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Multi-level thresholds of residential and agricultural land use for elk avoidance across the Greater Yellowstone Ecosystem

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Abstract

1. Conversion of land for settlements and agriculture is increasing globally and can influence wildlife space use. However, there is limited research to identify the thresholds of land-use change that incur wildlife avoidance and how these thresholds might vary across levels of selection.
2. We evaluated multi-level avoidance thresholds of elk *Cervus canadensis* impacted by residential development and irrigated agriculture across the Greater Yellowstone Ecosystem in Idaho, Montana and Wyoming. Using GPS data from 765 elk in 21 herds, we estimated habitat selection in relation to development and agriculture at three levels (home range selection, within home range selection and movement path selection). Next, using individual selection covariates and associated measures of land-use availability, we used functional-response models to evaluate how selection varied based on availability, and in turn, to estimate avoidance thresholds.
3. We found individual and level-specific variation in elk responses to environmental factors. Elk exhibited stronger responses (either selection or avoidance) when selecting home range locations (i.e. second-order selection) than when selecting areas within home ranges (i.e. third-order selection) or selecting movement paths (i.e. fourth-order selection). Importantly, elk avoidance of development and

agriculture changed as the amount of land in these categories changed. Across all levels of selection elk exhibited neutral selection for human development at low levels of availability (<1.1%–2.2% developed) but avoided areas that were >1.1%–2.2% developed. Conversely, elk selected positively for irrigated agriculture at low to moderate levels of availability (<52.0%–66.2% agriculture) but exhibited neutral selection in areas that were >52.0%–66.2% agriculture.

4. *Synthesis and applications*. Elk avoidance of low levels of human development suggests conservation efforts such as restrictions on future development or conservation easements could focus on areas that are still below 2% developed. Additionally, because elk selection was strongest at the landscape scale, conservation actions that are based on information about the overall landscape structure may be most impactful. Our results highlight the importance of understanding variability in wildlife habitat selection at multiple levels, particularly in relation to land-use change, and highlight how functional response modelling can help inform landscape conservation.

KEYWORDS
agriculture, *Cervus canadensis*, development, functional response, land-use change, thresholds

1 | INTRODUCTION

Understanding the habitat use of animals can help guide management and conservation decisions (Allen & Singh, 2016). Typical habitat selection analyses assume that animals select or avoid specific environmental features regardless of their availability on the landscape (Holbrook et al., 2019). However, selection of specific features might change based on availability, which is termed a functional response (Mysterud & Ims, 1998). Functional responses in habitat selection can occur when animals switch use of habitats at specific environmental conditions, or when tradeoffs between different types of habitats vary based on availability. For example, animals might use specific habitats more intensely when these habitats are scarce if they rely heavily on or are particularly attracted to specific conditions (e.g. cover, food availability) associated with that particular habitat type (Anderson et al., 2012). Alternatively, animals might use specific habitat types more intensely when these habitat types are relatively more common on the landscape because other areas of preferred habitats are less common (Hebblewhite & Merrill, 2008; Knopff et al., 2014).

Analysing functional responses with regards to habitat selection can be useful in the face of land-use change. Globally, native habitats have been converted to human development and agriculture (Venter et al., 2016), and many wildlife species have been found to alter their habitat use and movements in response to these anthropogenic habitat modifications (Doherty et al., 2021; Tucker et al., 2018). Although studies been conducted on how animals select or avoid areas that have underwent land-use change, limited research has focused on the magnitude of land-use change that alters animal space use patterns. Yet identifying thresholds of avoidance can be particularly useful for managers and land-use planners who are expected to balance multiple competing needs. For example, recent work in western Wyoming determined that mule deer *Odocoileus hemionus* use of migratory routes decreased when surface disturbance from natural gas development was greater than 3% (Sawyer et al., 2020), which in turn can help plan future development.

