Ecological traps in isodars: effects of tallgrass prairie management on bird nest success

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Ecological traps occur when habitat selection and habitat suitability (measured in terms of fitness) are decoupled. We developed a graphical model based on isodar theory to distinguish between an ideal distribution and an ecological trap. We tested the model's predictions using data on breeding bird populations in managed tallgrass prairie in Oklahoma. Between 1992 and 1996 we monitored success for 2600 nests of 26 breeding species in undisturbed, grazed, and burned and grazed plots. We also sampled arthropod biomass and nest predator abundance. Using the isodar model we determined that managed plots are ecological traps: compared with success on plots left undisturbed, nest success on plots that were only grazed was lower, and success on plots that were burned and grazed was substantially lower. Yet birds preferred to nest on managed plots, where arthropod abundance was measurably higher. Reptiles were the most abundant taxon of nest predators, and their abundance was highest in managed plots. Consequently, tree-nesting species had higher nest success than shrub- and ground-nesting birds. Nest success also increased with tree height. We concluded that isodar theory is a useful tool for detecting ecological traps if any component of fitness is measured in addition to animal densities. Our study also suggests that (1) human modification of the environment may alter simultaneously food and predator abundance, (2) the former affects nest site selection and the latter nest success, and (3) such ecosystems are likely to become traps for breeding birds.

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Continuous and rapid human modification of natural environments presents one of the biggest challenges for the persistence of wildlife populations (Morris and Kingston 2002). Altered environments require organisms to adapt rapidly else face extinction (Rice and Emery 2003, Stockwell and Ashley 2004). Ecological traps (Schlaepfer et al. 2002) represent particularly challenging environments for animals. Ecological traps are habitats retaining cues animals use to select breeding, foraging, or roosting sites but that have changed such that they now affect fitness and population dynamics negatively (Dwernychuk and Boag 1972, Schlaepfer et al. 2002, Kristan 2003). In other words, habitat selection has become decoupled from habitat quality. Because traps may affect population size or persistence in the long term, our understanding of conservation ecology and population biology will benefit from identifying factors that create ecological traps and ways to avoid their creation (Kokko and Sutherland 2001).

Although a good indication of a trap is a negative relation between habitat preference and reproductive success (Misenhelter and Rotenberry 2000, Remes 2003), the cues with which organisms select habitat and the factors that turn habitats into traps remain unclear. Specifically, bottom-up and top-down factors that could drive decision-making and affect fitness have not been linked to parameters such as density and reproduction. To this end, we need a clearer idea of how productivity, not just occupancy, is affected by current land use practices (Vickery and Herkert 2001).

Grasslands of the midwestern United States are among the world's most altered habitats (Flores 1996). North America's original tallgrass prairie has been devastated – only about 4% of it remains in small, widely scattered patches (Steinauer and Collins 1996). Populations of birds breeding in this habitat have declined sharply since the mid 1960s (Knopf 1996, Peterjohn and Sauer 1999, Murphy 2003). Extant Midwestern grasslands are also highly modified by humans, particularly in being subjected repeatedly to prescribed fires (Collins and Wallace 1990) and livestock grazing (Hartnett et al. 1996). These factors have complex direct and indirect effects on bird populations. Both fire (Niwa and Peck 2002) and grazing (Dennis et al. 1997) can induce bottom-up control of bird populations by increasing arthropod biomass (Warren et al. 1987, Evans 1988, Anderson et al. 1989), yet they can also induce top-down control as burned fields can facilitate predator access to nests (Jones et al. 2002) and grazing can increase cowbird density (Goguen and Mathews 2001). Under this scenario, if birds select nesting sites on the basis of food abundance and thus favor burned and grazed prairies, their populations might be "trapped" as a result of the overall increase in nest predation and brood parasitism.

We present results from a long term study in which we monitored nest success of forty species of birds in tallgrass prairie grasslands of Oklahoma. We tested the hypothesis that ubiquitous spring burning has created a mosaic of ecological traps in the tallgrass prairie ecosystem. Over five years (1992–1996) we compared bird abundance and nest success between undisturbed and managed (burned and/or grazed) plots. In addition we sampled arthropods and recorded nest predators to determine how habitat management affected their abundance, and how they in turn affected habitat selection and reproductive output of grassland birds. We extended the isodar theory of density dependent habitat selection (Morris 1987, 1988) as a means of generating expected associations between habitat selection and habitat quality and as a means of broadening the theoretical underpinnings of ecological traps.

An isodar theory of ecological traps

Fretwell and Lucas (1969) described how individuals distribute themselves in a system of two or more habitats of different qualities. At low population densities individuals occupy only the primary habitat. As population size increases, fitness will be depressed until some individuals can achieve equal fitness by occupying the secondary habitat. As population size increases further still, individuals will distribute themselves between the two habitats in a manner that equalizes their relative fitness. Under such equilibrium no individual enjoys a gain in fitness from moving to the other habitat. Fretwell and Lucas (1969) named this equilibrium an ideal free distribution (IFD), a system in which individuals are free to settle in any habitat. The IFD can be revealed by plotting the system's isodar, the set of densities in the two habitats such that an individual's expectation of fitness is the same in both (Morris 1987, 1988). Isodar theory can be applied to solve numerous problems in management and conservation (Morris 2003).

