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Trophic Ecology Warrants Multispecies Management in a Grassland Setting: Proposed Species Interactions on Black-tailed Prairie Dog Colonies

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On the Ground

- Trophic cascades occur when flora and fauna directly and/or indirectly influence co-occurring species populations at different levels of the food chain, and North American temperate grasslands provide an interesting case study to research these relationships.
- We briefly define trophic cascades in terrestrial systems and explore the potential for a cascading trophic interaction among grassland-associated swift fox (*Vulpes velox*), western burrowing owl (*Athene cunicularia hypugaea*), and mountain plover (*Charadrius montanus*), three rangeland species of conservation concern, on black-tailed prairie dog (*Cynomys ludovicianus*) colonies using two US Forest Service data sets.
- Historic patterns of occurrence and co-occurrence suggest top-down control governs the spatiotemporal distribution patterns of the three species and may be influenced by habitat fragmentation and management actions.
- Managing for interactive, multitrophic communities requires the identification of species interactions and the mechanisms that drive them.
- Long-term multispecies occupancy research, combined with hypothesized driving mechanisms and the co-occurrence of associated grassland species, is recommended for addressing these complex interactions moving forward.

Keywords: black-tailed prairie dog, burrowing owl, grasslands, mountain plover, swift fox, trophic cascades.

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North American temperate grasslands support high levels of species richness and diversity[1–3] and are an important resource for agricultural production, so research and appropriate management for these rangeland systems must focus on the interactions between species rather than on single-species populations. Because species-interaction paradigms are crucial for management in these systems, we present a theoretical framework to address a broad issue, which is cascading trophic interactions play a critical role in structuring populations of concern in grasslands. As a case study, we examine the hypothesis that co-occurring swift fox (*Vulpes velox*), western burrowing owl (*Athene cunicularia hypugaea*), and mountain plover (*Charadrius montanus*) are involved in a cascading trophic interaction on black-tailed prairie dog (*Cynomys ludovicianus*) colonies on North American temperate grasslands. Trophic cascades among these species remain undocumented and are worthy of investigation for effective multispecies management in these communities of conservation concern. We begin by introducing North American temperate grasslands and follow with short species accounts for prairie dogs, foxes, owls, and plovers. We then briefly define trophic interactions, followed by a case study on the Pawnee National Grassland (PNG) in Colorado and Thunder Basin National Grassland (TBNG) in Wyoming. Finally, we hypothesize potentially influencing mechanisms in a fox–owl–plover interaction. We fully acknowledge that inferences based on the trend data and literature cited in this paper are anecdotal and statistically insufficient and maintain that future investigation into this system is needed. Collectively, this paper serves as a proposal for future trophic-level research in this interactive community.

North American Temperate Grasslands

North American temperate grasslands historically covered 162 million hectares (ha) of central and western North America.[1]

These grasslands can be loosely subdivided based on characteristics of the dominant plant life forms into shortgrass, mixed-grass, or tall-grass prairies (Fig. 1).[1,4,5] In this review we focus our attention on the shortgrass and northern mixed-grass prairies of the Great Plains. The shortgrass prairie, or shortgrass steppe ecoregion, is dominated by C_4 grasses (typically 6–12 inches in height) including blue grama (*Bouteloua gracilis*), buffalo grass (*Bouteloua dactyloides*), and Western wheat grass (*Pascopyrum smithii*), and comprises the southwestern portion of North American temperate grasslands (Fig. 1).[5,6] Mixed-grass prairies are split into two subregions—northern mixed-grass and southern mixed-grass—extending north into Canada and south to northcentral Texas (Fig. 1).[5,6] Mixed-grass prairies are characterized by ecotones of shortgrass steppe and sagebrush shrubland, and support rich communities of forbs like goldenrod (*Solidago sp.*), slimflower scurfpea (*Psoralea tenuiflora*), and scarlet globemallow (*Sphaeralcea coccinea*).[6,7] Common shrub species may include Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and greasewood (*Sarcobatus vermiculatus*).[6,7] Collectively, the vegetation structure of these grasslands support diverse communities of interactive fauna,[1–3] presenting us with an opportunity to highlight potential trophic-level cascades that inform future grassland management objectives.

Focal Species

Our hypothesis concerning trophic cascades in this system hinges on the role of black-tailed prairie dogs in structuring requisite habitat for these species. The ecological benefits of black-tailed prairie dogs are extensive; the species engineers resource-rich environments for grassland birds, small- to medium-sized carnivores, and many burrowing species by providing habitat for breeding, rearing of offspring, foraging,