Although functional response modelling can be informative to management, it is often conducted at one of the following orders of selection: selection of home range locations (i.e. second-order selection; Johnson, 1980), selection of locations within home ranges (i.e. third-order selection; Johnson, 1980) or selection of movement paths (Thurfjell et al., 2014). However, animals can exhibit selection for different features at different orders of selection (Mayor et al., 2009). For example, theory suggests that selection against factors that are most limiting to fitness should be strongest at coarser scales (i.e. placement of home ranges within a landscape), whereas less important factors might influence finer-scale selection (Rettie & Messier, 2000). Thus, multi-level functional response modelling that captures orders of selection including path selection, selection of attributes within the home range, and selection of the home range within the landscape, could offer insight into hierarchical thresholds associated with land-use change. In turn, understanding multi-level thresholds could help guide conservation; thresholds associated with higher levels of selection could provide insight into landscape-scale land-use planning such as county-wide zoning regulations or prioritization of conservation easements, whereas thresholds at finer-levels could inform localized management actions such as small-scale habitat improvements.

We investigated hierarchical functional responses to land-use change by elk *Cervus canadensis* across the Greater Yellowstone

Ecosystem (GYE). A large portion of the major elk herds within the GYE migrate seasonally (Craighead et al., 1972; Rickbeil et al., 2019) between summer ranges in and around protected areas such as Yellowstone and Grand Teton National Parks and winter ranges on private lands that are experiencing significant change (Gigliotti et al., 2022; Hansen & Phillips, 2018). Conversion of habitats to residential development or irrigated agriculture within the GYE has the potential to affect elk. For example, in areas with high levels of human development elk might experience reduced foraging opportunities (Ciuti et al., 2012), lower survival or reproduction (Phillips & Alldredge, 2000; Webb et al., 2011) and might face increased levels of human conflict because of crop damage and disease transmission (Walter et al., 2010). Alternatively, elk might benefit from human development because of reduced predation risk (Muhly et al., 2011; Shannon et al., 2014) or nutritional subsides from agricultural areas (Barker et al., 2019).

Although land-use change has the potential to affect elk populations within the GYE, little is known about the magnitude of land-use change that alters the habitat selection of elk, particularly regarding the magnitude of land-use change associated with elk avoidance of an area. Because individual elk herds in the system use areas with vastly different land covers, there is a gradient of availability of developed and agricultural land which can be used to better understand elk responses to land use at multiple scales.

In this study, we investigated elk multi-level functional responses to human development and agriculture to obtain information on the thresholds of land-use change that might affect elk within the GYE. We tested several hypotheses related to functional responses of elk habitat selection in relation to land use:

1. Avoidance thresholds for both developed and agricultural land vary by selection order: We predicted that avoidance thresholds would be lowest at the second order (i.e. placement of home ranges), followed by the third order (i.e. selection of locations within home ranges) and the fourth order (i.e. selection of movement paths) because selection for factors affecting fitness should be strongest at the coarsest scale.
2. Elk habitat selection for developed land varies based on availability of developed land: Across all scales, we predicted that elk would select for areas closer to human development when availability of the developed area was high because areas of preferred habitats would be less common.
3. Elk habitat selection for irrigated agriculture varies based on availability of irrigated agriculture: Across all scales, we predicted that elk would select for areas closer to irrigated agriculture when availability of irrigated agriculture was low or moderate because elk would be able to take advantage of the nutritional benefits of the agriculture while still using nearby non-agricultural areas.
4. Elk habitat selection for development or irrigated agriculture varies based on an interaction between the availability of development and irrigated agriculture: Across all scales, we predicted that elk would select for areas closer to development when the availability of irrigated agriculture was high, or areas closer to agriculture when the availability of development was high, because the nutritional subsidies provided by the agriculture would outweigh the potential costs of being near development.