An ecological trap occurs when the cues that individuals use for selecting habitat (and, by proxy, to evaluate fitness) overestimate the habitat's true fitness value, a situation that may occur, for example, if site fidelity plays a key role in habitat selection (Knick and Rotenberry 2000). Individuals will be more abundant in the trap habitat than they should be; their fitness there will be lower than in alternative habitats, and the population's mean fitness will be reduced. Ecological traps are especially likely when previously reliable cues based on the short-term value of a habitat (such as resource supply or the density of predators) that influence settlement early in the breeding season become disconnected from the habitat's true value later in the breeding season (e.g. through unexpected changes in resource supply, cover, or predation).

Our first example imagines the following scenario. A habitat's quality is altered in some way that does not change the cues used by its would-be occupants. We start with a simple model of habitat selection where fitness of prey individuals in a pair of habitats represents a compromise between density-dependent population growth and incidental predation. The population growth rate of the prey will be reduced by the predator, but the serendipitous consumption of prey will have little influence on the predator's dynamics. We can model the prey's per capita population growth rate in habitats 1 and 2 as

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1\left(1 - \frac{N_1}{K_1}\right) - a_1 P_1 \tag{1}$$

and

$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2\left(1 - \frac{N_2}{K_2}\right) - a_2 P_2 \tag{2}$$

respectively, where subscripts denote the two habitats, N is the density of prey, r is the prey's per capita intrinsic rate of increase, K is the prey species' carrying capacity, P is predator density, and a is the predator's attack rate (searching efficiency). Setting Eq. 1 and 2 equal at the IFD yields the linear isodar

$$N_2 = \frac{K_2[(r_2 - r_1) + (a_1 P_1 - a_2 P_2)]}{r_2} + \frac{r_1}{r_2}\frac{K_2}{K_1}N_1 \qquad (3)$$

(Morris 2005). Now, imagine that instead of two habitats we simply have two nearby areas covered by a single habitat. One "replicate" is altered in a way that has potential to either increase or decrease parameter values as follows: $K_T = K + \alpha K$, $r_T = r + \beta r$, $a_T = a + \gamma a$, and $P_T = P + \varepsilon P$, where the subscript T corresponds to the value of the parameters in the altered habitat and Greek letters represent a coefficient of habitat change. We further assume that individuals selecting habitat can detect only the difference in r and K and that they alter their densities accordingly. Thus, from the habitat selector's perspective, the two habitats have equal predation rates, and the densities will be adjusted to fit an "apparent isodar" as

$$N = \frac{K(r - r_T)}{r} + \left(\frac{r_T}{K_T}\frac{K}{r}\right)N_T \qquad (4)$$

Note that the intercept of the apparent isodar will be negative (higher density in the altered habitat at low population size) whenever $\beta r > 0$ (Fig. 1). The slope will exceed unity when $\frac{r_T}{K_T} > \frac{K}{r}$ and be less than one when $\frac{r_T}{K_T} < \frac{K}{r}$. But the "apparently better" habitat T will be an ecological trap if the altered predation rate actually causes fitness to be lower than in the undisturbed "control"; i.e. if

$$r - \frac{r}{K}N - aP > r_T - \frac{r_T}{K_T}N_T - a_T P_T$$

which will occur when

$$a_T P_T - aP > r_T - r + \frac{r}{K}N - \frac{r_T}{K_T}N_T \qquad (5)$$

Substituting Eq. 4 for N in inequality (Eq. 5) and letting the difference in predation be represented by $\delta P = a_T P_T - aP$, habitat T will be a trap whenever $\delta P > 0$. More generally, individuals may be misled into occupying a trap whenever their estimate of the difference in predation between habitats $[E(\delta P)]$ is less than its true value. Under this scenario, the apparent isodar is given by

$$N = \frac{K[(r - r_T) + (a_T' P_T' - aP)]}{r} + \frac{r_T}{K_T}\frac{K}{r}N_T \qquad (6)$$

where the prime indicates the (under) estimated values for predation in habitat T. Note that the intercept of the
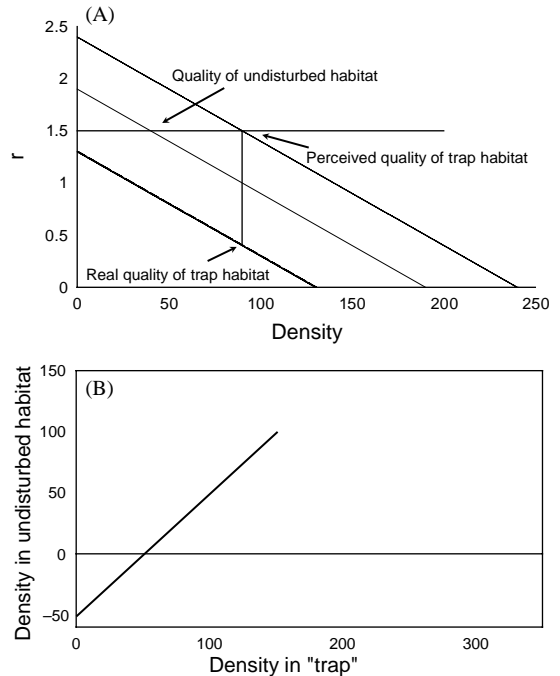

Fig. 1. An illustration demonstrating that a disturbed habitat can be turned into an ecological trap if habitat-selecting individuals cannot perceive an associated increase in predation. (A) The relationships between fitness and density. The horizontal line represents an example where the perceived fitness of an individual is the same in both habitats. Note that the real fitness in the trap habitat is much less than in the undisturbed control. (B) The apparent isodar representing the expected densities in the two habitats. Parameter values in the undisturbed habitat are r = 2, K = 200, a = 0.01, P = 10, and in the trap are $r_T = 2.5$, $K_T = 250$, $a_T = 0.06$, $P_T = 20$.

apparent isodar will now be greater than zero whenever the perceived difference in predation risk exceeds the increase in r (Fig. 2). Letting $\delta P'$ represent the difference in perceived predation, habitat T will be a trap whenever $\delta P > \delta P'$.