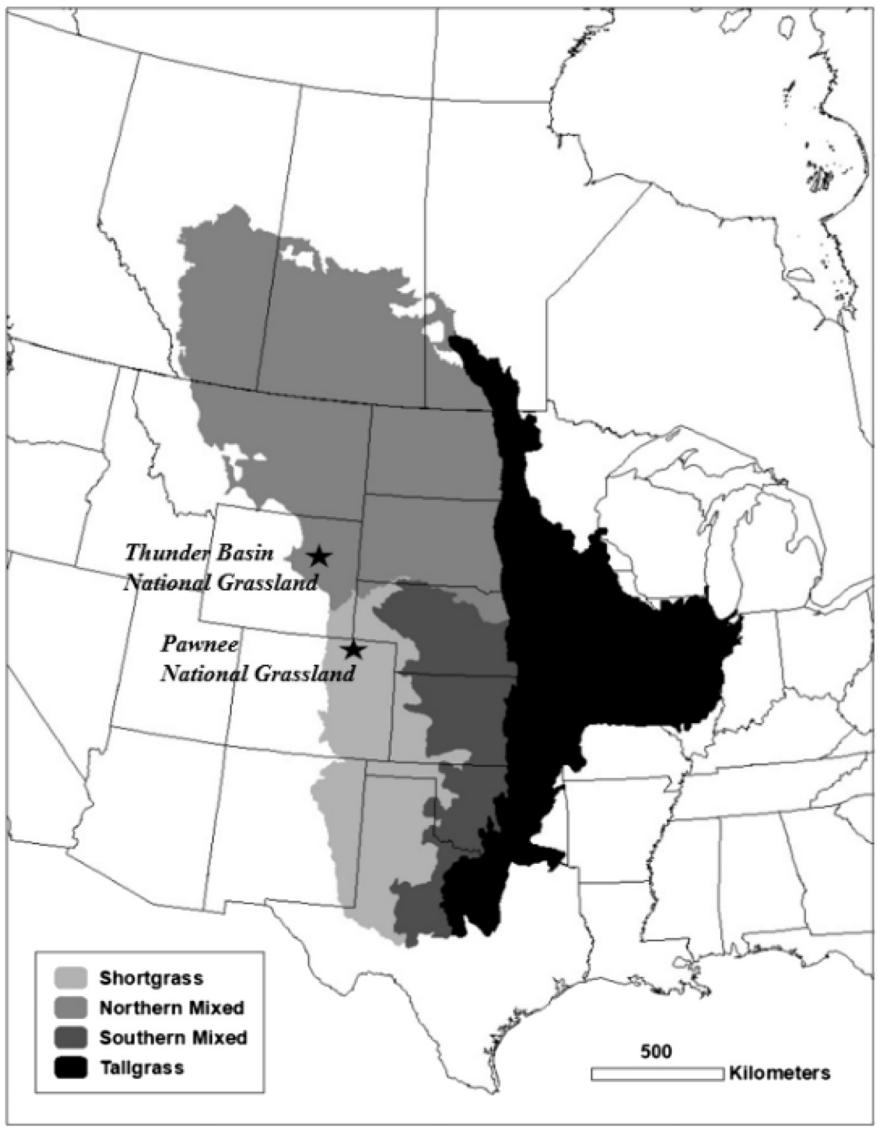

Figure 1. Map of North American temperate grassland categories and regions. Pawnee National Grassland represents a shortgrass prairie, and Thunder Basin National Grassland represents a northern mixed-grass prairie. Data retrieved from Esri REST Services Directory.

and cover from predators.[8–11] The US Fish and Wildlife Service (USFWS) reported a historically low 364,000 active ha of prairie dog colonies in 1961,[12,13] and more recent estimates suggest a range-wide decline of 90% to 98%,[2] leading to their status as species of conservation concern.[14–16] These declines have also been linked to decreasing populations of swift fox, burrowing owl, and mountain plover, three grassland species of conservation concern with the potential for trophic interactions.[17–20]

Swift Fox

The swift fox (*Vulpes velox*; Fig. 2) is a small predatory canid that frequently occupies prairie dog colonies and relies on denning opportunities and abundant prey resources therein.[21,22] Shrub-free expanses across the shortgrass prairie, such as open fields and burned areas, provide additional habitat for swift fox.[23] In regions characterized by mixed-grass prairie and sagebrush steppe, swift fox may be specifically tied to prairie dog colonies because shrub composition and structure in these landscapes are low. Swift fox is a species of conservation concern at both state and federal levels.[14–16]

Burrowing Owl

Western burrowing owls (*Athene cunicularia hypugaea*; Fig. 2) are small, fossorial raptors that lay eggs, rear chicks, and shelter in pre-excavated burrow systems.[24] Today, burrowing owls regularly colonize urban environments (e.g., golf courses, landfills, and storm drainage systems), remain abundant in agroecosystems, and frequently associate with both urban and rural prairie dog complexes.[25–29] In the Great Plains, owls have been documented to respond to prairie dog alarm calls, providing evolutionary evidence that owls use prairie dogs for detecting predators.[30] Prairie dog colonies also support populations of ground nesting birds and insects, both prey items for burrowing owls. Burrowing owls remain a species of conservation concern at state and federal levels,[14–16] and North American Breeding Bird Survey data between 1966 and 2011 estimate an annual population decline of 1.1%.[31]

