

# Habitat selection and the perceptual trap

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**Abstract.** The concept of “ecological traps” was introduced over three decades ago. An ecological trap occurs when, by various mechanisms, low-quality (yielding low fitness) habitat is more attractive than good habitat, thus coaxing individuals to settle there despite a resultant loss of fitness. Empirical work on such traps has increased dramatically in the past decade, but the converse—avoidance of high-quality habitat because it is less attractive, what we term a “perceptual trap”—has remained largely unexplored. Even so, depending on conditions (growth rate, strength of habitat preference, and mortality rate), such perceptual traps can be more limiting than ecological traps to population persistence. An example from field experiments with the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) lends empirical support to the concept, and several other potential examples suggest that these traps are perhaps more prevalent than has been appreciated. Because demographic Allee effects are expected to prevent a population from growing sufficiently in a habitat that is avoided, a perceptual trap may persist even though fitness is high. Unlike an ecological trap, which may be negated by increasing habitat quality, biologists will be hard pressed to negate a perceptual trap, which will require determining which cues an animal uses to select high-quality habitat and then devising a means of enhancing those cues so that an animal is lured into the habitat.

**Key words:** avoidance; ecological trap; habitat selection; Lesser Prairie-Chicken; shortgrass prairie, New Mexico, USA; *Tympanuchus pallidicinctus*; undervalued resource.

## INTRODUCTION

When the concept of an *ecological trap* was introduced, it was unclear whether it had any value for on-the-ground conservation, yet over the past 30 years the concept of ecological traps has become an important consideration in conservation planning, particularly because traps are thought to occur chiefly as a result of anthropogenic habitat change (Battin 2004, Robertson and Hutto 2006). As a result, conservation and management plans now more consistently devise mitigation strategies for habitats in which animals occur but either survive or reproduce poorly. Whereas some such habitats may be population sinks (Kristan 2003), others—habitats in which the animal prefers to settle—conform to the notion of an ecological trap. Such traps occur when habitat selection becomes decoupled from habitat quality (*sensu van Horne* 1983), so that an animal preferentially chooses a habitat that reduces its own fitness relative to what it would have been in other available habitats (e.g., Donovan and Thompson 2001, Schlaepfer et al. 2002, Shochat et al. 2005a, Robertson and Hutto 2006).

At its core, then, the concept of an ecological trap recognizes a disconnect between the act of habitat selection and the consequences of that act. We recognize a third step in this process, one involving the cognition

of the organism: its perception of habitat quality leads to a particular choice (habitat selection), which in turn has particular consequences. This cognitive step is not new. Building on groundwork laid by Schlaepfer et al. (2002), Robertson and Hutto (2006) summarized both the kinds of data needed for scientists to detect an ecological trap convincingly and the different means by which a trap could develop, each of which invoked perception in the form of habitat cues. In this view, an ecological trap can occur after (a) attractiveness of a selection cue is raised in a habitat with lower quality, (b) quality is lowered in a habitat with unchanged cues, or (c) attractiveness of cues is raised and habitat quality is lowered simultaneously. Any of these three scenarios creates requisite conditions for an ecological trap: given a suite of choices, an animal selects a habitat in which fitness is low (i.e., population growth rate  $\lambda < 1$ ).

Pulliam's (1988) model of source–sink dynamics did not include habitat selection, but ecological traps have been linked to sources and sinks (Kristan 2003). In this vein, Battin (2004) presented a simple  $2 \times 2$  table linking sources, sinks, and ecological traps (Fig. 1A); however, in both Battin's table and Robertson and Hutto's (2006) verbal model, a distinct combination of habitat preference and habitat quality was ignored until recently (Fig. 1B; Gilroy and Sutherland 2007). In either conception, a “source” occurs when preference and quality are high, a “sink” when preference and quality are low, and an ecological trap when preference is high and quality is low. Views diverge in the fourth cell: because  $\lambda > 1$ ,