To summarize, our model of an ecological trap assumes that the target species can assess some, but not all, components of fitness and that cues it can use are thereby incomplete estimates of the habitat's true quality. When the target species alters its habitat use according to increases in r and K, but not with changes in predation risk, a graph of density in unaltered versus disturbed habitats will reflect the change in habitat preference and the intercept will be negative. The graph will not be a true isodar because individual fitness is lower in the trap habitat. If the target species can detect no cues associated with habitat disturbance, the "isodar" will pass through the origin with slope 1 (because the two habitats appear identical) even though fitness is lower in the trap. And if the target species can perceive only some of the difference in predation, it is even
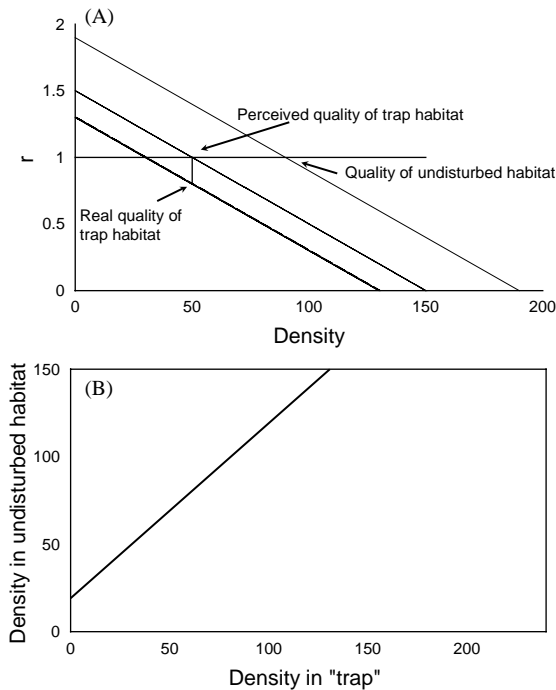
Fig. 2. An illustration demonstrating an ecological trap when habitat-selecting individuals perceive that the expected predation in the disturbed habitat is less than its actual value. (A) The relationships between fitness and density. The horizontal line represents an example where the perceived fitness of an individual is the same in both. Note that the real fitness and the perceived fitness in the trap are lower than in the undisturbed control. (B) The apparent isodar representing the expected densities in the two habitats. Parameter values are $r = 2$, $K = 200$, $a = 0.01$, $P = 10$ in the undisturbed habitat, and for the trap, $r_T = 2.5$, $K_T = 250$, $a_T = 0.06$, $P_T = 20$, $a'_T = 0.05$, and $P'_T = 20$.

possible that density at low population size will be higher in the control habitat.

We use isodar theory to explore differences in habitat selection consistent with an ecological trap. In the context of the theory, undisturbed tallgrass prairie represents the original habitat. Areas disturbed anthropogenically by grazing and/or fire may represent ecological traps. If breeding birds select territories only on the basis of food availability (alters r, K, or both) and if availability is increased by disturbance, then the isodar intercept should be negative (Fig. 1) and its slope may depart from unity. If disturbed habitats also yield higher rates of incidental predation or nest parasitism and if breeding birds cannot detect (all of) the increased risk, then the apparent isodar will be decoupled from nest success. Undisturbed prairie habitats may nonetheless have high densities of breeding birds whose nest success is higher than on disturbed areas (Fig. 2).

Our test is complicated by despotic theories of habitat selection that also predict differences in mean fitness between habitats (Fretwell and Lucas 1969). Dominant individuals interfere with the habitat choices of sub-ordinates. The perceived fitness of the habitat to subordinates is thereby devalued. The perceived value of alternative habitats with a lower density of dominant individuals remains high. But subordinates that equalize the perceived value of habitats will nevertheless have lower mean fitness than dominant individuals occupying the "best" habitats. One way to model the effect of despotism is to assume that the behavior of dominants reduces a habitat's perceived carrying capacity (increases the slope of fitness with density; Fretwell and Lucas 1969). Thus, in our example where prairie habitat is altered by disturbance, the apparent isodar will be given by

$$N = \frac{\hat{K}[(r - r_T) + (a'_T P'_T - aP)]}{r} + \frac{r_T}{\hat{K}_T} \frac{\hat{K}}{r} N_T \qquad (7)$$

where $\hat{K}$ represents the apparently reduced carrying capacity of habitat i caused by dominant behavior. Note that if disturbance alters r, then even in the absence of habitat differences in predation, the isodar intercept is less than it otherwise would have been (inflated density in the "trap" habitat).

Despotic behavior is one mechanism that leads to source and sink dynamics. If much of the landscape is disturbed and if a habitat's real quality is also reduced by the disturbance, then most individuals may occupy the low fitness disturbed habitat. Such populations can also be visualized as occupying an "ecological trap" where the population's future is jeopardized because recruitment depends on the success of the few individuals living in residual undisturbed habitat. But if disturbance also increases r, then a source–sink reversal (Boughton 1999) is possible because density will be greater in the disturbed habitat $[(r - r_T) < 0]$. It is thereby crucial that any test for an ecological trap must 1) demonstrate a difference in density between control and disturbed habitats (e.g. via isodars), 2) confirm that fitness is lower in the trap, and 3) identify the cause of the fitness difference.