2 | MATERIALS AND METHODS

2.1 | Study area

We focused our study within the GYE, which is an approximately 10.8 million ha ecosystem centered around the Yellowstone plateau and surrounding mountain ranges in Idaho, Montana and Wyoming (Noss et al., 2002). The GYE contains a mixture of land ownership including federally protected Yellowstone National Park, Grand Teton National Park, and several national forests, as well as land managed by the Bureau of Land Management and the US Fish and Wildlife Service, state-owned land in Idaho, Montana and Wyoming, and private land devoted to a variety of uses including agriculture, working and amenity ranches and residential housing. Habitat types within the GYE include high elevation alpine forests, mid-elevation coniferous and deciduous forests and low-elevation shrub-steppe and grasslands.

2.2 | Spatial data

We used GPS data, which were collected for a variety of previous research projects spanning from 2002 to 2020, from 765 elk in 21 herds within the GYE (Table S1; Figure S1). Given that we used historical data rather than collecting any new data, this research did not require institutional ethical approval. All data used in these analyses were collected by GPS collars that took locations at intervals ranging from 45 min to 3 h. To ensure that elk that were monitored for longer periods of time did not overly influence the results, we randomly selected a single year of data for elk that were monitored for more than 1 year. Because hunting can affect elk space use patterns (Proffitt et al., 2013), we restricted our analyses to January–March, avoiding the period when the majority of hunting in this area occurs, although hunting season lengths differ throughout the GYE. We only included elk that had more than 45 days of data during a given year (mean monitoring duration = 77.5 days; range = 45–91 days), and a GPS fix success greater than 90% (calculated by dividing the number of collected locations by the total number of location that would have been collected if every scheduled fix was successful).

To characterize land use within the GYE, we used yearly U.S. Geological Survey (USGS) Land Change, Monitoring, Assessment, and Protection (LCMAP) data (Collection 1.1; https://www.usgs.gov/core-science-systems/eros/lcmap) at a 30-m resolution. We specifically included forests, shrubland and development (which includes commercial and residential buildings, roads, utility corridors and industrial and mining infrastructure) and considered these land-use classes as distance covariates (e.g. distance to forest) to standardize across all elk herds. Because we were primarily interested in irrigated crops, we used yearly USDA Cropscape data (https://nassgeodata.gmu.edu/CropScape/) at a 30-m resolution. We selected the primary irrigated crops in the region (alfalfa, other hay/non-alfalfa, barley and spring wheat) to create both an agricultural presence raster and a distance to agriculture raster. Other spatial data included elevation that we obtained from a 30-m digital elevation model, and ruggedness that we calculated as the Terrain Ruggedness Index using the RASTER R package (Hijmans, 2020). We also included snow depth data on both a monthly and seasonal time-scale by averaging daily snow depth values at a 1-km resolution using National Oceanic and Atmospheric Administration (NOAA) SNODAS data (https://nsidc.org/data/g02158). We conducted all analyses in R version 4.0.5 (R Core Team, 2019).

2.3 | Second-order and third-order selection

To estimate selection of home range locations (i.e. second-order habitat selection) and selection of locations within home ranges (i.e. third-order habitat selection) for individual elk, we first estimated winter ranges for each individual elk using Brownian bridge movement models (BBMM), which estimate occurrence distributions based on estimated movement paths of individual animals (Horne et al., 2007), implemented using the BBMM R package (Nielson et al., 2013). For the second-order analysis, we then aggregated all points from individuals in the same herd in a given year and calculated the 95% quantile of distances between elk locations and the centroid of the herd's locations. We used this distance to define a "home range availability zone" for each individual elk. Specifically, we buffered the individual elk home ranges by the defined quantile distance for the elk's herd (O'Neill et al., 2020). Implicit in this calculation is the assumption that elk were able to select the location of their home range while controlling for the spatial extent requirements of the larger herd, and still including areas available to the herd that might be above the avoidance threshold. Although second-order selection is often conducted by estimating a study area-level home range (i.e. aggregating locations from all monitored individuals) and generating random points within that area, this method excludes areas that are not used by any monitored individuals (Buskirk & Millspaugh, 2006), and, therefore, would underrepresent areas that are accessible to elk but potentially avoided if they are above the avoidance threshold of a given habitat feature. On average, an individual animal's home range comprised only 9.51% of the home range availability zone (Table S2), indicating that availability at the second order differed from availability at the third order.