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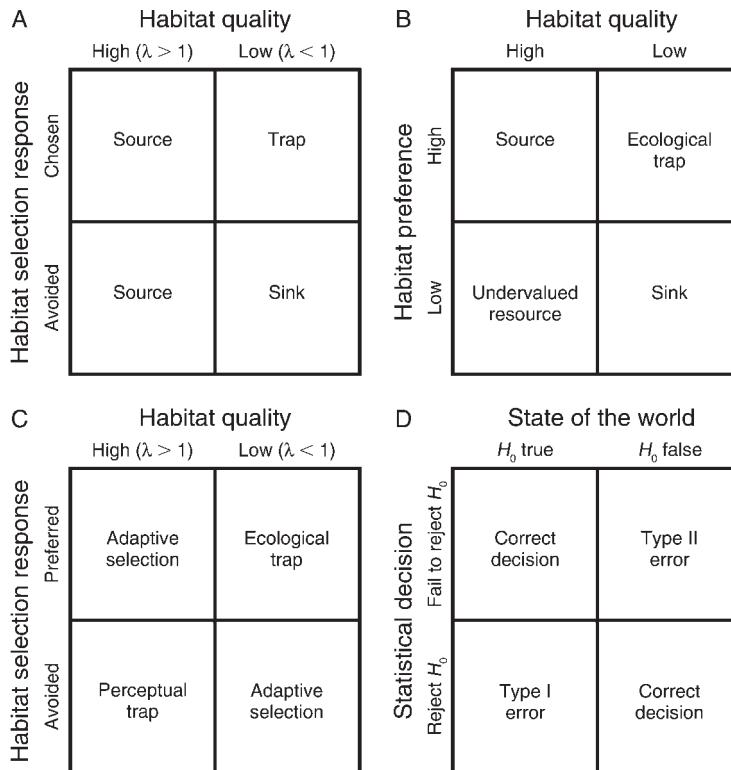


FIG. 1. Conceptual representations ( $2 \times 2$  tables) of sources, sinks, ecological traps, and perceptual traps. (A) For high-quality habitats, Battin (2004) did not distinguish between areas chosen or avoided. By contrast, (B) Gilroy and Sutherland (2007) recognized that high-quality areas that were avoided cannot be “sources.” (C) We argue that alignment of habitat selection and habitat quality defines adaptive choice, whereas if selection and quality are not aligned it defines an error in habitat selection. In this respect, our view shares more with a standard  $2 \times 2$  table of statistical error (D) than it does with tables in Battin (2004) or Gilroy and Sutherland (2007), which added source–sink dynamics.

Battin (2004) dubbed it another type of source, which gives primacy to consequence over choice (meaning an ecological trap ought to have been labeled a sink under the same logic). Gilroy and Sutherland (2007) recognized that the act of habitat avoidance led to a different condition—one they termed an “undervalued resource”—in which, given a suite of choices, an animal avoids a habitat in which its fitness would have been high (i.e., population  $\lambda > 1$ ). To emphasize its conceptual kinship with an ecological trap, we feel “perceptual trap” is a more fitting term for this phenomenon, as this new term emphasizes that it is a trap and perception of habitat cues is at its heart.

*Habitat preference*, an organism’s perception of whether a habitat is suitable or not, is the first step to recognizing either an ecological trap or a perceptual trap. Given a choice among distinct habitats, an animal may (a) show no preference, (b) prefer one or more of the habitats, or (c) avoid one or more of the habitats. Although at odds with Gates and Gysel’s (1978) formulation, Robertson and Hutto (2006) posited that choice (a) produces a type of ecological trap, which they termed an “equal-preference trap,” if by chance one

habitat is of lower quality. We disagree: this situation should not be termed a trap because the essential step of habitat selection was not exercised. (In our view, then, most plants cannot experience ecological traps because habitat occupancy typically is passive.) Option (b) yields what Robertson and Hutto (2006) called a “severe trap,” which matches standard definitions of an ecological trap because the preferred habitat is of lower quality. It is option (c) that had been ignored and what we term a *perceptual trap*. We can state that an ecological trap exists if organisms act in choosing low quality habitat perceived to be of high quality. Conversely, then, a perceptual trap exists if organisms act in avoiding high-quality habitat perceived to be of low quality. Moreover, akin to Robertson and Hutto (2006), we posit that a perceptual trap may arise in three ways that mirror ways in which an ecological (severe) trap may arise: (a) selection cues are made less attractive in a habitat with higher quality, (b) quality is raised in a habitat with unchanged selection cues, or (c) selection cues are made less attractive and habitat quality is raised simultaneously. The first condition—active avoidance of