Methods

Study area

Tallgrass prairie of northeastern Oklahoma is relatively homogenous with a low level of fragmentation by ranches and farms. Within this continuous habitat we selected eighteen 40 acre plots in Osage and Washington Counties. Half of the plots were located on the Nature Conservancy's Tallgrass Prairie Preserve in Osage County, while the other half were on private

ranches in either county. We identified three habitat types on the basis of management intensity: undisturbed, grazed, and burned. Burned plots represent the most disturbed habitat because their management includes prescribed fires in spring followed by moderate to intensive livestock grazing; thus, for this habitat the effects of burning and grazing cannot be partitioned. For each plot, there was a high treatment turnover between years, so that the title "burned", "grazed" or "undisturbed" was assigned on an annual basis. The rapid growth of grasses and corresponding increase in arthropods suggest that, relative to within-year effects, past-year fire and grazing effects are minor (Shochat et al. 2005).

Nest data

Each spring and summer (1992–1996) we surveyed each plot carefully every 3–4 days to find as many nests as possible. We searched for nests on the ground, in shrubs, and in the sparse trees. We monitored nests frequently until the end of the breeding season, ensuring sound data on nest initiation and nestling survival. We also noted nest location and height and whether the nest had been parasitized by the brown-headed cowbird (*Molothrus ater*). For unsuccessful nests we recorded whether failure was the result of predation, brood parasitism, or other reasons.

Because we were interested in monitoring only breeding individuals we did not use abundances in each habitat. Rather, we tallied the incidence of estimated first egg dates for all the nests we located. In most cases our nest searching frequency allowed us to determine first egg date with an error of ± 1 day. We assumed that birds laid eggs earlier in habitats they occupied earlier. We used these data to plot two isodars: undisturbed vs grazed and undisturbed vs burned (data pooled across years).

Predator and arthropod sampling

During the nesting seasons of 1995 and 1996 we recorded predators encountered during our regular plot censuses. We recorded species and abundances of all potential nest predators. We classified predators as reptilian, avian (Corvidae, Icteridae, and Accipitridae), and mammalian (Carnivora). As it was for nest surveys, predator surveys were also done long enough after re-growth of grasses in burned plots so that detectability was similar in all habitats.

Arthropods were sampled in the last three years of the study (1994–1996). We sampled each plot three times each summer, during the middle of May, June, and July. We placed four 6.4×7.6-cm adhesive flags (Thomson et al. 2004) coated with "Tangle-Trap"

in four corners of each plot, 67 m from the plot's two nearest borders, for 22–26 h. Two traps were oriented east–west, two north–south. If a flag was knocked over by cattle or wind we used data from the three other flags; if two or more flags were knocked over we repeated the sampling. Insects were counted on both sides of the flags and categorized by size class (<2, 2–5, 5–10, and >10 mm). We deleted the first class from our analysis because the birds we studied are unlikely to feed nestlings such small arthropods.

Statistical analysis

We compared nest density among the three treatments using the average nest density for each species/treatment/year; we then averaged the five yearly values for each treatment. We used randomized block ANOVA with the three treatments as the independent variable, nest density as the dependent variable, and the 12 most common species (accounting for $\sim 98\%$ of all nests) as the blocking factor. We used χ^2 tests to compare predator abundance and arthropod biomass between treatments.

Recently there have been several important advances in the statistical analysis of avian nest survival (Dinsmore et al. 2002, Nur et al. 2004, Shaffer 2004). Because we had success employing the technique previously (Shochat et al. 2005), we opted to use survival analysis (Nur et al. 2004), a powerful and conservative technique, to assess differences in nest success between treatments. We combined this analysis with Cox (proportional hazards) regression models (Muenchow 1986, Fox 1993) to determine the effects of particular independent variables on patterns of nest survival. We used the log-rank test (Pyke and Thompson 1986) to compare nest survival curves over exposure time, with degrees of freedom being the number of curves minus one (thus avoiding pseudoreplication). We compared nest survival curves between treatments (burned vs undisturbed, grazed vs undisturbed), nest height, tree height, arthropod biomass, and nesting substrate (ground, shrub, or tree). We adjusted type I error rates for multiple comparisons by calculating an experiment-wise error rate (Hardin et al. 1996).

We calculated arthropod abundance as the cumulative (throughout May, June and July) mean number of arthropods per treatment (standardized to 4 traps 24 h^{-1} plot^{-1}). We used a one-sample t-test to compare arthropod abundance in managed plots and undisturbed plots. Because our alternative hypothesis was that arthropod abundance is higher in managed plots, all tests were one-tailed.

Results

Nest surveys

We discovered 2747 nests of 40 species from 1992–1996 (Table 1). We excluded from the analyses three unidentified nests and 141 nests belonging to precocial, semi-precocial, raptorial, or cavity-nesting species (following Baicich and Harrison 1997; Table 1B). The final total used for analyses included 2603 nests of 26 bird species (Table 1A). Of these nests, 1713 (65.8%) failed, 745 (28%) fledged at least one young, and the outcome of 145 nests (5.6%) was unknown. Of the failed nests, 1327 (77.5%) failures were the results of predation, 157 (9.2%) were deserted, and 120 (7%) failed for unknown reason.