Mountain Plover

Mountain plover (*Charadrius montanus*; Fig. 2) are upland shorebirds that nest, rear young, and forage on landscapes with a relatively high bare-ground structure, taking advantage of a prairie dog's natural tendency to clip vegetation and create short-grass habitat.[2] Plovers do not exclusively depend on prairie dog colonies for breeding habitat, as pastures moderately to heavily grazed by cattle, burned areas, and fallow crop fields throughout the southern portion of the species range provide favored habitat requirements.[32–34] Prairie dog colonies, however, provide a greater source of habitat for breeding mountain plovers in the mixed-grass prairies of the Northern Great Plains (Wyoming, Montana, and Canada).[9,35] Here, shortgrass prairies transition into mixed-grass/sagebrush steppe landscapes where prairie dogs often create the only shortgrass/bare-ground habitat suitable for nesting. Mountain plovers remain a species of conservation concern throughout their range,[14–16] and North American Breeding Bird Survey data between 1966 and 2011 estimate an annual population decline of 3.0%.[31]

Understanding Trophic Ecology

Management objectives for prairie dogs should be geared toward meeting the requirements of multiple associated species of conservation concern. Reaching these objectives first requires a careful understanding of potential cascading trophic interactions among species.

Trophic Cascades

Trophic cascades can be classified as facilitating top-down or bottom-up responses.[36] Top-down control is driven by apex or dominant predators (predators at the top of the food chain with no direct threat of predation) or quaternary consumers (species at the top-level of the food chain capable of consuming all lower-level species),[37] triggering a response from lower-level predators, consumers, or producers in the food chain (Fig. 3).[36,38] Bottom-up control is characterized by primary producers or lower-level consumers driving changes to patterns in plant or wildlife populations and distributions higher up the food chain (Fig. 3).[36,38] Here, we focus on top-down trophic cascades facilitating responses in plant or wildlife communities that may in turn structure food chains and ecosystems.[36,38,39] We do not discount, however, that bottom-up mechanisms may be simultaneously at work, and we support this by evaluating impacts to the vegetation community that may cause upward influences along the food chain. Responses may manifest as

Figure 2. The swift fox (*Vulpes velox*; left), western burrowing owl (*Athene cunicularia hypugaea*; center) and mountain plover (*Charadrius montanus*; right) all directly benefit from black-tailed prairie dogs (*Cynomys ludovicianus*) where their respective ranges overlap. Photo courtesy of Cristi Painter.

oscillations over time, as constant increases or decreases, or as static in populations across all trophic levels.[40,41] These responses have repercussions for management, particularly when communities are comprised of multiple species of conservation concern.[42]

Intraguild Predation and Mesopredator Release

Top-down control occurs in many predator–prey relationships where intraguild predation and mesopredator release is present. We define intraguild predation as predators across different trophic levels competing for a shared prey resource, while the lower trophic level predators also risk predation from the upper trophic level predators.[40] This process fits within a broader, widely accepted predator–prey hypothesis commonly referred to as mesopredator release. Here, apex predators become rare or absent in an ecosystem, resulting in population spikes of smaller, medium-level (meso) predators.[43,44] Mesopredators exploit prey resources at little cost of predation or competition from apex predators and initiate top-down control[36,38] on lower trophic level prey communities (Fig. 3).[43,44] To further explore these hypotheses, we introduce a case study focusing on the dynamics between swift fox, burrowing owl, and mountain plover in the grasslands of the Great Plains.

Case Study

Trophic Interactions on the Pawnee and Thunder Basin National Grasslands

To examine potential cascading trophic interactions within grassland systems, we explored raw-data trends (Fig. 4) in annual prairie dog colony mapping (i.e., total colony boundary, surface area measured in hectares) and count data for swift fox, burrowing owl, and mountain plover for two federally managed US Forest Service (USFS) national grasslands: 1) the PNG in Weld County of northeastern Colorado, representing a shortgrass prairie (Fig. 1),[45] and 2) the TBNG in Converse, Weston, and Campbell Counties of eastern Wyoming, representing a northern mixed-grass prairie (Fig. 1).[46]

Data Collection

Both data sets are used annually by the USFS to inform management of viable populations of prairie dogs and associated species,[45,46] and are collected under a collaborative effort by university researchers, federal wildlife managers, and trained volunteers. Total prairie dog colony hectares on both USFS grasslands are obtained by driving the outer boundary of active colonies and mapping those boundaries with GPS (Global Positioning System) units between June and September. Active colonies are determined by the presence of prairie dogs, which includes: fresh scat, freshly clipped vegetation, fresh digging at burrow entrances, and visual and aural identification. Only burrows that indicate evidence of active prairie dogs are included in the mapping effort. Mountain plover and burrowing owl surveys occur in early morning and late evening by driving transects no more than 400 m apart across prairie dog colonies, stopping every 30 to 60 seconds to scan for the presence of adult birds during the breeding season (mid-May through mid-July). Swift fox surveys are conducted mid-August through September via spotlighting at night while driving transects across prairie dog colonies or along designated USFS grassland roads adjacent to prairie dog colonies to detect and confirm presence by eye shine. Surveys are conducted one time per colony, and total observations per colony are included into the annual data set. All survey methods follow USFS survey protocol.[45,46] Count data belongs to the USFS and will be made available upon request.