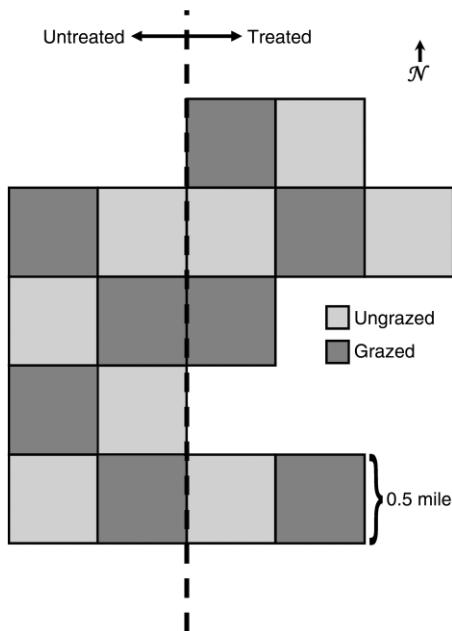


FIG. 2. Experimental design for examining the effects of tebuthiuron application ("treated") and cattle grazing on Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) reproduction in eastern Roosevelt County, New Mexico, USA. Each block is a section ( $0.5 \times 0.5$  mile), yielding a study area of  $\sim 16,000$  ha (1 mile  $\approx 1.6$  km). Tebuthiuron was also applied to other scattered blocks in the 52,000-ha study area.

high-quality habitat—fits most neatly into our idea of a perceptual trap.

Battin (2004) and Gilroy and Sutherland (2007) linked sources and sinks to ecological traps in their  $2 \times 2$  tables (Fig. 1A, B). As phenomena, source-sink dynamics differ fundamentally from traps, in large measure because the former emphasizes population consequences ( $\lambda$ ) as a function of density dependence. Traps, by contrast, emphasize behavior (perception of and selection of habitat) and consequences of that behavior (see Misenhelter and Rotenberry 2000), so conflating source-sink dynamics and traps may muddy theoretical and empirical advances. In our view, if preference coincides with high-quality habitat or avoidance coincides with low-quality habitat, then we have adaptive habitat selection (Fig. 1C), the "adaptive choice" of Misenhelter and Rotenberry (2000). The other two possibilities are errors, akin to the two types of errors in inferential statistics (Fig. 1D), which are related yet differ fundamentally. We thus feel that treating a perceptual trap as the inverse of an ecological trap (pace Gilroy and Sutherland 2007) would be like treating type I error as the inverse of type II error. In a perceptual trap stimuli for habitat selection are negative (avoidance) rather than positive (cf. Robertson and Hutto 2006): habitat of high quality is *perceived* to be of low quality, which is analogous to resources being undervalued (Gilroy and Sutherland 2007). In other words, an animal has three choices: active preference, do

nothing (i.e., exercise no choice), and active avoidance. That habitat is avoided for a perceptual trap implies a fundamental difference between it and an ecological trap: if avoidance is strong, a demographic Allee effect (i.e., negative density dependence) will hinder a population from establishing itself. Allee effects play no comparable role in an ecological trap.

Our goal is to shorten the gap between recognition of the concept of perceptual traps and incorporation of the concept into conservation strategies by providing a practical example and reviewing the ecological literature for other possible examples. Documenting a perceptual trap is a challenge, as it requires data in support of a negative (habitat avoidance) coupled with data from enough individuals that settled in the eschewed habitat to demonstrate that at least some component of fitness was no worse than in preferred habitat. Our example is a step in demonstrating the kinds of data needed.

## METHODS

### *Study system and field site*

In New Mexico, the rare and declining Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) occurs in *Quercus havardii* (shinnery oak) grassland (see Plate 1). It has been hypothesized that, in the past century, the oak has become more widespread and now occurs in denser stands, thus reducing grass cover and other forage for cattle (Peterson and Boyd 1998). To counteract this hypothesized effect, land stewards have used various techniques to reduce or remove oak and other shrubs. Among these techniques is the application of herbicides, chiefly tebuthiuron, which inhibits growth of woody vegetation. The Sutton Avian Research Center (Bartlesville, Oklahoma, USA) conducted a four-year study of the reproductive ecology of the prairie-chicken in response to tebuthiuron application.

The  $\sim 52,000$ -ha study area was located in eastern Roosevelt County (New Mexico, USA), on the western edge of the Llano Estacado, a region characterized by sandy soils atop caliche bedrock, sand dunes, and scattered playas (the only natural surface water). Vegetation is shortgrass prairie dominated by *Quercus havardii*; other woody vegetation included *Artemisia filifolia*, *Prosopis glandulosa*, *Opuntia imbricata*, *Gutierrezia sarothrae*, and several species of *Yucca*. Short bunch grasses (e.g., *Andropogon hallii*, *Bothriochloa laguroides*, *Schizachyrium scoparium*, *Sporobolus* spp., *Bouteloua* spp., and *Buchloe dactyloides*) predominate. Less than 10% of the area was cultivated, and well pads and roads supporting oil production accounted for  $\sim 5\%$  of the land area.