Table 1. (A) Results of the nest survey in tallgrass prairie plots, Washington and Osage Counties, Oklahoma, 1992–96. UD – undisturbed, GR –grazed, and BU – burned plots. (B) Species not included in the analysis.

A

Species common name	Latin name	Number of nests:			
		UD	GR	BU	Total
Ground nesting					
Eastern meadowlark	*Sturnella magna*	160	123	299	582
Grasshopper sparrow	*Ammodramus savannarum*	34	67	172	273
Henslow's sparrow	*Ammodramus henslowii*	24			24
Shrub nesting					
Bell's vireo	*Vireo bellii*		7	6	13
Grey catbird	*Dumetella carolinensis*		2	1	3
Field sparrow	*Spizella pusilla*		5	4	9
Blue grosbeak	*Passerina caerulea*		1	1	2
Dickcissel	*Spiza americana*	402	192	513	1107
Lark sparrow	*Chondested grammacus*	1	3	18	22
Tree nesting					
Mourning dove	*Zenaida macroura*	8	10	31	49
Yellow-billed cuckoo	*Coccyzus americanus*	1	4	14	19
Eastern kingbird	*Tyrannus tyrannus*	15	12	42	69
Scissor-tailed flycatcher	*Tyrannus forficatus*	5	10	20	35
Loggerhead shrike	*Lanius ludovicianus*		2	3	5
Blue-gray gnatcatcher	*Polioptila caerulea*		1	1	2
American robin	*Turdus migratorius*	1	1	5	7
Northern mockingbird	*Mimus polyglottos*		5	20	25
Brown thrasher	*Toxostoma rufum*	3	24	75	102
Common yellowthroat	*Geothlypis trichas*	2			2
Northern cardinal	*Cardinalis cardinalis*			2	2
Red-winged blackbird	*Agelaius phoeniceus*	111	31	84	226
Common grackle	*Quiscalus quiscula*		1	8	9
Great-tailed grackle	*Quiscalus mexicanus*	3			3
Orchard oriole	*Icterus spurius*	2	3	4	9
Summer tanager	*Piranga rubra*			2	2
American goldfinch	*Carduelis tristis*	1		1	2
Total		773	504	1326	2603

B

		UD	GR	BU	Total
Precocial/semi-precocial					
Green heron	*Butorides virescens*		1	1	2
Mallard	*Anas platyrhynchos*	2			2
Greater prairie-chicken	*Tympanuchus cupido*	12	4	6	22
Northern bobwhite	*Colinus virginianus*		3	10	13
Killdeer	*Charadrius vociferus*	3	11	6	20
Upland sandpiper	*Bartramia longicauda*	8	2	6	16
Common poorwill	*Phalaenoptilus nuttallii*	1			1
Common nighthawk	*Chordeiles minor*	21	9	25	55
Birds of prey					
Northern harrier	*Circus cyaneus*	2			2
American kestrel	*Falco sparverius*			1	1
Short-eared owl	*Asio flammeus*	1			1
Cavity nesting					
Belted kingfisher	*Ceryle alcyon*			1	1
Carolina chickadee	*Poecile carolinensis*		1		1
Eastern bluebird	*Sialia sialis*		3	1	4
Total		50	34	57	141

The other 109 nests (6.4%) failed as a result of bad weather, trampling by cows, or cowbird parasitism.

Nest success

Nest success differed among treatments (Fig. 3A, $\chi^2 = 7.81$, P = 0.02). Compared with undisturbed plots, nest success was similar in grazed plots but lower in burned plots (Fig. 3A). Because burned plots were always grazed it suggests that, more than grazing, burning is the major reason for the reduction in nest success. The crossover of curves after about 20 days probably has no biological meaning. At this stage sample size becomes too low, and each failure of a single nest adds a greater amount of bias; thus, interpretation of survival curves is best at the left part of survival curves. There were differences in nest success depending on nesting substrate. Nest success curves of ground- and shrub-nesting species were similar, and both were significantly lower than the nest success curve of tree-nesting species (Fig. 3B). For shrub- and tree-nesting species, nest survival increased with plant height ($\chi^2 = 6.20$, P = 0.01) but not with nest height ($\chi^2 = 0.02$, P > 0.85).
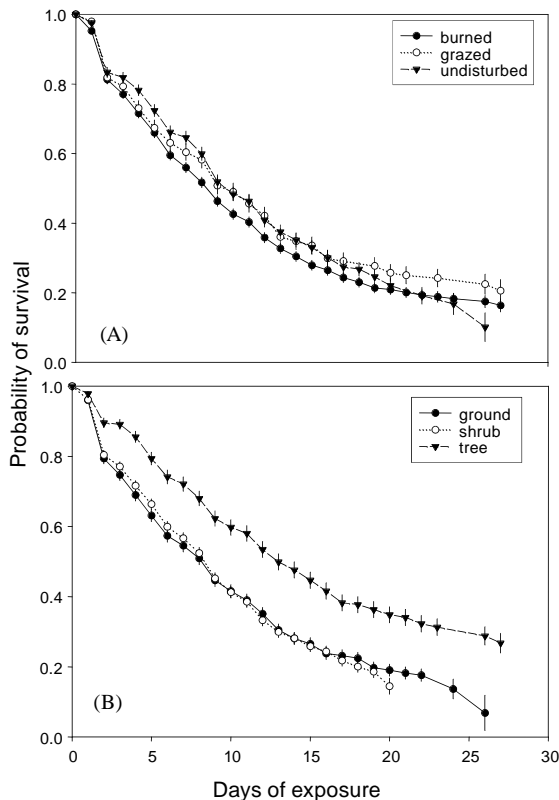

Fig. 3. Differences in nest survival between (A) undisturbed, grazed, and burned plots, and (B) ground-, shrub-, and tree-nesting species.

