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Shrub encroachment creates a dynamic landscape of fear for desert lagomorphs via multiple pathways

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Abstract. Shrub encroachment is transforming arid and semiarid grasslands worldwide. Such transitions should influence predator–prey interactions because vegetation cover often affects risk perception by prey and contributes to their landscape of fear. We examined how the landscape of fear of two desert lagomorphs (black-tailed jackrabbit, *Lepus californicus*; desert cottontail, *Sylvilagus audubonii*) changes across grassland-to-shrubland gradients at Jornada Basin Long Term Ecological Research site in the Chihuahuan Desert of southern New Mexico. We test whether shrub encroachment shapes risk differently for these two lagomorphs because of differences in body size and predator escape tactics. We also examine whether an ecosystem engineer of grasslands (banner-tailed kangaroo rat, *Dipodomys spectabilis*) mediates risk perception through the creation of escape refuge and whether trade-offs exist between shrub encroachment and the local reduction of banner-tailed kangaroo rats caused by shrub expansion. We measured perceived predation risk with flight initiation distances (FIDs) and then used structural equation modeling to tease apart the hypothesized direct and indirect pathways for how shrub encroachment could affect perceived risk. A total negative effect of shrub cover on FID was supported for jackrabbits and cottontails, suggesting both species perceive shrubbier habitat as safer. Increases in fine-scale concealment also reduced risk for cottontails, but not jackrabbits, likely because cottontails rely on crypsis to avoid predator detection whereas jackrabbits rely on speed and agility to outrun predators. Perceived risk was reduced when individuals were near kangaroo rat mounds only for cottontails because the smaller species can use banner-tailed kangaroo rat mounds as refuge. Shrub encroachment greatly reduced the availability of mounds. Thus, a trade-off exists for cottontails in which shrub encroachment directly reduced perceived risk, but indirectly increased perceived risk through the local extirpation of an ecosystem engineer. Our work illustrates how the expansion of shrub encroachment can create a dynamic landscape of fear for populations of prey species involving direct and indirect pathways contingent on prey body size, escape tactics, and activities of an ecosystem engineer.

Key words: black-tailed jackrabbit; Chihuahuan Desert; desert cottontail; ecosystem engineer; flight initiation distance; lagomorphs; landscape of fear; predation risk; shrub encroachment; Special Feature: Dynamic Deserts.

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Introduction

The landscape of fear model predicts prey animals perceive and respond to spatial variation in predation risk and adjust their antipredator behaviors accordingly to minimize the risk of predation (Laundré et al. 2001, 2010). The landscape of fear experienced by individuals can be dynamic across multiple timescales, for instance due to changes in daily predator activity (Kohl et al. 2018) or shifting risk from lunar cycles (Palmer et al. 2017). Moreover, the landscape of fear for prey populations can be dynamic over generational timescales because of longer-term structural changes to habitats (Wheeler and Hik 2014, Riginos 2015). Indeed, vegetation structure is an important landscape feature that often influences how prey perceive and respond to risk (Denno et al. 2005, Gorini et al. 2012), and ecological state transitions on dynamic landscapes should alter the landscape of fear for prey populations.

Shrub encroachment is a major driver of vegetation change worldwide with pronounced effects on arid and semiarid grasslands (Van Auken 2009, Eldridge et al. 2011, Ratajczak et al. 2012). Therefore, shrub encroachment into grasslands should shape perceived predation risk by prey. However, most research examining how animals respond to shrub encroachment does so through the lens of species diversity and population abundances or biomass (Bestelmeyer 2005, Blaum et al. 2007, Cosentino et al. 2013, Schooley et al. 2018, Stanton et al. 2018). Although shrubs can affect risk perception at the microhabitat scale (Longland and Price 1991, Bouskila 1995, Brown and Kotler 2004), mechanistic pathways for how shrub encroachment alters prey perception of risk at larger scales (Laundré et al. 2014, Wheeler and Hik 2014) remain poorly understood. Given the prevalence of shrub encroachment globally, understanding how encroachment alters the landscape of fear for prey animals is consequential because perceived predation risk affects habitat selection, individual fitness, population dynamics, and community interactions (Schmitz et al. 1997, Werner and Peacor 2003, Creel et al. 2007, Ford et al. 2014, Laundré et al. 2014).

Prey species may respond directly to changes in habitat structure caused by increased shrub cover. For instance, shrub encroachment could directly increase levels of perceived risk by increasing obstructive cover, precluding prey from seeing or escaping predators (Schooley et al. 1996, Blumstein et al. 2006, Camp et al. 2012). Conversely, shrubs may directly reduce levels of risk by increasing protective cover that hinders predators from seeing and attacking prey (Hannon et al. 2006, Camp et al. 2012). Greater shrub cover may also reduce perceived risk directly by increasing the amount of escape refuge (e.g., increased access to the interior of shrubs) available to prey (Wirsing et al. 2010).

Shrub encroachment could also have indirect effects on perceived predation risk, and these pathways could be distinct for different species. Sympatric prey species encountering similar habitat conditions but differing in body size and antipredator behavior may have dissimilar perceptions of risk (Heithaus et al. 2009, Wirsing et al. 2010, Dellinger et al. 2019, Weterings et al. 2019). Smaller prey may be more efficient at using fine-scale concealment cover and using refuges for escape (Camp et al. 2012, Crowell et al. 2016), and the availability of either could be affected by shrub encroachment. For example, shrub encroachment may reduce fine-scale concealment via decreases in herbaceous cover and increases in bare ground (Huenneke et al. 2002, Gillette and Pitchford 2004). Effects of shrub encroachment on smaller prey also could be mediated by ecosystem engineers that modify habitat structure. For example, some burrowing mammals are strong modifiers of grassland habitats, in part, because they construct extensive mound systems that smaller prey can use as escape refuge (Davidson and Lightfoot 2007, Davidson et al. 2012, 2018, Cosentino et al. 2013). Shrub encroachment can cause local declines of ecosystem engineers in grasslands (Cosentino et al. 2014), indirectly altering perceived predation risk by changing the landscape of refuge for smaller prey. In contrast, larger prey may not respond to changes in fine-scale concealment or escape refuges because of body size constraints. In sum, effects of shrub encroachment on the landscape of fear may be complex and involve direct and indirect mechanisms, potentially mediated by the body size and antipredator behavior of prey species.