These raw data (Fig. 4) were collected under protocols targeted for agency-management purposes and were not designed to address research objectives[45,46]; therefore, inferences concerning processes in trophic ecology are purely speculative. We fitted an exponential curve to the data (Fig. 5) to heuristically observe patterns suggesting that the total area of active prairie dog colonies has increased across the PNG, with the number of observed burrowing owls increasing and the number of swift

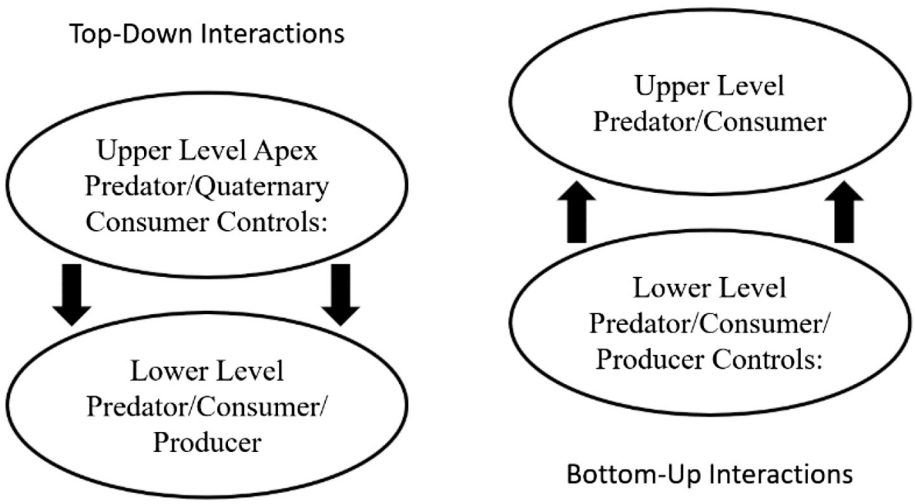

Figure 3. General processes of top-down interactions (left) where upper trophic level species control populations of lower trophic level species, and bottom-up interactions (right) where lower trophic level species control populations of upper trophic level species.[36,38]

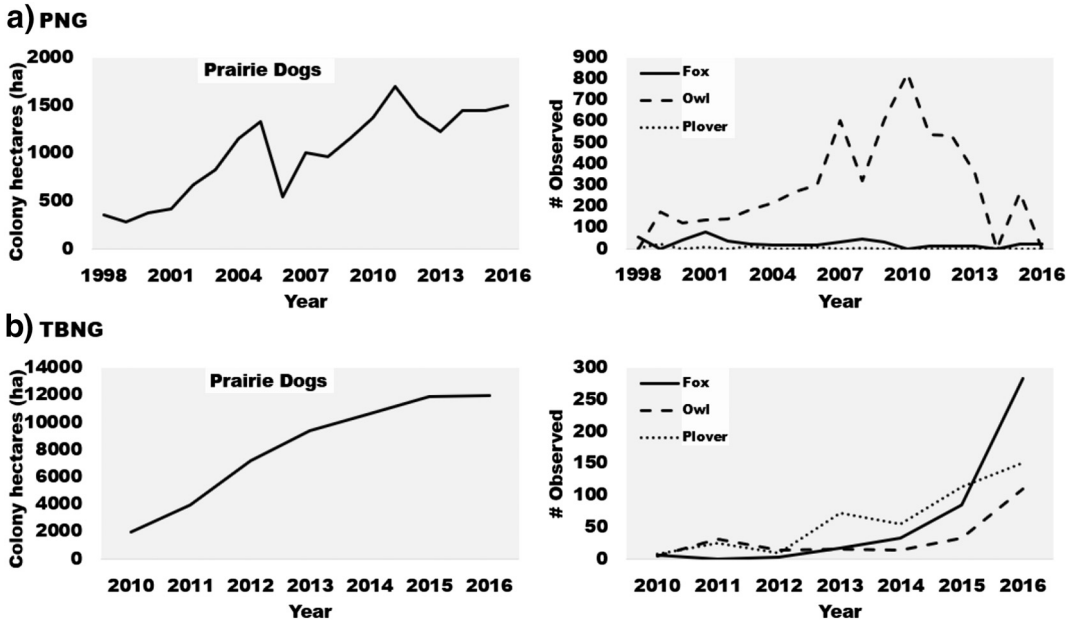

Figure 4. Annual count data in raw form collected on A, the Pawnee National Grassland (PNG) from 1998 to 2016 and B, the Thunder Basin National grassland (TBNG) from 2010 to 2016 for total active prairie dog colonies measured in hectares (ha) and population counts for swift fox, burrowing owl, and mountain plover.[45,46]

foxes and mountain plovers remaining uncommon and moderately declining (1998–2016; Fig. 5A). Total area of active prairie dog colonies has also increased across TBNG; however, the number of observed swift fox and mountain plover is increasing, and the number of burrowing owls is only responding weakly (2010–2016; Fig. 5B). Combining these observed co-occurrence patterns with examples of trophic ecology defined in the literature suggests the possibility of a cascading trophic interaction in this system, where the presence or absence of swift fox directly influences the abundance of mountain plovers by controlling burrowing owl mesopredators. Factors beyond increased prairie dog colony area are likely at play because species' responses differ markedly between the PNG and TBNG during the same period.

