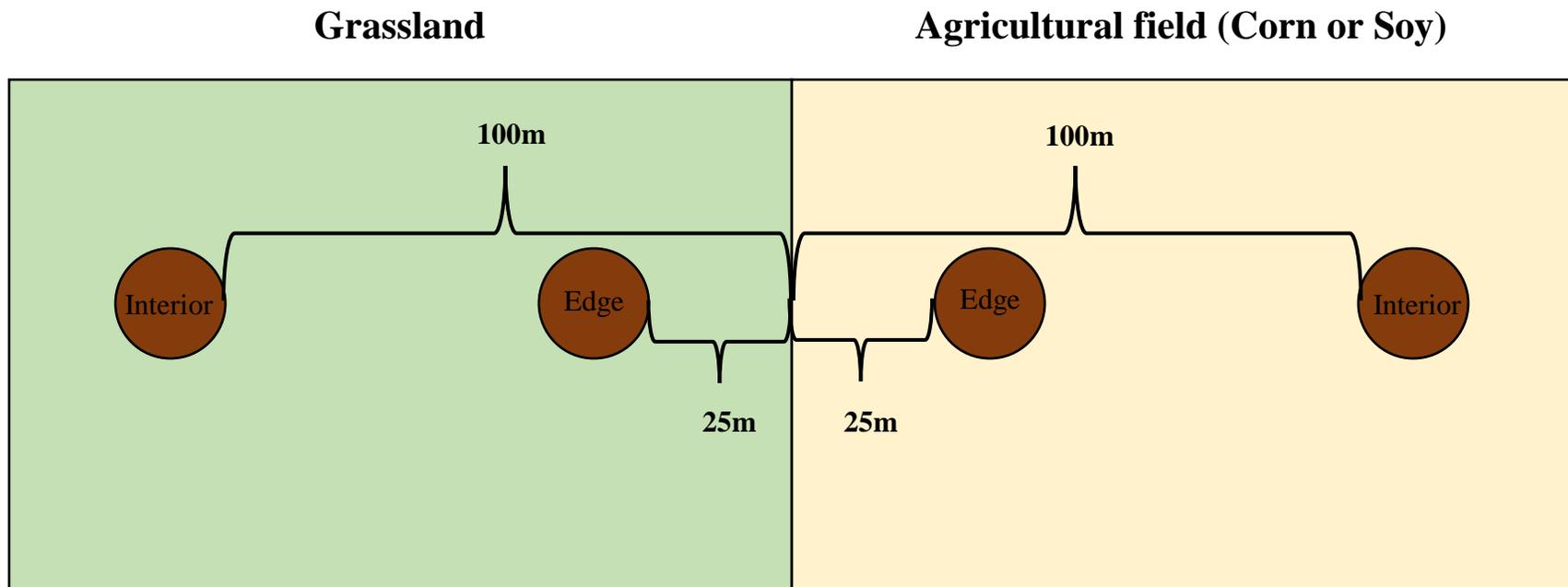
Model	$\Delta$ AICc	AICc Weights	K	Deviance
season + sex + grass + (sex x season) + (sex x grass)	0	0.324	6	582.105
season + sex + grass + (sex x season)	2.776	0.081	5	586.894
season + grass	2.912	0.075	3	591.051
season + sex + corn + soy + dev + (season x corn) + (season x soy) + (season x dev) + (sex x season)	3.264	0.063	10	577.293
season + sex + mass + grass + (sex x season)	3.555	0.055	6	585.660
mass(kg) + grass	3.689	0.051	3	591.828
season + corn + soy + dev	3.894	0.046	5	588.013
season + sex + corn + soy + dev + (sex x season)	3.926	0.045	7	584.015
season + sex + mass + corn + soy + dev + (sex x season)	4.039	0.043	8	582.110
season + sex + corn + soy + dev + (sex x corn) + (sex x soy) + (sex x dev) + (sex x season)	4.169	0.040	10	578.198
season + sex + grass + (sex x season) + (season x grass)	4.600	0.032	6	586.704
season + grass + (season x grass)	4.921	0.028	4	591.051
season + corn + soy + dev + (season x corn) + (season x soy) + (season x dev)	5.106	0.025	8	583.177
season + sex + corn + soy + (sex x season) + (season x corn) + (season x soy)	5.163	0.025	8	583.234
season+ corn + soy + (season x corn) + (season x soy)	6.759	0.011	6	588.864
sex + grass + (sex x grass)	7.091	0.009	4	593.221
season + corn + soy	7.150	0.009	4	593.280
season + sex + corn + soy + (sex x season)	7.465	0.008	6	589.570
season + sex + corn + (sex x season) + (season x corn)	7.652	0.007	6	589.757
season + sex + mass + corn + soy + (sex x season)	7.986	0.006	7	588.075
mass(kg) + corn + soy + dev	9.078	0.003	5	593.196