Shrub encroachment is exceedingly evident in the northern Chihuahuan Desert of the

southwestern United States (Van Auken 2000, Peters et al. 2012, Bestelmeyer et al. 2018, Ji et al. 2019). Over the last 150 yr, perennial grasslands have been invaded by native honey mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*) producing dramatic ecological state transitions (Buffington and Herbel 1965, Grover and Musick 1990, Peters et al. 2006, 2012, Bestelmeyer et al. 2018). Potential mechanisms promoting shrub invasion in the Chihuahuan Desert include interactions between overgrazing and prolonged drought, altered fire regimes, the redistribution of soil resources (Grover and Musick 1990, Schlesinger et al. 1990), and feedbacks dependent on connectivity (Okin et al. 2015).

Our objective was to evaluate how shrub encroachment in the Chihuahuan Desert alters the landscape of fear for two sympatric prey species: black-tailed jackrabbits (*Lepus californicus*; hereafter jackrabbits) and desert cottontails (*Sylvilagus audubonii*; hereafter cottontails). Both lagomorph species are widespread native herbivores in the Chihuahuan Desert (Whitford 2002, Lightfoot et al. 2011). Coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) are their primary predators (Wagner and Stoddart 1972, White and Garrott 1997, Dennis and Otten 2000). Both canids exhibit active hunting modes and can exert intense predation pressure on lagomorph prey (White and Garrott 1997, Dennis and Otten 2000, Arias-Del Razo et al. 2012, Ripple et al. 2013). Indeed, jackrabbits and cottontails experience high annual mortality from canids and other predators (Chapman and Willner 1978, Best 1996, Simes et al. 2015), and thus are expected to respond strongly to perceived predation risk. A mechanistic understanding of how shrub encroachment affects perceived risk for these lagomorphs is relevant to the conservation and restoration of grasslands because both species can exacerbate shrub encroachment due to selective herbivory on grasses (Norris 1950, Havstad et al. 1999, Bestelmeyer et al. 2007, Abercrombie et al. 2019).

We measured perceived predation risk with flight initiation distances (FIDs; Stankowich and Blumstein 2005) and then employed structural equation modeling (SEM; Grace 2006) to tease apart the direct and indirect effects of shrub encroachment on the landscape of fear for jackrabbits and cottontails. The two lagomorphs differ markedly in body size and predator escape tactics (Harrison 2019). Jackrabbits are nearly three times the size of cottontails and morphologically adapted for long flight distances with speed and agility to escape predators (Hoffmeister 1986, Simes et al. 2015). In contrast, antipredator behavior of cottontails involves remaining still and relying on crypsis (Ingles 1941) or depending on short bursts of speed and dodging into high cover or burrows (Orr 1940, Ingles 1941, Harrison 2019). We tested the contrasting hypotheses that shrub cover at the patch scale may directly increase perceived risk for both lagomorphs by increasing obstructive cover, or shrub cover may reduce perceived risk by providing protective or escape cover. We also hypothesized that shrub encroachment indirectly mediates perceived risk for the smaller cottontails that can use fine-scale concealment or burrows to reduce risk (Camp et al. 2012, 2013, Crowell et al. 2016). Shrub encroachment should increase perceived risk for cottontails by reducing herbaceous cover, increasing bare ground, and reducing refuges created by banner-tailed kangaroo rats (*Dipodomys spectabilis*), a desert rodent and ecosystem engineer (Cosentino et al. 2013). Banner-tailed kangaroo rats change the composition of grassland vegetation by selectively harvesting large seeds and by building large mounds (~4 m diameter) that provide resource-rich patches on the landscape (Brown and Heske 1990, Schooley and Wiens 2001, Davidson and Lightfoot 2007). The mounds of banner-tailed kangaroo rats have multiple entrances (≤12) that the smaller cottontail may use for shelter. However, shrub encroachment greatly reduces the density of banner-tailed kangaroo rat mounds (Krogh et al. 2002, Waser and Ayers 2003, Cosentino et al. 2014).

Materials and Methods

Study site

We conducted our research at the Jornada Basin Long Term Ecological Research (LTER) site in southern New Mexico, USA (32°35′ N, 106°51′ W; 1334 m a.s.l). The Jornada Basin site includes the Jornada Experimental Range (USDA Agriculture Research Service, 783 km^2) and the Chihuahuan Desert Rangeland Research Center (New Mexico State University, 259 km^2). The

Jornada Basin represents an unequivocal example of grassland loss in the region (Peters et al. 2012). From 1858 to 1998, the land area estimated to be grassland decreased from 82% to 8%, which paralleled an increase in cover by honey mesquite from 15% to 59% (Peters et al. 2012). The remaining dominant perennial grasses included black grama (*Bouteloua eriopoda*), dropseed (*Sporobolus* spp.), threeawn (*Aristida* spp.), and tobosa (*Pleuraphis mutica*). The dominant shrubs included honey mesquite, creosote bush, and tarbush (*Flourensia cernua*). Our study sites were on similar soils consisting of sandy to sandy loam surface soils with a petrocalcic horizon layer at depths of 30–100 cm (Schooley et al. 2018). Long-term mean annual precipitation is 245 mm and >50% falls in July–September during the seasonal monsoon. Mean monthly temperature ranges from 3.8°C in January to 26.1°C in June.