Hypotheses Concerning Trophic Ecology on Pawnee and Thunder Basin National Grasslands

Mesopredator Release on the PNG

Mesopredator release may explain the increase of burrowing owls on the PNG and their co-occurrence patterns with swift fox and mountain plover. Burrowing owls may respond positively to declining swift fox populations (Fig. 5A), "releasing" them from the predation pressure of a higher-level predator. Hunting and trapping presents an annual additive mortality factor for swift fox in Colorado with an estimated harvest of over 600 individuals in the 2014 to 2015 season[47,48]; however, uncertainty around how to obtain accurate harvest estimates of swift fox remains a challenge for state wildlife agencies.[47] The current population of swift fox in eastern Colorado is unclear; however, state-managed occupancy surveys occurring every 5 years suggest that eastern Colorado still supports the largest population of swift fox throughout their range.[49] Predation from coyotes is also a driver of swift fox mortality in Eastern Colorado.[21,50] Kitchen et al.[21] found that coyotes contributed to 48% of swift fox mortality in a resource partitioning study in southeastern Colorado. Complex trophic interactions between canid species are documented in the literature[51,52]; however, the extent to which coyotes currently impact swift fox on the PNG remains uncertain. Because coyotes have been documented to influence swift fox abundance,[21,50] coyote presence should be considered as a driving mechanism in future trophic research between foxes, owls, and plovers (Fig. 6) on black-tailed prairie dog colonies on the PNG.

Regardless of the cause, a decline in the count of swift fox on the PNG is concurrent with the increased count of burrowing owls and decreased count of mountain plover (Fig. 5A).[45] Release of owl mesopredators may be linked to increasing infrequency of mountain plovers on prairie dog colonies on the PNG despite expansion of suitable habitat. Lower trophic level prey resources often decline after the eruption of a mesopredator due to increased predation.[43,44] Burrowing owls consume mountain plover nestlings,[53] supporting this hypothesized trophic cascade between foxes, owls, and plovers (Fig. 6). We also note that radio transmitters attached to plovers have been recovered inside swift fox dens, suggesting that plovers are a shared prey resource for both foxes and owls.[53,54] Under this scenario, an increased predation effect on plovers by owls may outcompete a predation effect on plovers by foxes.

Mesopredator Release on the TBNG

Predator–prey dynamics consistent with intraguild predation[40] compare with co-occurrence patterns seen on TBNG. Swift foxes remain common and are protected from