Predator abundance and influence

We recorded 736 predator observations in the study plots, including 551 reptiles (79%), 95 mammals (14%), and 54 birds (8%). Abundances of reptilian and avian predators, but not mammalian predators, differed among treatments. Avian predators were least abundant in grazed plots, but it is difficult to draw conclusions about their real effect because of the small sample size. In contrast, the incidence of reptiles recorded was highly skewed towards managed plots, especially burned ones (Table 2). Because the surveys were done after grass growth, it is unlikely that these differences were due differences in detectability among treatments. Of the reptiles recorded, most were snakes (28%) and box turtles (*Terrapene* spp. 70%). Both groups are considered to be major nest predators in the study area.

Nest success decreased with predator abundance (Wald's $\chi^2 = 4.46$, P = 0.03). Of the three predator taxa, only reptiles had a significant effect (Wald's $\chi^2 = 4.78$, P = 0.03). Reptiles negatively affected nest success when plots were classified on the basis of a grazing-only regime (Wald's $\chi^2 = 3.96$, P < 0.05) but not when they were classified by burning + grazing (Wald's $\chi^2 = 1.00$, P = 0.31). This result probably indicates that the difference in failures resulting from predation is greater between disturbed (whether burned or grazed) and undisturbed plots than between burned and unburned plots.

Habitat selection

We calculated isodars for two ground-nesting species (grasshopper sparrow, Fig. 4A; eastern meadowlark, Fig. 4B), one shrub-nesting species (dickcissel, Fig. 4C), and three tree nesting species (scissor-tailed flycatcher + eastern kingbird, Fig. 4D; red-winged blackbird, Fig. 4E). We placed the native habitat of higher fitness on the ordinate and removed all data points where one habitat had zero values, ensuring that we detected regression line intercepts properly. Each figure shows two isodars: grazed only vs undisturbed and burned + grazed vs undisturbed. The isodar intercepts of most species indicate preference for the managed habitats (Table 3) as follows: burned > grazed > undisturbed. Slopes of the isodars indicate that the perceived habitat quality is in a similar order. The location of the eastern meadowlark isodar intercepts on the y-axis (Fig. 4B) is the result of the nonlinear shape of the data, as the data

Table 2. Results of χ^2 tests on the differences of three taxa of nest predators between undisturbed, grazed and burned plots.

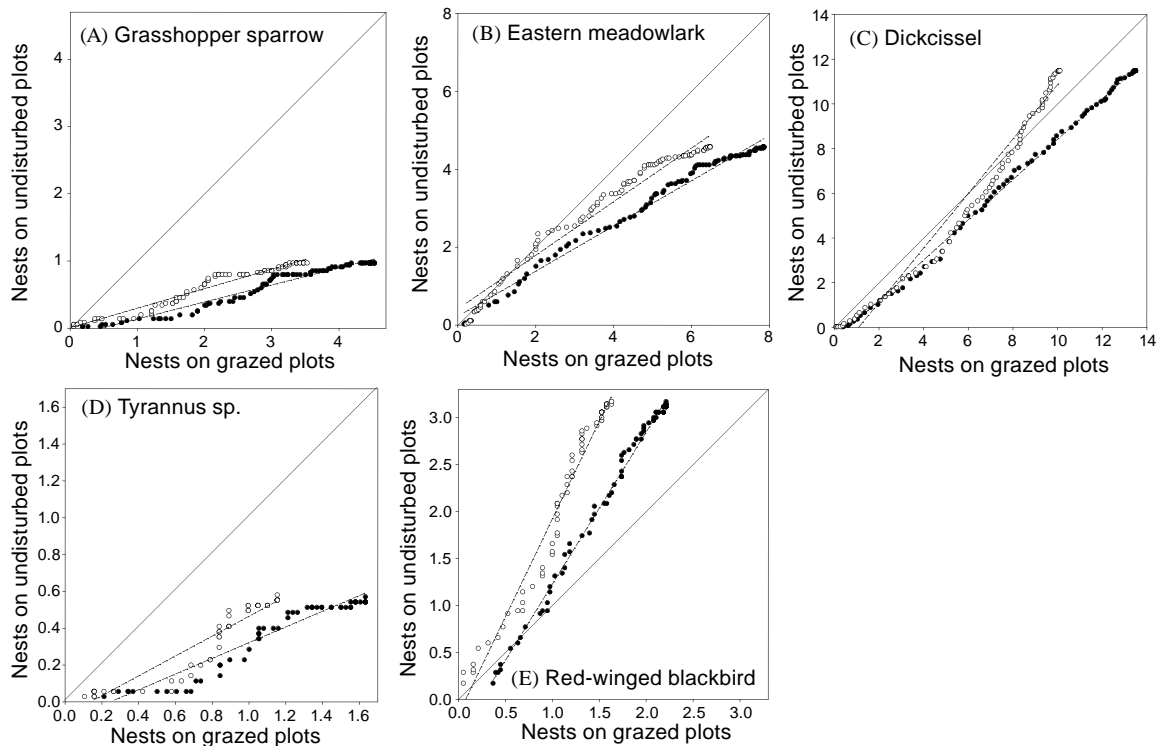| Predator taxa	% of all predators	χ^2	P
Reptilian	79	118.03	<0.001
Avian	14	8.26	<0.05
Mammalian	8	1.37	=0.50