The experimental study focused on the  $\sim 16,500$  ha area centered at the north end of the North Bluff Prairie-Chicken Area. Tebuthiuron (0.67 kg/ha) was applied to the portions of the study area late October–early November 2000 (Fig. 2). Field work began in March 2001, the first growing season after treatment. Oaks and other shrubs died back in May 2001, shortly

after the first prairie-chicken eggs were laid. As a result, in that year it is possible that some females chose a nest site that looked suitable to them when it was chosen but later would have looked unsuitable (e.g., more exposed) because of defoliation (i.e., treatment effects became apparent). This potential problem occurred only in the first year of the study—defoliation from tebuthiuron treatment was readily apparent during 2002–2005. Another key aspect of this study design was to determine the effects of cattle grazing on the prairie-chicken (Fig. 2), but grazing treatments were not implemented until after the 2002 breeding season and are considered only briefly herein. See Patten et al. (2005a, b) for details of trapping, radiotracking, nest monitoring, and vegetation sampling, the last including how we sampled random vs. occupied locations.

### Statistical analyses

Nest placement with respect to tebuthiuron treatment was analyzed with the Wilcoxon two-sample test on nest number/block in the experimental area (Fig. 2). We treated each nest as an independent event and combined data across years. *P* values were derived from a *t* approximation.

Failure-time analysis and Cox regression were used to explore patterns of nest survival (Nur et al. 2004, Shochat et al. 2005b). Failure-time analysis is advantageous because with it one can build heuristic graphics that compare nest success, and it has a well-established statistical foundation, including ready incorporation of right-censored data. Cox regression, for example, allows one to associate predictors with survival curves. Use of the technique requires an assumption that errors are distributed evenly across treatments; i.e., nests were no more or less likely to be found *at a given stage* on any of the treatments or with respect to any other of the comparison variables. We feel that this assumption was met, largely because we located almost all nests at an early stage via tracking radio-collared females. By definition, left-censored data will not be incorporated fully, absolute nest survival times will be biased downward, but with the assumption of equally distributed errors, valid comparisons of relative survival between treatments can be made.

We used path analysis to model potential cause-and-effect pathways in the ecosystem; i.e., with it we could deduce effects of tebuthiuron on fledgling productivity (number of hatched chicks/nest). As with the analysis of nest survival, we used all available nests from the 52 000-ha study area to ensure an adequate sample size. We treated a path model as “valid” only if the model’s  $\chi^2$  was nonsignificant, an indication that the actual and model correlation matrices do not differ (Mitchell 1993). In the case of multiple “valid” models, we accepted the simplest one (lowest AIC<sub>c</sub>). Resultant models are not meant to be a full explanation of cause-and-effect relationships; rather, they are plausible (simplified) models for the system. The overall effect of tebuthiuron

TABLE 1. Vegetation at Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nest sites ( $n = 45$ ) relative to availability ( $n = 414$  random vegetation surveys) in the experimental area (Fig. 2) in *Quercus havardii* (shinnery oak) grassland in New Mexico (USA), 2001–2005.

Measure	Nest site mean	Random mean	Effect size§
Cover†			
Shrubs (%)	<b>53.82</b>	29.47	0.98
Grasses (%)	<b>47.31</b>	34.67	0.55
<i>Quercus havardii</i> (%)	<b>41.01</b>	20.22	0.95
Canopy height (cm)	<b>63.82</b>	24.21	1.44
Density‡			
<10 cm	<b>1.18</b>	0.71	0.36
10–50 cm	<b>6.57</b>	1.75	1.52
>50 cm	<b>0.66</b>	0.26	0.47

Notes: Post hoc significance tests (Tukey’s hsd) control for experimentwise  $\alpha$  at 0.05; significantly larger means are boldfaced. Separate analysis by each year does not materially change these results.

† Shrub and grass values were transformed to percentages post hoc.

‡ Density was estimated as the number of contacts on a vertical rod.

§ Effect size was estimated as *d* (Cohen 1988).

on fledgling production could be calculated through paths by means of a point-biserial correlation ( $r_{pb}$ ), a Pearson’s *r* with one variable continuous and the other dichotomous (Howell 1992:267). Cox regression (proc phreg) and path analysis (proc calis) were performed in SAS version 9.1 (SAS 2003).