Sampling design

We focused our sampling of lagomorphs across grassland-to-shrubland transitions associated with long-term monitoring of mammals and their feedbacks to vegetation dynamics at the Jornada Basin site (i.e., the Ecotone Study; Bestelmeyer et al. 2007, Schooley et al. 2018, Svejcar et al. 2019). Specifically, we sampled individuals on 24 sites that represented a broad gradient of encroachment by honey mesquite. For each of the 24 sites, the area sampled was ~3 km^2. The minimum distances between edges of sites ranged from 188 to 4400 m. If sites were adjacent and the distance between sites was <3 km, we deliberately focused our sampling on nonoverlapping 3-km^2 areas. The spatial extent of our study area was 200 km^2. The 24 sites provided a strong gradient of perennial grass cover (range = 1.7–50.2%, mean = 14.5%) and shrub cover (range = 1.5–27.1%, mean = 12.3%). We used this gradient across sites only to guide sampling of individuals (our replicates), and we measured vegetation locally for each FID trial.

Flight initiation distance

Flight initiation distance—the distance at which an animal initiates escape from an approaching human—is commonly used to quantify perceived risk of predation under different circumstances (Ydenberg and Dill 1986, Stankowich and Blumstein 2005). Because prey have evolved antipredator behaviors to generalized threat stimuli, such as loud noises and rapidly approaching objects, the threat of an approaching human should be analogous to predation risk (Frid and Dill 2002). Moreover, lagomorphs in our rural study area are not habituated to humans. Flight initiation distances reflect the costs and benefits of staying in a resource patch vs. fleeing the approaching threat (Ydenberg and Dill 1986). Longer FIDs indicate greater perceived predation risk assuming equal resource quality.

Flight initiation distance trials were conducted by five observers during the dry season (June 1–July 15) and wet season (July 16–October 24) in 2017 and 2018. All trials were conducted from sunrise to 10:00, which are the daylight hours when lagomorphs were most active at the Jornada Basin site (C. J. Wagnon, *unpublished data*). Each observer wore the same attire during sampling and followed a standardized protocol. A single observer slowly and haphazardly walked until they identified a solitary, adult (based on size and pelage color) jackrabbit or cottontail using binoculars. We did not conduct trials on lagomorphs in groups. When an animal was detected, the observer positioned themselves to have a direct line of approach to the animal and marked the start position. Staring distance (SD) is the distance between the start position of the observer and the focal animal before the FID trial begins. Once aligned, the observer approached the animal at a standard pace (0.5 m/s) while maintaining eye contact and marked the distance at which the animal took flight (FID). Following a flight response, defined as any movement >1 m by the focal animal from its original position, we marked the original position of the focal animal and then recorded SD and FID to the nearest meter with a laser range finder (Nikon 8397 ACULON AL11: Nikon Inc., Melville, New York, USA). We attempted to record alert distances (i.e., distance at which an animal first becomes alert to the approaching observer) for each trial but were only successful for a small percentage of trials (jackrabbit = 28%, cottontail = 21%). Thus, we only included SD in our analysis, which is an appropriate proxy for alert distance because the two measures often are highly correlated (Dumont et al. 2012).

Observers attempted to avoid resampling individuals by moving >300 m from a jackrabbit or >150 m from a cottontail, in the opposite direction in which the animal fled during the FID trial, before conducting a new trial on the same species. These separation distances were based on species-specific daily movements (Orr 1940, Ingles 1941, Chapman and Willner 1978, Best 1996, Simes et al. 2015). We also did not conduct new trials on a different species that was <50 m from a previous trial to avoid sampling individuals with altered behavior. There is a small chance that animals sampled in 2017 might have been resampled in 2018. However, annual mortality is generally high for both species (Chapman and Willner 1978, Best 1996, Simes et al. 2015), and we also restricted trials in 2018 to be >300 m from trials conducted in 2017 to increase the probability of independence between years. Flight initiation distance trials were discarded if there was any doubt of the original location, if a focal animal was alarmed by an external stimulus during the approach (e.g., passing car or predator vocalization), or if a different individual was flushed while approaching the focal animal.

Environmental covariates

We characterized vegetation cover at two spatial scales to assess how shrub encroachment might shape perceived predation risk for lagomorphs. At the patch scale, we established a 20 × 20 m plot centered on the original location of the focal animal and then used step-point intercept methods (Herrick et al. 2005). We used five 20-m transects, offset by 5 m, and we recorded shrub cover every 1 m on the five transects (100 points total) and calculated the percentage of points with shrubs. To assess effects of vegetation cover at a finer scale, we recorded concealment cover for each FID trial. Concealment was defined as the extent to which vegetation would obscure a focal individual from an approaching predator (Camp et al. 2012). We used a 50 × 50 cm cover board with 25 alternating 10 × 10 cm red and white squares to measure concealment. Along the compass azimuth of approach taken by the observer, we viewed the cover board from a horizontal distance of 15 m and a height of 0.5 m. We used 0.5 m because it is the mean head height of coyotes (Arias-Del Razo et al. 2012), which is the primary predator of lagomorphs in the Chihuahuan Desert (Hoffmeister 1986, Cypher and Spencer 1998, Hernández et al. 2002). We recorded the number of 10 × 10 cm squares that were ≥50% concealed by vegetation and converted that count to a percentage. A single observer (CJW) measured all vegetation indices to eliminate observer bias.