Fig. 4. Isodars of grazed only (open circles) and burned+grazed (closed circles) vs undisturbed plots for the (A) grasshopper sparrow, (B) eastern meadowlark, (C) dickcissel, (D) eastern kingbird+scissor-tailed flycatcher, and (E) red-winged blackbird. Densities are calculated as the mean number of nests with first egg 40 acres^{-1} to avoid counting non-breeding individuals. Solid lines represent the expected isodar if managed and undisturbed plots were identical quantitatively and qualitatively. In practice, the habitat of higher fitness is located on the y-axis as in ideal distribution models. The intercepts of most species fall on the x-axis, implying that managed plots are ecological traps. The slopes of most isodars indicate that the rate of establishing territories in managed plots is faster than in undisturbed plots. The red-winged blackbird is the only species that clearly prefers undisturbed plots, while the dickcissel changes its selection to prefer undisturbed plots over unburned grazed plots at high nest density.

show clearly that meadowlarks enter the managed habitats first. The red-winged blackbird (Fig. 4E) is the only species that clearly prefers the undisturbed habitat, despite the apparent preference for burned plots in the early stage. The dickcissel changes its preference of undisturbed vs grazed plots in late season, but burned plots remain the primary habitat throughout the breeding season (Fig. 4C).

Overall nest density supports these results: average nest density in undisturbed plots (0.95 nest plot^{-1} species^{-1}) was lower than in managed plots, with 2.57 and 3.14 nest plot^{-1} species^{-1} in burned plots and grazed plots respectively (randomized block ANOVA: $F_{2,\,10} = 3.43$, $P < 0.05$).

Food abundance

To assess whether habitat selection was based on food abundance we compared arthropod abundance between undisturbed and managed plots. Arthropod abundance was always higher in managed plots than in undisturbed

Table 3. Statistical analysis of the isodars presented in Fig. 4. Slopes bigger than 1 and positive intercepts indicate preference for undisturbed plots (but see text for discussion on eastern meadowlark).

Species	Burned					Grazed				
	slope	intercept	t	r^2	P	slope	intercept	t	r^2	P
A. grasshopper sparrow	0.25	−0.11	−6.81	0.96	<0.0001	0.29	0.01	0.57	0.96	>0.5000
B. eastern meadowlark	0.58	0.22	5.86	0.98	<0.0001	0.69	0.42	7.27	0.97	<0.0001
C. dickcissel	0.90	−0.59	−13.68	1.00	<0.0001	1.22	−1.32	−8.17	0.97	<0.0001
D. Tyrannus spp.	0.43	−0.12	−6.25	0.93	<0.0001	0.54	−0.09	−4.26	0.91	<0.0001
E. red-winged blackbird	1.62	−0.40	−15.82	0.99	<0.0001	2.08	−0.16	−3.00	0.97	<0.0100

plots, with the differences becoming larger with time (May through July). We present the results as the cumulative arthropod abundance so the data are comparable to the bird isodars shown in Fig. 4 (Fig. 5). Cumulative arthropod abundance was higher in managed plots than in undisturbed plots, with a higher ratio for burned vs undisturbed than for grazed vs undisturbed (Fig. 5).

Discussion

In this study we used data from a large sample of nest monitoring, predator census and arthropod sampling to compare habitat selection between managed and undisturbed plots. We also extended the well-established isodar theory to include ecological traps. The importance of gathering data on any component of fitness (e.g. energy gain or reproductive output) in addition to measuring densities has been demonstrated in the past (Morris and Davidson 2000, Shochat et al. 2002). Such information may be crucial for assessing different models of habitat selection. Our study demonstrates, in addition, that fitness may not only differ between habitats, it can also be decoupled from habitat selection. Future studies using the isodar method, especially in human-managed environments, should consider such processes.

Remes (2003) distinguished among three different scenarios of habitat selection, each yielding a different set of predictions for primary vs secondary habitats: (1) the ideal free distribution (Fretwell and Lucas 1969), with higher density in the primary habitat and equal reproductive success across habitats, (2) the ideal despotic distribution (Fretwell and Lucas 1969), with higher

density and success in the primary habitat, and (3) ecological traps (Dwernychuk and Boag 1972), with higher density and lower success in the secondary habitat. We demonstrate that when the suitability of each habitat is measured, isodar theory can be used to detect the third scenario on the basis of the isodar's unique intercept. Measuring habitat suitability is essential in studies on ecological traps, because plotting the isodar solely on the basis of an animal's habitat choice may yield the wrong conclusion that choice is coupled with fitness. In other words, knowing nothing about suitability, densities in ecological traps may be plotted on the wrong axes.

To plot the isodars we used data on first egg day (Fig. 4). This may introduce some bias to the data because a pair may make more than one nesting attempt and therefore be tallied as two pairs. Yet, we believe that such bias is minor compared with the bias emerging from relative abundance estimates that may include many individuals passing through the area during spring migration or floating between territories. Further, a second nesting attempt may not take place in the same habitat as the first. The change in dickcissel's habitat preference between grazed and undisturbed plots hints that some birds failing to breed successfully on grazed plots make a second attempt on undisturbed plots.