Within the home range availability zone for the second-order analysis, or within home ranges for the third-order analysis, we generated random points for each elk equal to their number of used points using the *spsample* function in the SP R package (Bivand & Pebesma, 2013) and extracted all environmental covariates (distance to development, distance to forest, distance to irrigated agriculture, distance to shrubland, elevation, ruggedness, snow depth) for both used and random points using the RASTER R package (Hijmans, 2020). To capture temporal variation in snow depth, we split the random points to correspond to the number of used points during each month and extracted the snow depth data from the associated monthly raster. We ran second-order and third-order resource selection function (RSF) models containing all covariates for each individual elk using logistic regression models and retained the beta coefficient values for distance to development and distance to agriculture to use in the functional response modelling.

2.4 | Fourth-order selection

To investigate fourth-order habitat selection, we estimated selection of movement paths. To standardize across elk with different GPS fix rates, we resampled GPS tracks to 3h using the *redisltraj* function in the ADEHABITATLT R package (Calenge, 2006). For each movement step within a track, we generated 10 random steps drawn from a gamma distribution of observed step lengths (mean ± SD across all animals: $k = 0.74 \pm 0.14$, $\theta = 537.34 \pm 217.34$) and a von Mises distribution of observed turning angles (mean ± SD across all animals: $\kappa = 0.49 \pm 0.19$, $\mu = 0$), based on all GPS data from the given individual (Duchesne et al., 2015). We extracted covariates at the end point of each used and available step. We analysed selection of individual elk using step-selection functions (SSFs) containing all covariates, implemented in the AMT R package (Signer et al., 2019) and retained the beta coefficient values for distance to development and distance to agriculture to use in the subsequent functional response modelling. For all orders of selection, we considered beta coefficients to indicate negative selection if β and 95% CI <0, positive if β and 95% CI >0 and neutral if 95% CI overlaps 0.

2.5 | Functional response modelling

To estimate functional responses of habitat selection and determine avoidance thresholds at all orders of selection, we determined availability related to distance to agriculture and distance to development for each individual elk. We first tested for a potential correlation between distance to agriculture and distance to development using a Pearson correlation test on all used and available points included in the second, third and fourth order models separately and considered values >0.75 to indicate strong correlation. Based on this analysis, distance to agriculture and distance to development were not strongly correlated at the second order ($r = 0.49$), third order ($r = 0.31$) or fourth order ($r = 0.31$).

For availability at the second order, we calculated the percent irrigated agriculture and percent development within each animal's home range availability zone. Similarly, we determined availability at the third order related to distance to agriculture and development by calculating the percent irrigated agriculture and percent development within each individual animal's home range. To determine availability at the fourth order, we created a buffer around each used location equal to the mean step length of the individual animal. We extracted the percent irrigated agriculture and percent development within all buffers and obtained an average value across all buffers for each individual elk. For all three levels of selection, we associated the level-specific individual availability with the distance to irrigated agriculture and distance to development beta coefficients from the corresponding RSF or SSF models. We removed animals that had 0% availability of either agriculture or development at a specific level because we assumed that some level of availability was needed to influence selection.

Across all three levels of selection, we tested for the presence of a functional response by running generalized linear mixed models with selection coefficient as the response variable and availability as the predictor variable. We compared a null model (i.e. no functional response), with a linear model of availability as well as a quadratic model of availability, given that functional responses often follow a curvilinear form since use typically equals availability at extreme high and low levels of availability (Holbrook et al., 2019; Mysterud & Ims, 1998). We included herd ID as a random effect in all models to account for potential within-herd selection similarity. We investigated functional responses in relation to availability of a land use affecting selection for that land use (e.g. availability of development affecting selection for development), as well as availability of irrigated agriculture affecting selection for development and vice versa. We conducted the model ranking separately for each availability-selection pair at each level of selection and considered models within 2 delta AIC of the top model to be competitive.