### RESULTS

Relative to availability, females selected nest sites with higher cover, greater canopy height, and higher vegetation density (Table 1). In particular, shrub cover (especially of *Quercus havardii*), canopy height, and mid-height (10–50 cm above ground) density are markedly higher at nest sites ( $P < 0.0001$  for each univariate ANOVA, plus generally large effect sizes). By contrast, females avoided blocks with low shrub cover, such as those treated with herbicide (Wilcoxon two-sample:  $C = 99.0$ ,  $P = 0.005$ ). Avoidance can be linked directly to the expected reduction in shrub cover resulting from treatment with tebuthiuron (Fig. 3). Sample size was low ( $n = 18$ ), but placement of 2003–2005 nests was not associated with grazing ( $C = 75.0$ ,  $P > 0.40$ ), yet the effect of tebuthiuron on nest placement was apparent even within this small sample ( $C = 94.0$ ,  $P < 0.02$ ).

Using data from all nests ( $n = 126$ ) from the 52 000-ha study area, nest survival did not differ between areas treated with tebuthiuron or not (Fig. 4)—i.e., nests were as likely to succeed and survived roughly equally long regardless of whether herbicide was applied. Likewise, clutch size did not differ for nests in treated vs. untreated areas (one-way ANOVA:  $F_{1,86} = 0.36$ ,  $P > 0.50$ ). Although tebuthiuron had the expected effect of greatly

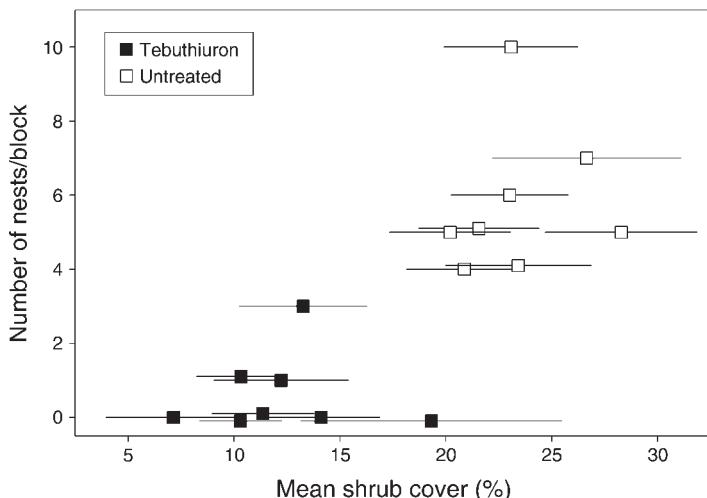


FIG. 3. Total number of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nests per block (Fig. 2) as a function of shrub cover (mean  $\pm$  SE), estimated from 414 random vegetation surveys. Mean shrub cover accounts for  $\sim$ 51.5% of variation in nest number, as estimated using the method of Mittlböck (2002) for a Poisson regression (offset by number of vegetation surveys/block:  $y = 0.13x - 4.72$ ).

reducing shrub cover, reducing the density of shinnery oak, and increasing grass cover, nest survival was not associated with the extent of shrub cover (Cox regression:  $\chi^2 = 1.43$ ,  $df = 1$ ,  $P > 0.20$ ), grass cover ( $\chi^2 = 2.14$ ,  $df = 1$ ,  $P > 0.10$ ), or oak density ( $\chi^2 = 0.37$ ,  $df = 1$ ,  $P > 0.50$ ).

Nest survival, which did not vary with female age (log-rank  $\chi^2 = 2.29$ ,  $df = 1$ ,  $P > 0.10$ ), was, however, associated with how well the nest was concealed ( $\chi^2 = 3.84$ ,  $df = 1$ ,  $P = 0.05$ ), which itself was associated with both oak density and grass cover (Fig. 5). Path analysis offered a plausible reason why fledgling production differed little between treatments: the resultant model implies that the herbicide has a complex relationship with fledgling production, such that tebuthiuron traces both positive and negative paths to this endpoint; e.g.,

tebuthiuron reduces shrub cover and oak density, but the latter is a key component of nest concealment. Tebuthiuron also increases grass cover, both directly and mediated through the reduction of oak density. Grass is also an important component of nest cover, but grass cover per se has an additional negative effect on fledgling production (Fig. 5). We suggest that tebuthiuron had an insignificant effect on fledgling production ( $r_{pb} = -0.03$ ) because its effects were dampened or countered through a sequence of causes and effects.