Our data indicate that the perceived habitat quality of traps exceeds that of undisturbed prairie for several species. The ecological trap we describe involves bottom-up cues upon which birds select nest sites and top-down control of nest success, with both bottom-up and top-down processes varying across the landscape (Patten and Bolger 2003). Management of tallgrass prairie that includes prescribed fires in spring followed by high intensity livestock grazing increases the abundances of arthropods and predators. The major consequence is that individuals breeding in the ''secondary'' (in terms of choice) unmanaged habitat may have a higher fitness in the long term. The main cause for nest failure is predation, accounting for more than 80% of all failures. Differences in nest success among substrates support this idea: nest success for tree-nesting birds is much higher than for ground- or shrub-nesting birds (Fig. 3B), and tree height is a good indicator of nest success. These results are similar to the results of a study on breeding birds in northern hardwood forest edge (Flaspohler et al. 2001), where brood parasitism was also high. In our study it was hard to assess the effect of brood parasitism on nest success because it is not clear how many of the abandoned nests were the result of parasitism. Yet, parasitism rates in managed plots are higher than in undisturbed plots, likely adding to the negative effect of predation. It is possible that the habitat selection by the red-winged blackbird is based on cowbird avoidance and not on food abundance, as this species is a major host for
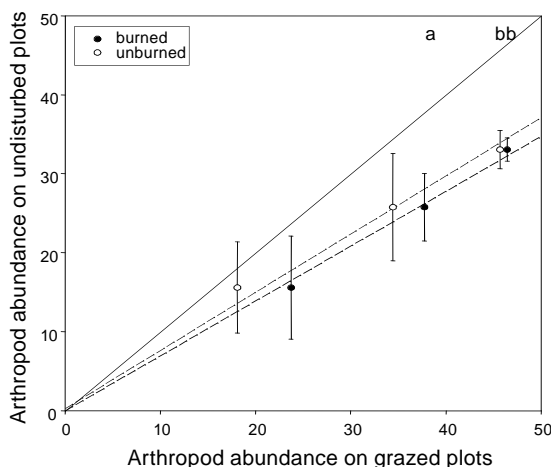

Fig. 5. The ratio between average cumulative numbers of arthropods 40 acres^{-1} in managed and undisturbed plots. Letters above points indicate a significant deviation from 1:1 ratio (solid line), with a $=P <0.02$ and b $=P <0.001$.

cowbird parasitism (Ward et al. 1996, Clotfelter and Yasukawa 1999), especially when nests are scattered (Friedmann 1963), as they are in the Oklahoma tallgrass prairie. Rates of brood parasitism of the dickcissel and red-winged blackbird were 6–7% higher than for the rest of the species in our study.

The high proportion of reptilian predators observed (79%) may explain the low success of ground and shrub nesting species. Box turtles appear to be major nest predators in the study area (Sutton Avian Research Center, unpubl.). The relatively low proportion of mammalian predators may be biased because many mammals are nocturnal; nonetheless, we found no difference among treatments for the mammals we did record. The overall low abundance of avian predators may, in turn, explain the relatively high nest success of tree-nesting species. Differences in reptile abundance appear to drive the differences in nest success between this study and a simultaneous one on nest success along roadsides in the same tallgrass prairie (Shochat et al. 2005). Along roadsides there is a positive relationship between burning, arthropod abundance, and nest success. We speculate that the abundance of reptilian predators may be lower near roads as a result of collisions with vehicles, thereby preventing the ecological trap we observe in roadless prairie.

If predation decreases nest success, then the scenario in managed tallgrass prairie in Oklahoma is similar to what Misenhelter and Rotenberry (2000) described for sage sparrows (*Amphispiza belli*) in southern California. The sparrows preferred habitats where snakes were more abundant, resulting in decreased nest success; however, although the study was also done in a disturbed landscape, in contrast to the tallgrass prairie species we describe, both the sparrows and snakes were more abundant in the undisturbed habitat. Misenhelter and Rotenberry (2000) speculated that the preference for the undisturbed habitat was based on vegetation structure, which indirectly determined foraging opportunities. Despite differences in habitat preference between sage sparrows and tallgrass prairie birds, there are important similarities between the studies: (a) human modification of the environment may alter both food abundance and predator abundance, (b) the former affects nest site selection and the latter nest success, and (c) such ecosystems are likely to become ecological traps for breeding birds. Our results, together with those of other studies, (Best 1986, Misenhelter and Rotenberry 2000, Kolbe and Janzen 2002, Remes 2003), indicate that ecological traps are especially common in managed and altered ecosystems.

Although ecological traps have negative effects on wild populations their effects depend on differences in suitability between habitats and populations size. Where differences in suitability are subtle, large enough populations may adapt to ecological traps and overcome their negative effects where spatial or temporal instability is moderate (Schlaepfer et al. 2002, Holt et al. 2004). Specifically, the response to tallgrass burning and grazing intensity probably differs among species, depending on their life history. As a result, conservation plans must consider whether a given species is caught in an ecological or evolutionary trap (sensu Schlaepfer et al. 2002) and formulate solutions accordingly. For example, ground nesters like the grasshopper sparrow that show high preference for burned plots over undisturbed plots may not adapt to the high predation and thus may vanish or exist only in sinks in places where burned prairie is in supernormal abundance. In contrast, a species like Henslow's sparrow that is restricted to unburned plots (Reinking et al. 2000) may benefit from being a habitat specialist, especially as a ground nester. Yet because undisturbed prairie became fairly rare in Oklahoma, the grasshopper sparrow is much more abundant than Henslow's sparrow. Future studies should identify those species most sensitive to grassland management and concentrate on their conservation based on their specific responses to anthropogenic activities.

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