When there was evidence of a functional response (i.e. the null model was not the best supported model), we determined thresholds associated with a change in selection by examining the 95% confidence interval (CI) around the predicted estimate. We considered availability values when the 95% CI included zero to be indictive of neutral selection and, therefore, identified availability thresholds as values when the 95% CI did not overlap zero.

3 | RESULTS

Across all levels of analysis, we included 765 elk from 21 different herds. We found individual and level-specific variation in selection of environmental factors. Elk exhibited stronger selection (either positive or negative) at the second order than at the third or fourth order; in particular, the majority of elk exhibited neutral selection for 6 out of 7 environmental factors (with the exception of ruggedness) at the fourth order (Figure 1). At the second order, the largest proportion of elk selected areas further from human development, closer to forests, closer to irrigated agriculture, closer to shrubland, at higher elevations, in areas of lower ruggedness and in areas with shallower snow (Figure 1).

3.1 | Functional responses to development

We found evidence for a quadratic functional response at all orders in relation to development (Table 1). Across all levels of selection, elk exhibited neutral selection for development at low levels of availability but selected for areas further from development at availability thresholds of >1.6% (Figure 2a), >2.2% (Figure 2b) and >1.1% (Figure 2c) at the second, third and fourth order, respectively. Although the overall pattern of the functional response was similar across levels, we observed a slightly weaker response with increasing levels (Figure 2).

We also found evidence for a quadratic functional response at all orders, when considering how the availability of irrigated agriculture affected selection for development (Table S3). Although elk typically selected areas further from development regardless of availability of irrigated agriculture, elk exhibited neutral selection for development when availability of irrigated agriculture was low (Figure 3a–c; second order: <7.0% irrigated agriculture, third order: <7.4% irrigated agriculture, fourth order: <30.0% irrigated agriculture). Additionally, at the second order, elk exhibited neutral selection for development at high levels of irrigated agriculture availability (>48.2% irrigated agriculture).

3.2 | Functional responses to irrigated agriculture

Similar to development, we found evidence for a quadratic function response at the second, third and fourth order in relation to irrigated agriculture (Table 1). Across all levels of selection, elk selected for areas closer to irrigated agriculture when agriculture availability was low to medium but exhibited neutral selection for irrigated agriculture at availability thresholds of >52.0% (Figure 2d), >59.1% (Figure 2e) and >66.2% (Figure 2f) at the second, third and fourth order, respectively. Additionally, at the third order, elk selected for areas further from irrigated agriculture when irrigated agriculture comprised >74.9% of a home range (Figure 2e). Although the overall pattern of the functional response was similar across levels, we observed a slightly weaker response with increasing levels (Figure 2).

At the second and fourth orders, we did not find evidence of a functional response, when considering how the availability of development affected selection for irrigated agriculture, but we did find evidence for a quadratic response at the third order (Table S3). At the third order, elk selected areas closer to irrigated agriculture when development comprised either <0.7% or >4.9% of an individual's home range, with strongest selection for irrigated agriculture occurring at the highest availabilities of development (Figure 3d).

4 | DISCUSSION

We found high individual variation in selection for different landscape features among elk in the GYE, leading to multi-level functional responses to human development and irrigated agriculture. We found stronger responses at the second order (selection of home ranges), compared consecutively to the third order (selection within home ranges) or movement-level (Figure 1). Regardless of the level of selection, elk avoided human development at low