DISCUSSION

Tebuthiuron had a negative effect on reproduction of the Lesser Prairie-Chicken, although not in the way typically considered. Tebuthiuron, via its effects on shrub cover, does not affect nest survival (Fig. 4), clutch

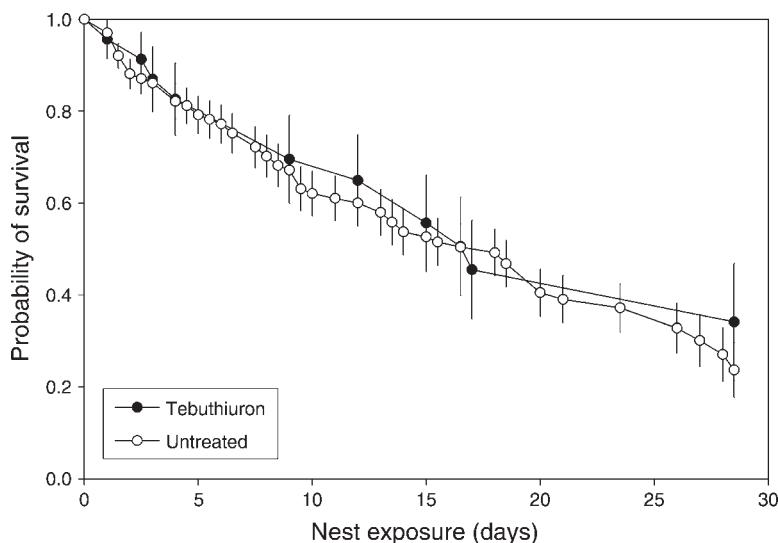


FIG. 4. Survival (mean  $\pm$  SE ) of Lesser Prairie-Chicken nests by tebuthiuron application. Nests either fledged or were depredated (none were abandoned). These Kaplan-Meier curves display the amount of time nests survived from inception to fate, and do not differ (log-rank test:  $\chi^2 = 0.56$ ,  $df = 1$ ,  $P > 0.40$ ).

size, or fledgling production (Fig. 5). Nonetheless, female prairie-chickens avoid nesting in areas with low shrub cover (Johnson et al. 2004, Davis 2009), which is the chief consequence of tebuthiuron application (Fig. 3); indeed, the percentage of prairie-chickens tracked year round in treated blocks declined over time: 25.3% in 2001 to 16.2% in 2002 to 3.1% in 2003 to 1.2% in 2004. We conclude that females perceive tebuthiuron-treated habitat to be of low quality even though reproductive data ( $n = 126$  nests) suggest it is not. It is possible that adult survival (Patten et al. 2005b, Hagen et al. 2007) or some other component of fitness offsets this apparent maladaptive behavior. An effect on survival would have been difficult to detect because only 8 of 40 birds (20%) with at least 15 tracking locations occupied untreated prairie exclusively, and none occupied treated habitat exclusively. Nonetheless, if tebuthiuron had an effect, the proportion of tracking locations in treated blocks (time spent in treatment) ought to be correlated negatively with survival (days elapsed from capture until disappearance or death), but there was no such correlation ( $r_{55} = -0.07$ ,  $P > 0.25$ ).

The consequences of habitat avoidance are potentially manifold. Reducing shrub cover may force female prairie-chickens to move farther to find what they perceive to be suitable nesting habitat, but increased motility leads to increased mortality (Patten et al. 2005a, Wolfe et al. 2007). If the practice of herbicide application spreads, then nesting prairie-chickens may abandon areas where their perception of habitat quality drops below some threshold, a common response to habitat loss, wherein habitat perceived to be unsuitable is avoided and, consequently, populations and ranges shrink as a result of fragmentation (Fahrig 2003).

Our study doubtless is not the sole instance of a perceptual trap, but locating potential examples in the literature is hampered by the concept not being articulated until recently (Gilroy and Sutherland 2007). We nonetheless note a few instances, largely from our own work, that may have qualified as perceptual traps: key elements of habitat avoidance are in place and available data on habitat quality suggests that an animal's fitness would not have suffered had the habitat in question not been avoided. For example, Pruett et al. (2009) documented that the Lesser Prairie-Chicken avoids habitats near both high-tension power lines and wide highways with modest amounts of traffic. Only 16 of 107 nests (~15%) were placed within 2 km of a power line in a three-county area of northwestern Oklahoma (USA), yet the proportion of these nests that fledged at least one chick (0.375) did not differ from the proportion across the entire study area (0.397; Patten et al. 2005a). Waders nesting in pastures in coastal Sweden also avoided placing nests near man-made structures even though nests nearer structures were no more likely to be depredated than nests farther away (Wallander et al. 2006). A study of the Greater Prairie-Chicken (*T. cupido*)—a denizen of tallgrass prairie and