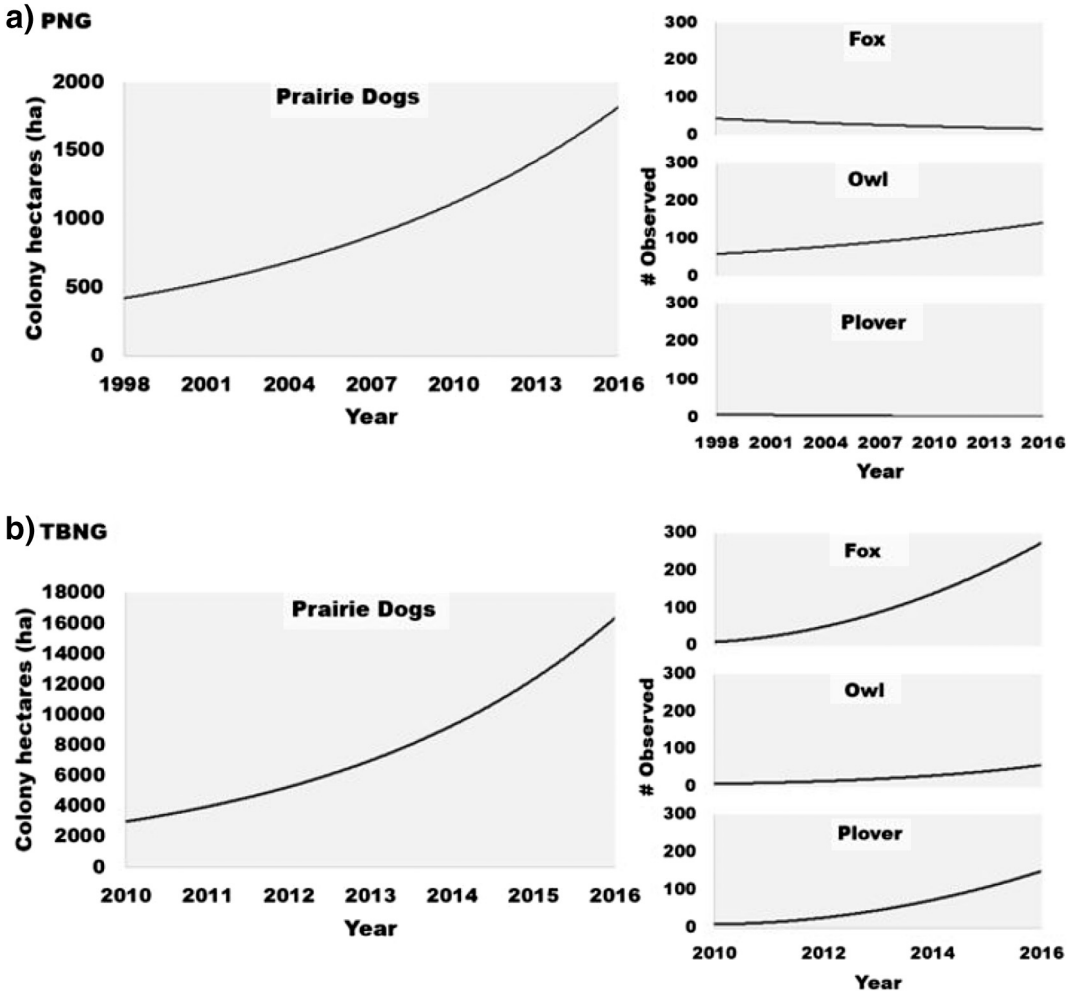

Figure 5. An exponential curve fitted to annual trend data collected on A, the Pawnee National Grassland (PNG) from 1998 to 2016 and B, the Thunder Basin National grassland (TBNG) from 2010 to 2016 for total active prairie dog colonies measured in hectares (ha) and population counts for swift fox, burrowing owl, and mountain plover.[45,46]

hunting and trapping in the northern mixed-grass prairies of eastern Wyoming,[16,46] and spotlight surveys suggest that this region remains a stronghold for swift fox. Although burrowing owl presence indicates a moderate increase on TBNG, trends remain low despite increasing availability of suitable habitat (Fig. 5B).[46] Mountain plover populations mirror the trend of swift fox, suggesting that even a minor increase in the count of burrowing owls still potentially alleviates predation on plovers, which allows them to take advantage of expanding prairie dog colonies, reflecting patterns of intraguild predation between owls and foxes (Fig. 5B).[46] Anecdotally, burrowing owls are selecting for resource deficient habitats where swift foxes are less likely to persist; the shared prey resource, mountain plover, is responding positively to the owls' change in habitat selection and the increased acreage of prairie dog colonies.

Coyotes are also present on the landscape on TBNG; however, the degree of impact on lower trophic level canid species remains undocumented. Coyote populations are lethally controlled in eastern Wyoming by local landowners, hunters, and predator control groups, and are infrequently documented on prairie dog colonies during associated species abundance surveys.[46] Successfully controlled coyote populations on the TBNG provide support for an increased abundance of swift fox; however, this inference remains speculative based on conversations with USFS biologists.[46] Because coyotes have been documented to influence swift fox abundance in Colorado,[21,50] coyote presence should be considered as a driving mechanism in future trophic research between foxes, owls, and plovers (Fig. 6) on the TBNG in Wyoming.

Landscape Fragmentation Driving Mesopredator Release

Conversion of grassland habitats may be an important driver of predator–prey dynamics because cascading trophic interactions have been linked to landscape fragmentation.[43,44] Prugh et al.[44] point to three factors that lead to declines in populations of top-level predators in fragmented landscapes: 1) apex predators have expansive territories and need large, connected areas of intact habitat. Therefore, as landscapes become fragmented, apex predators are less likely to meet resource requirements and become uncommon or absent from