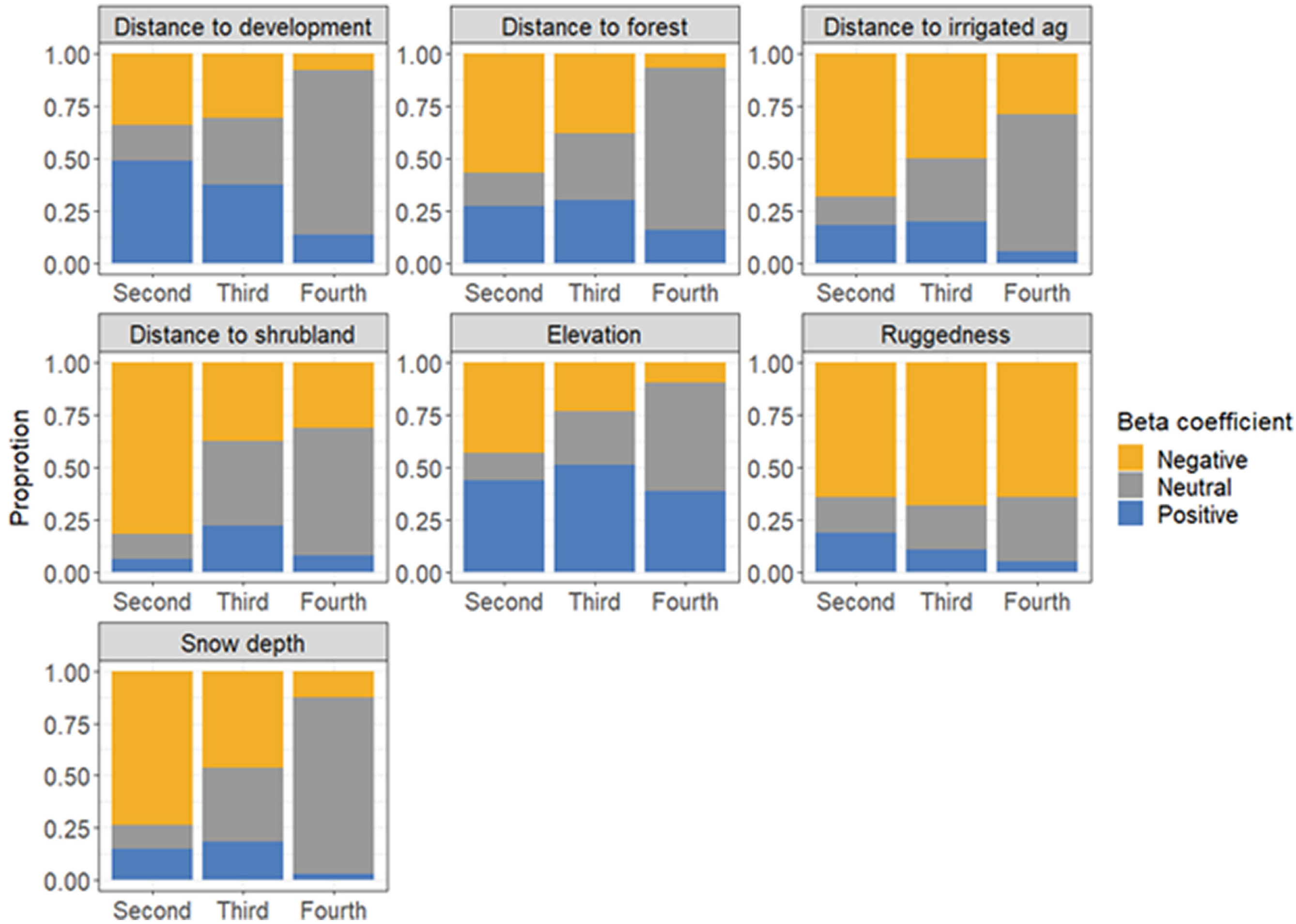

FIGURE 1 Proportion of individual elk *Cervus canadensis* exhibiting negative (β and 95% CI <0), positive (β and 95% CI >0), or neutral selection (95% CI overlaps zero) for different habitat factors based on selection coefficients, at levels of second (selection of home range locations), third (selection within home ranges) and fourth orders (selection of movement paths), Greater Yellowstone Ecosystem, 2002–2020.

TABLE 1 Model selection results for elk winter functional response models in relation to irrigated agriculture and development, Greater Yellowstone Ecosystem, 2002–2020.