To evaluate the influence of banner-tailed kangaroo rat mounds on risk perception, we measured the distance to the nearest mound within 50 m of the original position of each focal animal with a range finder. We included all mounds of kangaroo rats, whether currently occupied or not based on sign (Schooley and Wiens 2001, Cosentino et al. 2014), because both types could provide refuge from predators. Distances for trials with no mounds within 50 m were recorded as 51 m. We chose 50 m as the cutoff because we assumed mounds beyond this distance were unlikely to affect FIDs, and due to time restraints that occurred because of extremely low densities of mounds in shrubbier areas.

We hypothesized that the costs and benefits of escape decisions by lagomorphs would be altered by hotter ambient air temperatures because of increased metabolic costs required for cooling after moving from a thermal refuge (Hinds 1970, Caraco et al. 1990). To control for changes in escape decisions related to temperatures, we not only constrained our sampling to morning hours but also ceased sampling if air temperatures reached ≥32°C. Finally, we recorded ambient air temperature for each trial with a Kestrel weather unit and evaluated temperature as a predictor for FID.

Data analysis

We applied SEMs (Grace 2006, Grace et al. 2010) to the FID data to evaluate our a priori hypotheses of how shrub cover affects the landscape of fear for lagomorphs (Fig. 1). We chose a SEM framework because it allows factors to be modeled simultaneously as both predictors and explanatory variables and permits one to examine a network of hypothesized direct and indirect effects (Grace 2006, Grace et al. 2010). To evaluate our main hypotheses, we included a direct effect from shrub cover to FID and indirect effects from shrub cover to FID through SD, concealment, and distance to refuge provided by banner-tailed kangaroo rat mounds (Fig. 1). Flight initiation

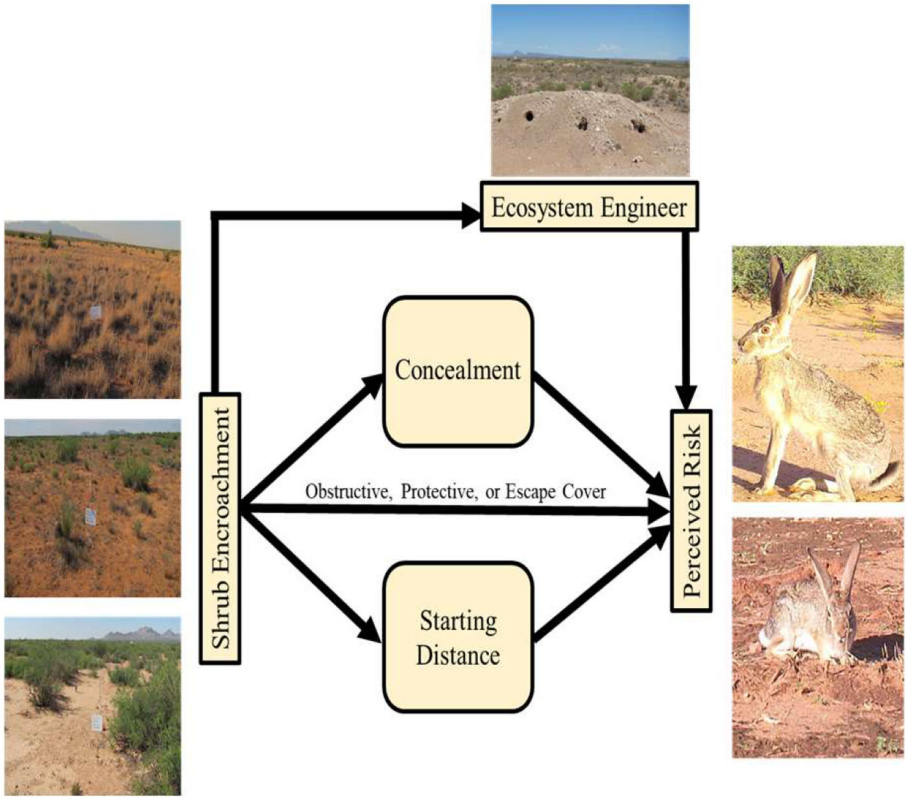

Fig. 1. The a priori structural equation meta-model describing interaction pathways through which shrub cover was predicted to influence the landscape of fear of black-tailed jackrabbits and desert cottontails. Shrub encroachment could directly affect perceived predation risk by increasing obstructive, protective, or escape cover at the patch scale. Shrub encroachment also could shape risk perception indirectly through (1) fine-scale concealment, (2) starting distance, and (3) densities of an ecosystem engineer that creates mounds for refuge.

distance can be positively correlated with SD in part due to a mathematical artifact, in addition to a biological effect, because of the constraint that SD ≥ FID (Dumont et al. 2012). However, a meta-analysis across multiple taxa found that only 7 of 87 (8%) estimates of the relationship between FID and SD could be solely attributed to the mathematical artifact (Samia et al. 2013). Thus, we assumed that the relationship in our study was not entirely artifactual and included a biological component. We predicted that FID would be strongly correlated with SD, as in many taxa (Samia et al. 2013), and that greater shrub cover would shorten SDs because it would reduce the ability of an observer to initially detect prey.

In addition to our main pathways (Fig. 1), we anticipated that observer, temperature, and season could influence perceived risk. Thus, we assessed these variables by adding direct paths from them to FID in our SEM. We evaluated observer effects by creating a binary variable that partitioned observers into the primary observer (CJW) and all other observers. We split observers this way because CJW completed most of the FID trials for jackrabbits (54%) and cottontails (75%). Resource availability (i.e., grasses and forbs) should be greater in the wet season when plant productivity is higher (Whitford 2002), which could influence missed opportunity costs and escape decisions for lagomorphs. That is, when forage is more abundant during the wet season, the cost of leaving a patch is reduced because of greater opportunities to locate other patches with equal or greater forage. Thus, the cost of escaping an approaching threat during the wet season would likely be lower than during the dry season when forage is scarce,

resulting in longer FIDs during the wet season. To account for such changes in missed opportunity costs, we included season as a binary variable (wet vs. dry). Temperature was also included in SEMs to control for increased metabolic costs of fleeing at higher temperatures.