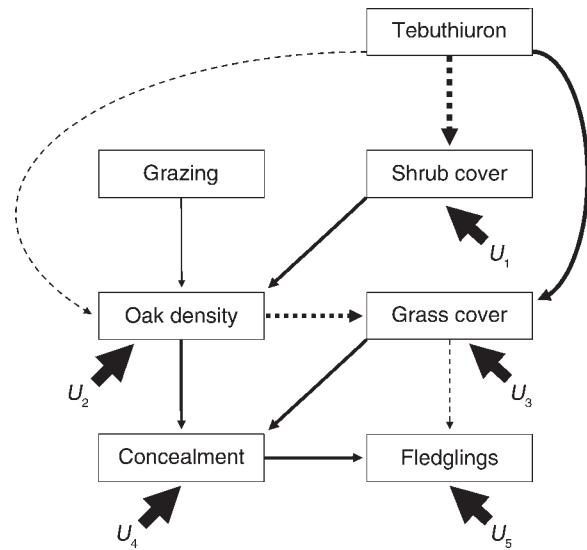


FIG. 5. Path analysis of effects of tebuthiuron on Lesser Prairie-Chicken fledgling production. The model provided a good fit for the data ( $\chi^2 = 6.00$ ,  $df = 10$ ,  $P > 0.80$ ). The width of a postulated cause-effect path corresponds to the strength of the relationship, with negative relationships shown by dashed lines.  $U_i$  refer to unknown sources of variation (i.e., not explained by the model).

sister species of the Lesser Prairie-Chicken—revealed a similar pattern of habitat avoidance, in that case in response to spring burning of prairie to increase forage for cattle (Patten et al. 2007). Annually ~60–80% of the ~40 000-ha study area was burned in March or April, just prior to nesting. Only 14 of 74 nests (~19%) were placed on burned prairie, yet nest success on burned prairie did not differ from that on unburned prairie (Patten et al. 2007).

The above studies are examples in which reproductive components of fitness are not lower in an avoided habitat. A putative example of a perceptual trap in which higher-quality habitat is avoided comes from a study of how habitat fragmentation affects nesting passerines in an urban area (Patten and Bolger 2003). Two ground nesters, the Spotted Towhee (*Pipilo maculatus*) and Rufous-crowned Sparrow (*Aimophila ruficeps*), are largely absent from habitat fragments (they occur along edges or in the core of large blocks of habitat), but those that nested on fragments had markedly higher nest success by virtue of a great reduction in snakes, their chief nest predator (Patten and Bolger 2003). Yet despite this advantage, even year-to-year populations on fragments do not persist, suggesting the possibility that these species avoid patches of habitat they perceive as being too small (see Bolger et al. 1991, 1997).

Another sparrow also may experience a perceptual trap: a study of landscape ecology of the Black-throated Sparrow (*Amphispiza bilineata*) identified a putative ecological trap in that mean nest density was highest (15.9 nests/100 ha) where mesquite (*Prosopis* sp.)

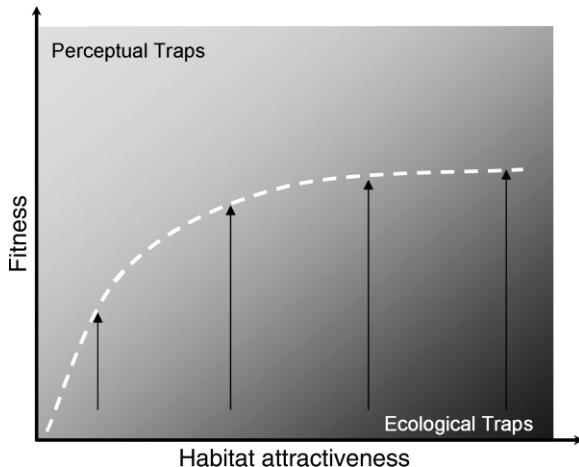


FIG. 6. Optimality modeling of habitat selection (e.g., ideal free and ideal despotic distributions) predicts that an organism will settle in habitats that maximize its fitness, meaning that there ought to be strong directional selection (arrows) favoring organisms attracted to optimal habitats (light shading) and against those attracted to suboptimal ones (dark shading). Selection produces a positive relationship between perceived attractiveness of a habitat and fitness of organisms that settle in that habitat (dashed curve). Attractive, albeit often human-modified, habitats with low fitness are ecological traps, and there is strong selection against organisms caught in them. Largely unrecognized are habitats (again often human modified) that are unattractive to organisms despite high fitness potential. Productivity lost in these perceptual traps may be substantial because few individuals occupy such sites (Allee effects), and the positive-fitness differential enjoyed by these few organisms may not be enough to influence habitat selection in large, well-mixed populations.