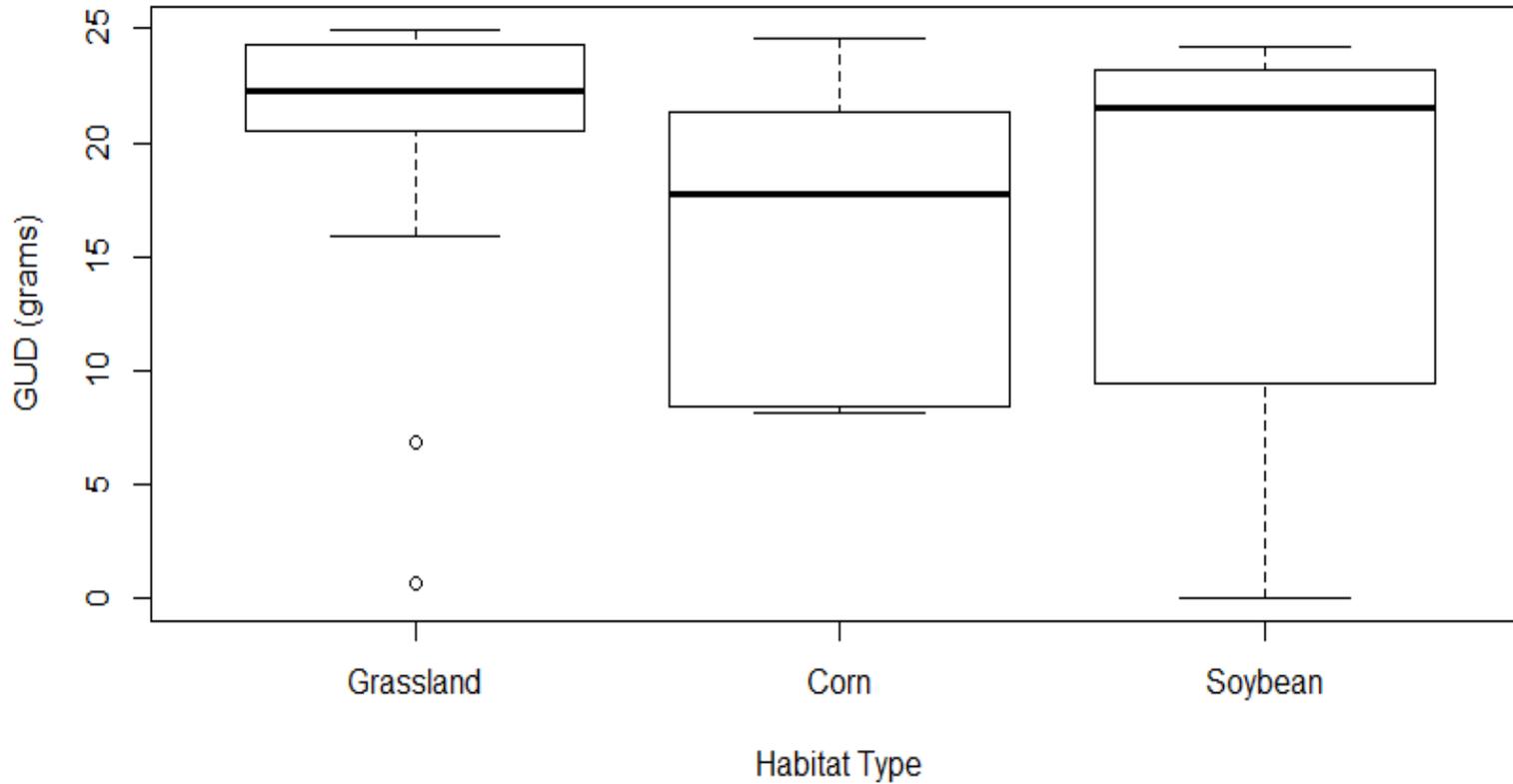
**Table A4 (cont.)**

season + corn + (season x corn)	9.849	0.002	4	595.979
season + sex + corn + (season x sex)	9.929	0.002	5	594.048
season + sex + mass + corn + (sex x season)	10.667	0.002	6	592.772
season + sex + corn + soy + (sex x corn) + (sex x soy) + (sex x season)	10.981	0.001	8	589.052
sex + corn + soy + dev + (sex x corn) + (sex x soy) + (sex x dev)	11.188	0.001	8	589.260
season + sex + corn + (sex x corn) + (sex x season)	11.550	0.001	6	593.654
season + corn	11.975	0.0008	3	600.113
mass(kg) + corn + soy	12.935	0.0005	4	599.065
mass(kg) + corn	13.717	0.0003	3	601.856
season + sex + soy + (sex x season) + (season x soy)	15.120	0.0001	6	597.225
sex + corn + (sex x corn)	16.454	0.00009	4	602.584
season + sex + soy + (sex x season)	16.575	0.00008	5	600.693
season + sex + (sex x season)	16.626	0.00008	4	602.755
season + sex + mass + soy + (sex x season)	16.673	0.00008	6	598.777
season + soy	16.769	0.00007	3	604.907
mass(kg) + soy	16.851	0.00007	3	604.989
season + sex + mass(kg) + (sex x season)	16.914	0.00007	5	601.032
season + soy + (season x soy)	16.960	0.00007	4	603.090
mass(kg)	17.223	0.00006	2	607.369
{.}	18.127	0.00004	1	610.277
season + sex + soy + (sex x soy) + (sex x season)	18.132	0.00004	6	600.237
sex + corn + soy + (sex x corn) + (sex x soy)	18.315	0.00003	6	600.420
season	18.962	0.00002	2	609.108
sex + soy + (sex x soy)	20.974	0.00001	4	607.104

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**Figure A1.** Diagram of the experimental design for measuring giving-up densities for cottontail rabbits. Shown is one transect (spatial block) that was replicated 15 times. Each 37.3-cm diameter nursery tray (circles) was filled with 25 g of dried alfalfa pellets designed for pet rabbits (Oxbow Essential Young Rabbit Food, Oxbow Animal Health, Murdock, Nebraska) and 4 cups of a sand substrate.





**Figure A2.** Giving-up density (GUD) of eastern cottontails in restored grasslands and adjacent agricultural fields. GUDs are from experiments conducted at Sibley and Saybrook Habitat Areas in Illinois during September 2015 when crops were present in the agricultural fields. The thick horizontal lines represent medians, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers indicate minimums and maximums (excluding outliers.) Mean GUD of grassland was 21.18 (SE= 0.99), corn was 16.19 (SE=1.66), and soy was 16.47 (SE=1.87). Only trays that were foraged were included in the data set.