We used a global estimation approach for SEM in which data–model relationships for the entire model are summarized by a variance–covariance matrix, and maximum likelihood procedures are used to estimate path coefficients by minimizing the total deviation between the observed and model-implied matrices (Grace et al. 2015). For interpretability of the final model, we compared the strength of direct and indirect pathways by comparing the strength and significance of standardized path coefficients (Grace and Bollen 2005). We also reported unstandardized coefficients because standardized coefficients can depend on variation in each variable (Grace and Bollen 2005). We used a maximum-likelihood estimator to estimate robust standard errors (SEs), 95% confidence intervals (CIs), and P values for direct, indirect, and total effects of shrub cover on FID using bootstrapping of standardized estimates with 1000 simulations. We used robust SEs to account for unequal error variance. The significance of path coefficients was evaluated at $\alpha = 0.05$. We used a chi-square goodness-of-fit test to assess model fit with $P < 0.05$ indicating inconsistencies between observed and model-implied matrices. That is, the chi-square test evaluates the null hypothesis that there is no difference between the expected and observed covariance matrices, and an SEM is considered a good fit when the test fails to reject the null (i.e., $P > 0.05$; Grace et al. 2015). We ran our core model (Fig. 1) with observer, temperature, and season added separately, and we excluded those paths if they were nonsignificant or did not substantially increase the amount of variation explained (R^2) in perceived risk. Our intent was to exclude any nonsignificant paths to fulfill the requirement that the ratio of sample size to the number of estimated paths is >5 (Grace et al. 2015). All SEM analyses were conducted using the lavaan (Rosseel 2012) package in R (R Core Team 2019).

Results

We conducted FID trials on 156 jackrabbits (51 in 2017, 105 in 2018) and on 48 cottontails (15 in 2017, 33 in 2018). Overall, the mean FID was 56.2 m (SE = 2.2 m) for jackrabbits and 40.0 m (SE = 3.3 m) for cottontails (Appendix S1: Table S1). Mean shrub cover was 14.0% (SE = 0.63) for trials of jackrabbits and 16.2% (SE = 1.66) for trials of cottontails. Mounds of banner-tailed kangaroo rats were within 50 m of focal animals for 100 trials for jackrabbits (64.1%) and for 31 trials for cottontails (64.6%).

Perceived risk for both species was unaffected by observer, season, or temperature. These variables were not significant pathways to FID, and they did not substantially increase the amount of variation explained in FID (Appendix S1: Table S2). Hence, we did not add these three variables to our core model.

For both species, the finalized SEM fit the data well and explained a considerable amount of variation in perceived risk (Fig. 2; $R^2 = 0.58$–0.60). A direct negative effect of shrub cover on FID was strongly supported in the jackrabbit model, indicating perceived predation risk decreased as shrub cover increased at the patch scale (Figs. 2, 3A). A direct effect of shrub cover on perceived risk for cottontails was weakly supported in the SEM (Fig. 2), but the pattern indicated perceived risk decreased as shrub cover increased (Fig. 3B). Start distance had a strong positive effect on FID for both species (Fig. 2). The path from shrub cover to SD was negative for both species (Fig. 2), indicating shrub cover mediates perceived risk through SD. For both species, the path from shrub cover to fine-scale concealment was weak and explained little variation (Fig. 2). Hence, shrub cover did not mediate perceived risk through fine-scale concealment for either species. However, fine-scale concealment had a negative effect on FID for cottontails (Fig. 3C), but not for jackrabbits.

As predicted, shrub cover had a strong positive effect on distance to mounds of banner-tailed kangaroo rats in both models (i.e., distance to these potential refuges increased in shrubbier areas). However, the effect of distance to mounds on perceived risk was only supported for the smaller cottontail. Cottontails farther from mounds had greater perceived risk (Fig. 4). Moreover, during FID trials, 35% of cottontails initially located within 50 m of a mound subsequently flushed into a mound entrance, whereas no jackrabbits flushed into a mound created by a