dominated, but mean nest success rate (0.10) was lowest in that habitat (Pidgeon et al. 2003). Not surprisingly, the authors did not name the converse, yet they provided data that nest density was lowest in black grama (*Bouteloua eriopoda*) grassland (5.3 nests/100 ha). Nest success rate (0.37) was second highest in black grama of the six habitats studied, and the success rate for one year was the highest recorded (0.47; Pidgeon et al. 2003). We posit that black grama grassland is a perceptual trap for the Black-throated Sparrow, and in this case the cue may be the perceived paucity of suitable nesting shrubs (Pidgeon et al. 2003).

Lastly, an intriguing example considers spatial ecology of the vervet monkey (*Cercopithecus aethiops*) in South Africa (Willems and Hill 2009). Monkeys avoid areas where perceived risk of predation by the chacma baboon (*Papio ursinus*) or common leopard (*Panthera pardus*) is high—the “landscape of fear.” For our purposes, “Of particular importance was the finding that the effects of fear can exceed those of local resource availability” (Willems and Hill 2009:553). Thus, even when resources important to maintenance and survival are abundant—resources putatively with a direct bearing on fitness—an animal perhaps avoids a habitat if perceived risk is high.

### Conclusions

A perceptual trap occurs when an animal avoids a habitat that, had it been occupied, would have yielded higher fitness than in the more preferred habitats. It thus differs from simple habitat avoidance, which likely often involves a correct decision (Fig. 1C, D). For example, that lizards avoid habitats with the nonnative vine *Cryptostegia grandiflora* where it has invaded northern Australia could be an example of adaptive selection because “the apparent avoidance of rubber vine habitat by lizards suggests that rubber vine may contain underlying characteristics that are unfavourable for lizards” (Valentine 2006:734). In other words, if cues used to select a habitat jibe with that habitat’s quality, then a trap does not exist; instead, avoidance is an instance of adaptive choice.

In contrast to an ecological trap, against which there is expected to be strong natural selection (Fig. 6; Kokko and Sutherland 2001), selection may be weak against a perceptual trap because if avoidance is strong, demographic Allee effects (*sensu* Stephens et al. 1999) are expected to hinder a population’s ability to establish itself in the habitat (Fig. 6). Either weak avoidance or extremely high population growth rate ought to overcome initial Allee effects and allow a species to enjoy fitness benefits in the habitat and establish a population. Nonetheless, sustained high growth rates are unlikely in most species that actively select habitat, and perceptual traps will be detected most readily when avoidance is strong.

As Kristan (2003) noted, animals use discrete environmental cues to select habitat. If an animal perceives habitat as unsuitable, then whether or not habitat quality is high is moot. This problem is one that conservation biologists and land managers cannot resolve easily, for it requires “convincing” the target animal that a habitat is suitable. In this respect applied issues of a perceptual trap differ fundamentally from those of an ecological trap. In both traps habitat-selection behavior can be viewed as maladaptive and (in most cases) largely the result of anthropogenic modification, but in an ecological trap conservationists may “fix” a “bad” habitat by elevating its quality (e.g., removing predators or supplementing food). In a perceptual trap the trick lies in fixing the cues or attempting to attract individuals, using song playback or decoys, to what appears to us to be suitable habitat (e.g., Ward and Schlossberg 2004, Ahlering et al. 2006). Yet without detailed knowledge of how habitats are selected—knowledge of which cues lure an animal to a site vs. which discourage settlement—it will be all but impossible to “fix” the habitat, which in this case we mean creating suitable cues. Worse, if avoidance is complete, biologists would have no data on relative fitness in a particular habitat and thus be unaware that the habitat had high fitness potential. Only detailed research on specific cues used in habitat selection will resolve this conundrum, and we echo Kokko and Sutherland (2001:537) that “conservation biologists



PLATE 1. A small motte of shinnery oak (*Quercus havardii*) on the study area in Roosevelt County, eastern New Mexico, USA. Such mottes are important as nest sites and roost sites for the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Photo credit: Donald H. Wolfe.

need to ensure that cues for habitat choice correlate with habitat quality.” Furthermore, both ecological traps and perceptual traps require in-depth empirical research that addresses all components of fitness. We hope that the concept of perceptual traps will both spur and help guide that research.

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