Covariate	Model	*K*	ΔAIC_c (second order)	ΔAIC_c (third order)	ΔAIC_c (fourth order)
Irrigated agriculture[a]	Quadratic	6	0	0	0
	Linear	5	20.26	76.26	39.1
	Null	4	30.82	78.67	49.81
Development[b]	Quadratic	6	0	0	0
	Linear	5	9.19	21.26	7.84
	Null	4	106	111.87	52.7

[a]The Akaike's information criterion corrected for sample size (AIC_c) for the top irrigated agriculture models are 4698.15, 3660.23. and 3285.86 for second, third and fourth order, respectively.
[b]The Akaike's information criterion corrected for sample size (AIC_c) for the top development models are 3454.11, 2635.10. and 1507.85 for second, third and fourth order, respectively.

thresholds of availability (1.1%–2.2% developed) and selected for agricultural land at low to medium availability (<52%–66% agricultural land). Additionally, elk selection for irrigated agriculture was strongest when individuals' home ranges had higher levels of development. Collectively, our results highlight the complexities of how wildlife respond to land use and the effects of multi-level habitat features in conservation actions across various management scales. Importantly, we show how functional response modelling can be beneficial in informing landscape conservation.

Consistent with the hypothesis that selection for or against factors that are most limiting to fitness occurs at coarser levels (Rettie & Messier, 2000), we found that most elk selection (either positive