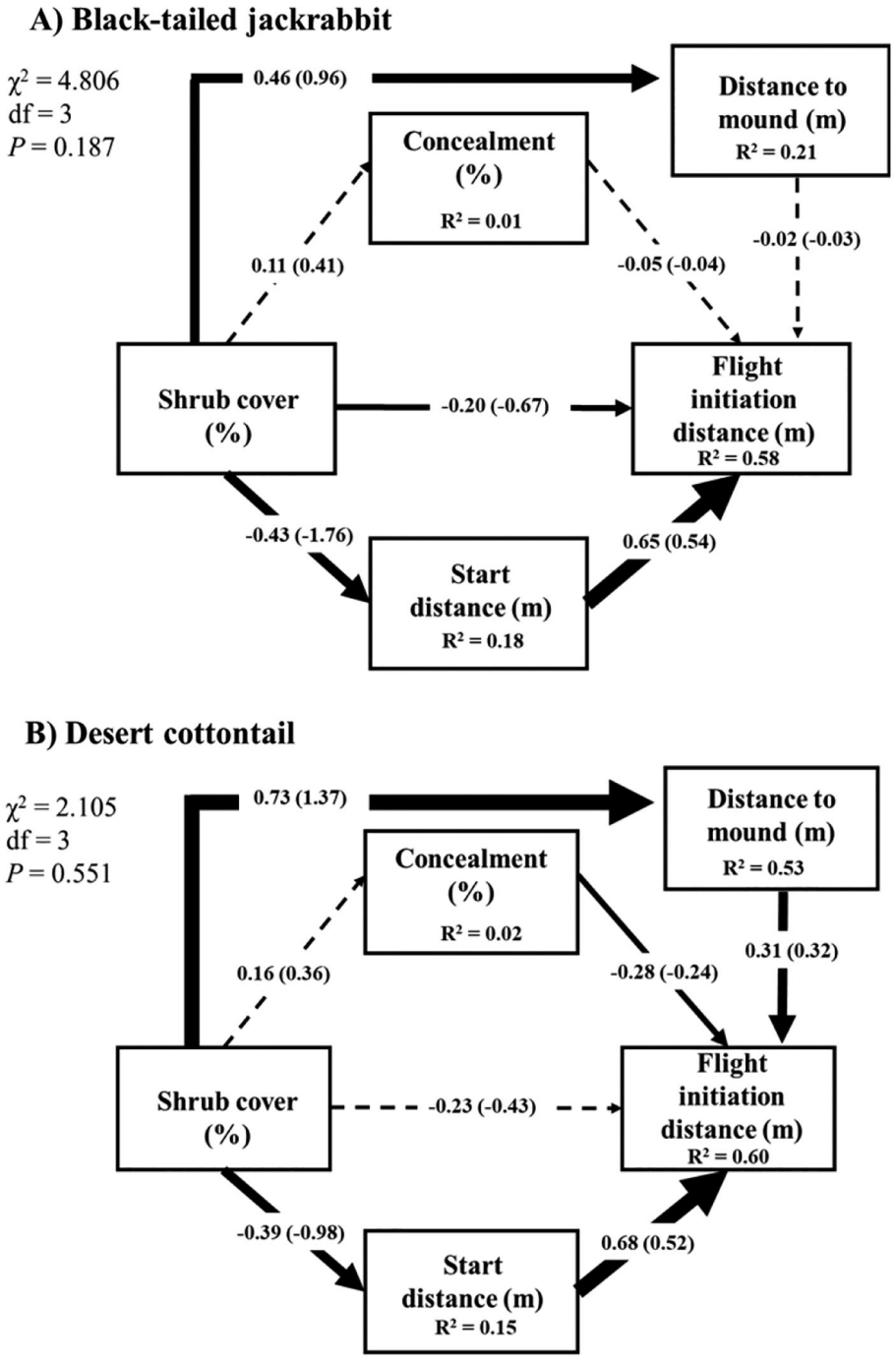

Fig. 2. Final structural equation models for (A) black-tailed jackrabbit and (B) desert cottontail showing effects of shrub encroachment on perceived predation risk at the Jornada Basin Long Term Ecological Research site, New Mexico, 2017–2018. Solid arrows represent significant pathways ($P < 0.05$). Dashed arrows represent non-significant effects ($P > 0.05$). Thickness of pathways is scaled to the magnitude of standardized coefficients, which are given for each pathway. Unstandardized coefficients are given in parentheses. R^2 values are displayed below endogenous variables (i.e., response variables). Model fit statistics are displayed in the upper left corner for each model.

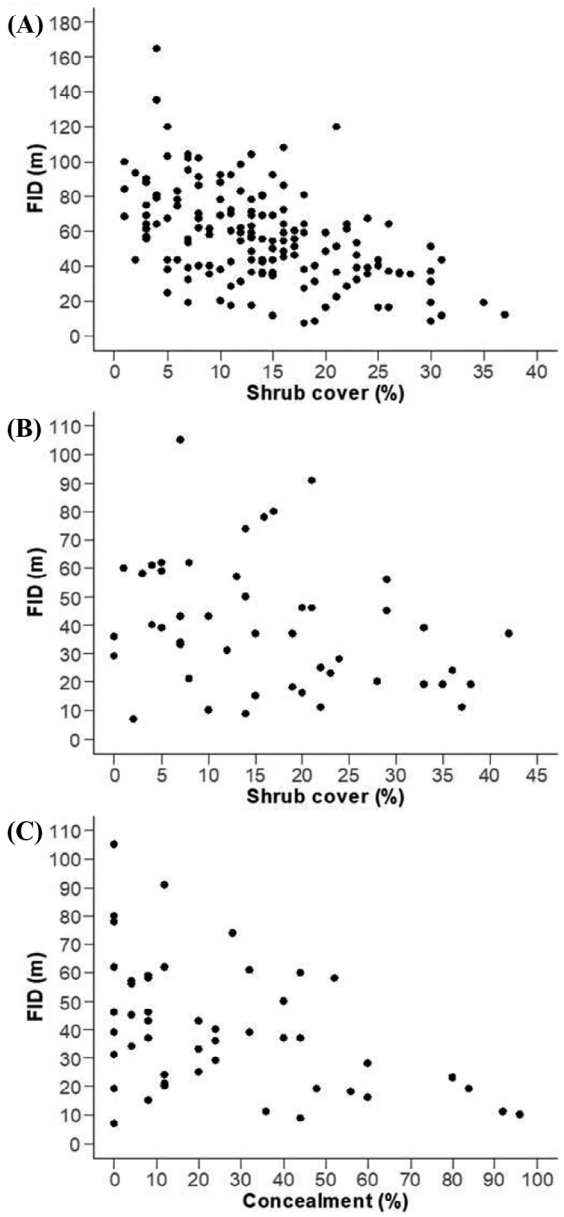

Fig. 3. Flight initiation distance (FID) relative to patch-scale shrub cover for (A) black-tailed jackrabbit and (B) desert cottontail, and (C) FID relative to fine-scale concealment for desert cottontail from Jornada Basin Long Term Ecological Research site, New Mexico, 2017–2018.

banner-tailed kangaroo rat (C. J. Wagnon, *unpublished data*).