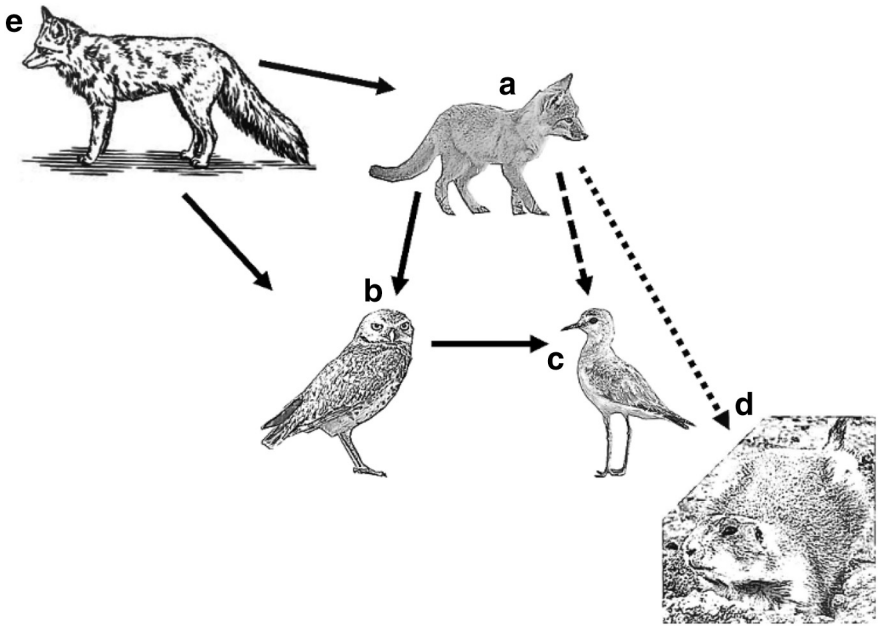

Figure 6. A, Swift fox (*Vulpes velox*), **B,** Western burrowing owl (*Athene cunicularia hypugaea*)**,** and **C,** mountain plover (*Charadrius montanus*) are all associated species of **D,** black-tailed prairie dog (*Cynomys ludovicianus*) colonies. We hypothesize that foxes consume owls (solid arrow) and owls consume plovers (solid arrow). Foxes also consume plovers (dashed arrow) and prairie dogs (dotted arrow), making this a highly interactive predator-prey community. **E,** Coyotes (*Canis latrans*) are also present in the system and play an unknown role in the hypothesized cascade by potentially influencing swift fox abundance and preying opportunistically on all species. Image courtesy of Cristi Painter, Ryan A. Parker, and Can Stock Photo Inc.

the area. 2) Fragmented landscapes provide attractive habitat for mesopredators because apex predators become rare and food resources in the form of human waste or crop fields become plentiful. And 3), in fragmented landscapes, apex predators experience frequent human conflict leading to lethal predator control. Thus, we uphold that predator-driven dynamics and the degree of habitat fragmentation could also support our hypothesis that swift fox, burrowing owl, and mountain plover are involved in a complex trophic interaction on black-tailed prairie dog colonies (Fig. 6).

Landscape Fragmentation on the PNG

Shortgrass prairie on the PNG is intermixed with independently managed rangeland and privately owned agricultural cropland; the latter fragments the landscape by transforming native grassland into cropland. Here, individual prairie dog colonies remain small (~0.5–138 ha, 2016 mapping data) and dispersed.[45] Spatial and temporal changes to prairie dog colonies partly result from agricultural development, but also from *Yersinia pestis*, an infectious bacterium that causes sylvatic plague (a disease often lethal to prairie dogs).[55] Plague is present annually on the PNG, clearing out over 95% of the prairie dogs in any given colony.[55,56] Annual prairie dog mapping reveals periodic appearance and disappearance of individual active colonies that shift geographically across the landscape between years.[45] Thus, a combination of agricultural development and plague contributes to the fragmentation and small size of prairie dog colonies.

The total number of small, isolated colonies are rising on the PNG,[45] however, suggesting that benefits to swift fox from prairie dogs may be negated by the surrounding landscape fragmentation. The transformation of grassland into agricultural cropland has removed expanses of swift fox habitat,[57] and small colony sizes combined with annual geographical changes in colony placement may further influence swift fox presence. These impacts may describe the increasing trend of burrowing owls (Fig. 5A).[45] Given that owls cue in on prairie dogs,[30] geographical changes in colony placement may not impact owl presence, provided prairie dogs remain on the landscape. Additionally, owls will continue to breed on colonies impacted by plague providing burrows remain intact, vegetation does not reach excessive heights, and prairie dogs recolonize shortly after.[20,53,58] This suggests that fragmented prairie dog colonies on the PNG have little impact on burrowing owls, further supporting the mesopredator release hypothesis.[43,44] Considering these fragmentation effects, mountain plover declines on prairie dog colonies may be in response to top-down control due to increased predation or selection of other suitable nesting habitat in the vicinity, such as prescribed burns and fallow crop fields. Regardless, the conversion of shortgrass prairie to agricultural cropland potentially benefits mountain plovers and alludes to a case of landscape fragmentation that both negatively and positively impacts different levels of the potential trophic cascade.

Landscape Fragmentation on the TBNG

Landscape fragmentation impacts the northern mixed-grass prairie to a lesser extent. The soil structure is unsuitable for producing crops, leaving cattle ranching as the primary agricultural practice.[59] On the TBNG, black-tailed prairie

dog colonies comprise large complexes upward of ~12,000 ha spanning public and privately owned land. Annual mapping efforts dating to 1999 indicate that these expanses oscillate over time (Fig. 4), declining when epizootics of plague sweep through the landscape.[46] Plague is less prevalent on an annual basis on TBNG and instead reflects patterns of density dependence.[60] Prairie dog colonies were recovering from a plague epizootic at the start of the trend data in 2010 (Fig. 5B),[46] and so using plague as a driver of fragmentation on TBNG helps address fox, owl, and plover interactions.

Prairie dog colonies expanded across the grassland post-2010 (Fig. 5B),[46] creating large, intact habitat patches for associated species. Systems with intraguild predation are frequently documented occurring on intact habitat patches,[51,52] providing an explanation for the relationship between co-occurring foxes and owls. Foxes on the TBNG are found almost exclusively on prairie dog colonies and presence has increased following the prairie dog expansion.[46] Burrowing owls are sparsely distributed across the prairie dog complexes and remain uncommon relative to the available habitat. If swift fox and burrowing owls are indicative of intraguild predation on TBNG, patterns in mountain plover trends follow suit: as fox occurrence increases, owls only slightly increase, and plovers increase (Fig. 5B). Plovers still risk predation by swift fox and other grassland predators; however, predation risk from owls is reduced. Thus, these potential cascading trophic interactions may be facilitated, in part, by the availability of intact patches of habitat created by prairie dogs.