Shrub cover had a significant indirect effect on FID for jackrabbits (Table 1), primarily mediated through SD (Fig. 2). The indirect effect of shrub cover on FID for cottontails was not supported (Table 1), reflecting the neutralizing effect that shrub cover had on refuge availability through the local reduction of banner-tailed kangaroo rat mounds. The total effect of shrub cover on perceived risk was significant and negative for both species, but jackrabbits responded more strongly to shrubs than did cottontails (Table 1). For

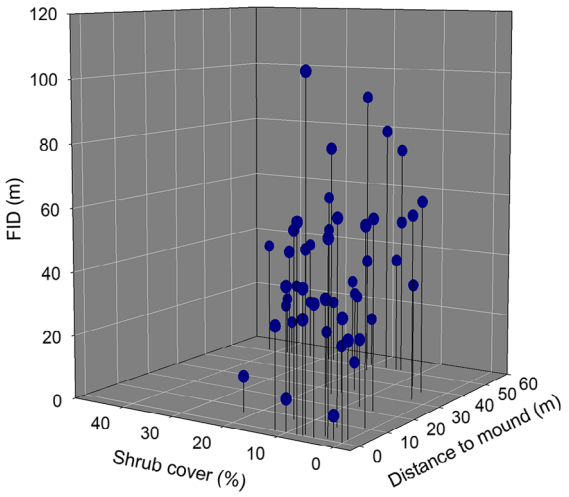

Fig. 4. Flight initiation distance (FID) of desert cottontail relative to shrub cover and distance to banner-tailed kangaroo mounds from Jornada Basin Long Term Ecological Research site, New Mexico, 2017–2018.

Table 1. Direct, indirect, and total standardized effects of shrub cover on flight initiation distance in the final structural equation model for black-tailed jackrabbits and desert cottontails at Jornada Basin Long Term Ecological Research site, New Mexico, 2017–2018.

Effect	Estimate	SE	Lower CI	Upper CI	*P*
Jackrabbit					
Direct	−0.195	0.064	−0.320	−0.070	0.002
Indirect	−0.289	0.052	−0.391	−0.187	<0.001
Total	−0.484	0.050	−0.583	−0.385	<0.001
Cottontail					
Direct	−0.225	0.147	−0.513	0.064	0.127
Indirect	−0.081	0.160	−0.394	0.233	0.613
Total	−0.306	0.110	−0.521	−0.090	0.005

Note: CI, confidence interval; SE, standard error.

cottontails, the nonsignificance of the direct and indirect effects indicates that within the precision with which we were able to estimate these effects separately, they were non-distinguishable from zero. However, when the direct and indirect effects were combined (i.e., total effects), the effect size was then large enough for us to detect a significant, and negative, total effect of shrub cover on perceived risk for cottontail.

Discussion

Capitalizing on grassland-to-shrubland gradients over a large spatial extent, we provide evidence linking shrub encroachment to a dynamic landscape of fear for desert lagomorphs. We also demonstrate species-specific responses to landscape change with some involving complex interactions with an ecosystem engineer. Specifically, shrub encroachment directly affected perceived risk in jackrabbits, whereas the effect of shrub encroachment on risk perception by cottontails was mediated by proximity to refuges created by banner-tailed kangaroo rats. More broadly, we show that prey body size and escape tactic could strongly affect how prey species respond to landscape change (Heithaus et al. 2009, Wirsing et al. 2010) and that shrub encroachment can influence the landscape of fear of prey via multiple pathways.

Our SEMs support the hypothesis that shrub cover decreases perceived risk at the patch scale for desert lagomorphs because of greater availability of protective or escape cover. Both prey species reduced their overall levels of risk in shrubbier habitats, as indicated by the total and direct negative effects of shrub cover on perceived risk (Table 1), albeit with weaker support for a direct effect for cottontails. Importantly, however, the estimated direct effect on cottontail risk was moderate in strength (−0.225), with some uncertainty reflected in its precision likely due to a small sample size (SE = 0.147; CI = −0.513, 0.064 that barely overlapped zero), leading us to conclude that shrub cover may directly reduce risk in cottontails.

At the microhabitat scale, perceived predation risk for both species increases with distance from shrub canopies (Longland 1991, Abu Baker et al. 2015), suggesting shrubs provide protective cover while foraging. By implication, shrub encroachment into desert grasslands may diminish perceived risk at the patch scale in lagomorphs by providing better protective cover during foraging bouts. Increases in shrubs may also provide better escape cover for cottontails because they are small enough to use the interior of shrubs, and they often run into dense cover to evade predators (Orr 1940, Chapman and Litvaitis 2003, Harrison 2019). In contrast, the large size of adult jackrabbits precludes them from effectively using the interior of shrubs (Harrison 2019). Thus, shrub encroachment may simultaneously increase protective and escape cover for cottontails but only function as protective cover for jackrabbits.

Shrub cover was not a good predictor of fine-scale concealment, suggesting shrub encroachment does not constrain the availability of concealment cover for prey. As expected, however, lagomorphs elicited divergent responses to fine-scale concealment. Cottontails had reduced perceived risk when fine-scale concealment cover was high, whereas perceived risk in jackrabbits was unrelated to concealment. This disparity in the importance of concealment is in accord with their respective antipredator behaviors. Because of their small size, cottontails rely on crypsis and remaining still to avoid predator detection (Camp et al. 2012, Harrison 2019), and increases in concealment likely facilitate their ability to evade detection. In contrast, jackrabbits are larger, rely on speed to outrun predators, and may not respond to concealment because of preferences for open spaces that improve predator detection and running ability (Brown and Krausman 2003, Flinders and Chapman 2003). These results are consistent with microsite selection by lagomorphs in southern New Mexico where cottontails select sites in the centers of shrub patches with greater concealment cover, and jackrabbits select sites on the periphery of shrubs with more open space (Harrison 2019). Likewise, perceived risk of other rabbit species is linked to concealment cover. For example, pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontails (*Sylvilagus nuttallii*) prefer food patches that offer better concealment (Crowell et al. 2016), and pygmy rabbits have lower perceived risk when they are better concealed by sagebrush (*Artemisia* spp.; Camp et al. 2012). Accordingly, concealment appears to be important for assessing predation risk in multiple

rabbit species, including desert cottontails, but it may not be as relevant for risk in larger hare species.

We predicted an ecosystem engineer in desert grasslands may shape risk perception in lagomorphs by providing escape refuge, but that this effect would depend on body size and escape tactic. Indeed, perceived predation risk in the smaller cottontail was strongly influenced by distance to escape refuge created by banner-tailed kangaroo rats, whereas the larger jackrabbit exhibited no response to proximity to mounds. Proximity to a mound was as strong of a predictor of risk in cottontails when compared to concealment, and a better predictor than the direct effect of shrub cover, indicating distance to refuges may be as important as vegetation structure for risk assessment in cottontails. Moreover, we modeled distances >50 m as 51 m, which may make the quantified relationship conservative and thus strengthen our argument that proximity to refuge is a critical factor affecting risk in cottontails. Proximity to refuge influences perceived risk in several taxa (Stankowich and Blumstein 2005), including other rabbit species (Bakker et al. 2005, Camp et al. 2012, Crowell et al. 2016). Namely, the obligate burrowing pygmy rabbit of the sagebrush steppe has a strong preference for food patches closer to their own burrows, and their perceived risk increases with distance to their burrows (Camp et al. 2012, Crowell et al. 2016). Our study may be unique by documenting the role of an ecosystem engineer in shaping risk perception for mammal prey through the creation of refuges. We also demonstrate that the importance of the landscape of refuge created by ecosystem engineers can be constrained by prey body size.

There is strong evidence linking shrub encroachment to the local decline of banner-tailed kangaroo rats (Krogh et al. 2002, Waser and Ayers 2003, Cosentino et al. 2014), and our SEMs are in accord with those findings. Because of this negative association, we predicted that escape refuge created by banner-tailed kangaroo rats would indirectly mediate the effect of shrub encroachment on lagomorph perceived risk. Indeed, our results illuminated a complex relationship between shrub encroachment and risk perception in prey that produced a trade-off involving increased protective and escape cover provided by shrubs at the cost of reduced refuge availability. However, this trade-off was only important for cottontails because of their smaller size and ability to use mounds to evade predators. The loss of ecosystem engineers may have implications that reverberate to other species and ecosystem processes (Hale and Koprowski 2018), and we extend these consequences to dynamic changes in perceived risk in prey animals.

The SEM for both species showed a strong relationship between FID and SD, which is consistent with the "flush early and avoid the rush" (FEAR) hypothesis (Blumstein 2010, Samia et al. 2013). The FEAR hypothesis proposes that when a threat (e.g., predator or human) begins an approach from greater distances (i.e., longer SD), prey will flee sooner to avoid higher costs associated with monitoring the threat, or because threats that continue an approach toward prey from greater distances are more likely to detect and attack prey (Blumstein 2010, Cooper et al. 2015). The biological interpretation of this positive relationship has been supported in several taxa including mammals, birds, and lizards (Samia et al. 2013). Thus, we suggest that the FEAR hypothesis could explain the strong effect of SD on FID for desert lagomorphs.

Combining SEM with FIDs allowed us to disentangle confounding relationships between shrub cover, SD, and FID. For example, we predicted that observers would have shorter SD in shrubbier habitats because high shrub cover would reduce their ability to detect animals. Because SD will always be greater than or equal to FID, this relationship could have biased the direct effect between shrub cover and FID because SD is shorter in shrubbier areas. However, using an SEM approach enabled us to tease apart those relationships because SEM allows for statistical control when estimating the direct effects of a predictor variable, thereby providing unbiased estimates (Grace 2006, Grace et al. 2015). Thus, we highlight a novel approach for uncoupling confounding relationships between SD, FID, and other variables using SEM, potentially providing an effective framework for analyzing FID data in future studies.

There is now broad agreement that the ecological impacts of herbivores on vegetation can be predicted, in part, by understanding the landscape of fear that herbivores experience

(Terborgh and Estes 2010). Lagomorph densities can influence herbivory pressure on rangelands (Norris 1950, Johnson and Anderson 1984, Mcadoo et al. 1987, Havstad et al. 1999), and shrub encroachment can intensify herbivory rates and potentially reinforce grassland loss (Bestelmeyer et al. 2007, Kerley and Whitford 2009, Abercrombie et al. 2019). If shrub cover is a good predictor of perceived risk, then mapping shrub cover via remote sensing (Ji et al. 2019) could predict where seedling establishment for grasses will be constrained on the landscape, which could then inform state transition dynamics.

Quantifying changes in perceived risk in prey is an essential first step to understand how shrub encroachment modifies predator–prey dynamics. A critical next step in our system will be to evaluate whether perceived predation risk of lagomorphs predicts their spatial abundance patterns and those of their main canid predators. Furthermore, integrating bottom-up and top-down pathways, including perceived risk, across shrub encroachment gradients should provide insights into how landscape change modifies trophic controls including the strength of density- or trait-mediated trophic cascades (Schmitz et al. 2004, Laundré et al. 2014).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3240/full