Bottom-Up Control

We have primarily focused on top-down control as a leading hypothesis to explain the trophic ecology behind swift fox, burrowing owl, and mountain plover interactions on black-tailed prairie dog colonies. However, we cannot discount alternative ecological processes at work. Bottom-up control is characterized by primary producers or lower-level consumers driving changes to patterns in plant or wildlife populations and distributions at higher levels in the food web (Fig. 3).[36,38] Both the shortgrass and mixed-grass prairie communities are subject to changes in climate, which change plant composition and structure.[61] Here, an increase in percent precipitation may lead to taller grasses and forbs across prairie dog colonies, changing the habitat conditions required by associated species. Vegetation structure on a colony is also influenced by plague, when prairie dogs are no longer present to clip the vegetation back to a shortgrass, bare-ground state.[62] Changes to plant composition and structure lead to changes in the insect community,[63] or may represent an absence of prairie dogs, which may then cascade up the food web, impacting species from the bottom up. We argue that it is likely never the case where only top-down or bottom-up control is at work, but instead both trophic level processes are working concurrently to influence the biotic state of the community. Therefore, carefully considering all factors that may contribute to a bottom-up effect on a swift fox-burrowing owl-mountain plover interaction is critical for understanding all dynamics of the system.

Additional Influences from USFS Grassland Management Techniques

The PNG and TBNG manage for prairie dogs, and to varying degrees, associated species. Prairie dog management consists of both lethal and nonlethal management strategies. Lethal strategies on the PNG include nonregulated prairie dog shooting and poisoning of colonies that interfere with agricultural operations. TBNG has regulated a prairie dog shooting closure on colonies that are considered core areas for associated species. Local stakeholders successfully removed the shooting closure in recent history, and poisoning of prairie dogs on the grassland has increased. Nonlethal prairie dog management includes structural (e.g., vegetation or fence) barriers on colony edges to prevent dispersal in any given direction on both grasslands and translocation of prairie dogs from unsuitable areas to patches of core area habitat on the TBNG.

Plague mitigation in the form of application of an insecticide, deltamethrin, that targets fleas (order *Siphonaptera*—the vector of sylvatic plague)[55] on prairie dogs has occurred on both the PNG and TBNG. Prescribed burns that create temporary habitat for mountain plover and swift fox have occurred on both USFS grasslands. Finally, grazing of domestic cattle occurs on pastures that overlap prairie dog colonies on both USFS grasslands. In areas where heavy grazing occurs outside of prairie dog colonies, bare ground habitat can result, which may attract dispersing prairie dogs and breeding plovers. Grazing periods, stocking rates, and densities may have an impact on the likelihood of prairie dog and associated species' occurrence and all yield varying levels of success. Thus, it is likely that management actions influence cascading trophic interactions by altering habitat composition and co-occurrence between species.

Conclusions

Trophic cascades occur in a diverse range of ecosystems and exist between flora and fauna at all trophic levels.[36,38,39] Cascading trophic interactions in North American temperate grasslands remain poorly described despite a heavy management focus on many individual species in the system. The theoretical framework presented here provides a starting point for research on species interactions between swift fox, burrowing owl, and mountain plover on prairie dog dominated rangeland communities. We add that there are many alternative, plausible hypotheses that we do not describe in detail in this manuscript. For example, mountain plover populations on both grasslands may be largely driven by nesting habitat availability, to include insect availability, and populations may reflect these factors more so than direct or indirect influences from co-occurring species. Also, burrowing owl populations may increase with a direct correlation to nesting habitat availability independent from a decrease in swift fox populations. We also acknowledge that it remains unclear at which life-stage predation on owls and plovers predominantly occurs.

We fully acknowledge that inferences made in this paper are anecdotal and maintain that future investigation into this system

is needed. Trophic cascades are a driving force in community ecology that cannot be defined by any one mechanism. The presence or absence of top-level consumers, hunting, disease, management strategies, agricultural production, habitat fragmentation, or deviations in resource availability, all of which change temporally, contribute to the dynamics of trophic cascades. Other environmental variables not discussed here, such as climate, should also be considered. We propose targeted long-term multispecies occupancy research that combines the hypothesized mechanisms specified previously with presence and co-occurrence of associated grassland species. This level of analysis is recommended for exploring these complex interactions moving forward, and this manuscript only serves as a prelude to this suggestion. Relationships between prairie dogs and associated species are highly interactive, so managing prairie dog colonies for viable populations of associated grassland wildlife is recommended from a conservation perspective. This promotes species richness, rangeland health, and diversity in shortgrass and mixed-grass prairies, and highlights opportunities for investigating multispecies interactions across all trophic levels.

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