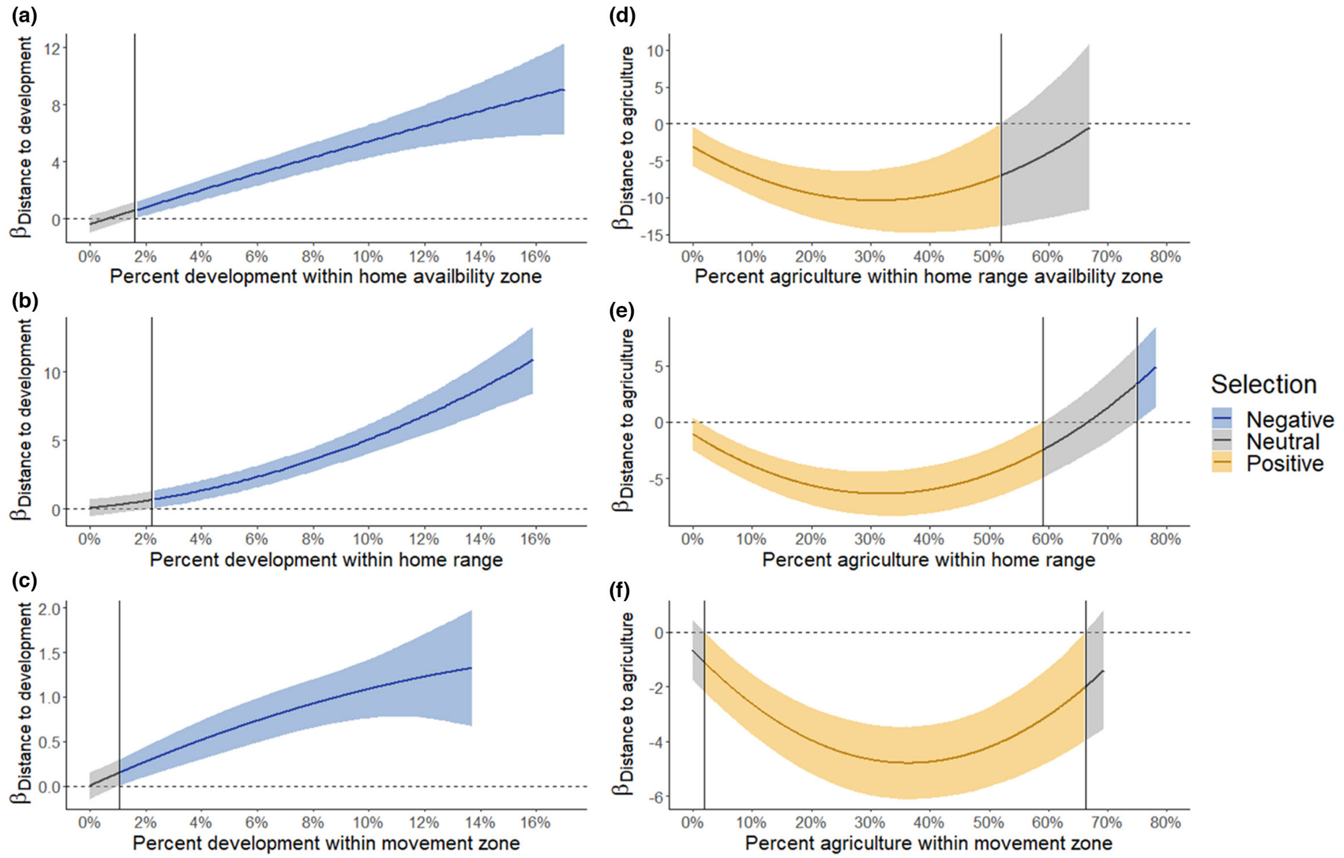

FIGURE 2 Level-specific functional responses (mean ± 95% CI) in elk *Cervus canadensis* winter habitat selection in relation to development (a = second order, b = third order, c = movement path) and irrigated agriculture (d = second order, e = third order, f = movement path); solid vertical lines identify thresholds associated with shifts in selection which are defined by availability values where the 95% CI does not overlap zero, Greater Yellowstone Ecosystem, 2002–2020. Note that the *y*-axis differs for each panel.

or negative) occurred at the second order, compared with the third or fourth order. Additionally, our findings add to the knowledge of level-dependent habitat selection by illustrating that the strength of functional responses can also vary by level, with stronger functional responses occurring at coarser levels. Both agriculture and human development could affect the survival and reproduction of elk (Cook et al., 2013; Phillips & Alldredge, 2000; Webb et al., 2011). Thus, it is logical that elk select locations for home ranges in areas closer to agriculture and further from development and that neutral selection at lower levels (i.e. third and fourth order) might be indicative of elk having already selected for or against specific habitat features when establishing home ranges.

Regardless of the scale, we found low avoidance thresholds of developed areas (1.1%–2.2% developed). At no level of availability did elk select for human development, but neutral responses to development at low levels of availability suggest that elk can tolerate small amounts of development. The observed avoidance of human development (>2.2% of developed land) could be a result of several processes. First, elk might be responding negatively to physical features of developed areas. Land conversion from forests or shrubland to human development reduces natural forage for herbivores (McCleery, 2010) and, therefore, reduces the energetic benefits that elk can gain in an area. Human development in the form of fences, roads, or paved surfaces can also create barriers to movement for wildlife (Prokopenko et al., 2017; Xu et al., 2021). Therefore, using these areas could be energetically costly for elk. Second, elk might display avoidance behaviours to reduce the risk of encountering humans. We conducted our analyses during a time of the year when hunting does not occur, yet elk have been found to exhibit avoidance behaviours in areas of higher human activity outside of hunting whether incidental (Rogala et al., 2011; Wisdom et al., 2018) or prescribed to minimize risk of disease transmission (Jones et al., 2021) Although our results suggest elk avoid highly developed areas, other research indicates that elk might benefit from human development as a means to avoid predators (Muhly et al., 2011; Shannon et al., 2014) or as refuge from human hunting pressure during the hunting season (Proffitt et al., 2010, 2013). We were unable to incorporate risk from predators and humans into our study. Clarifying how risk from predators and hunters affects avoidance thresholds of human development is an area for future research.

Our observed development avoidance threshold was similar to that of mule deer avoidance of energy infrastructure during migration in southwestern Wyoming, where deer migratory use decreased when disturbance exceeded 3% (Sawyer et al., 2020). Taken together, these findings suggest that avoidance thresholds are not unique to migratory ranges or species but similarly

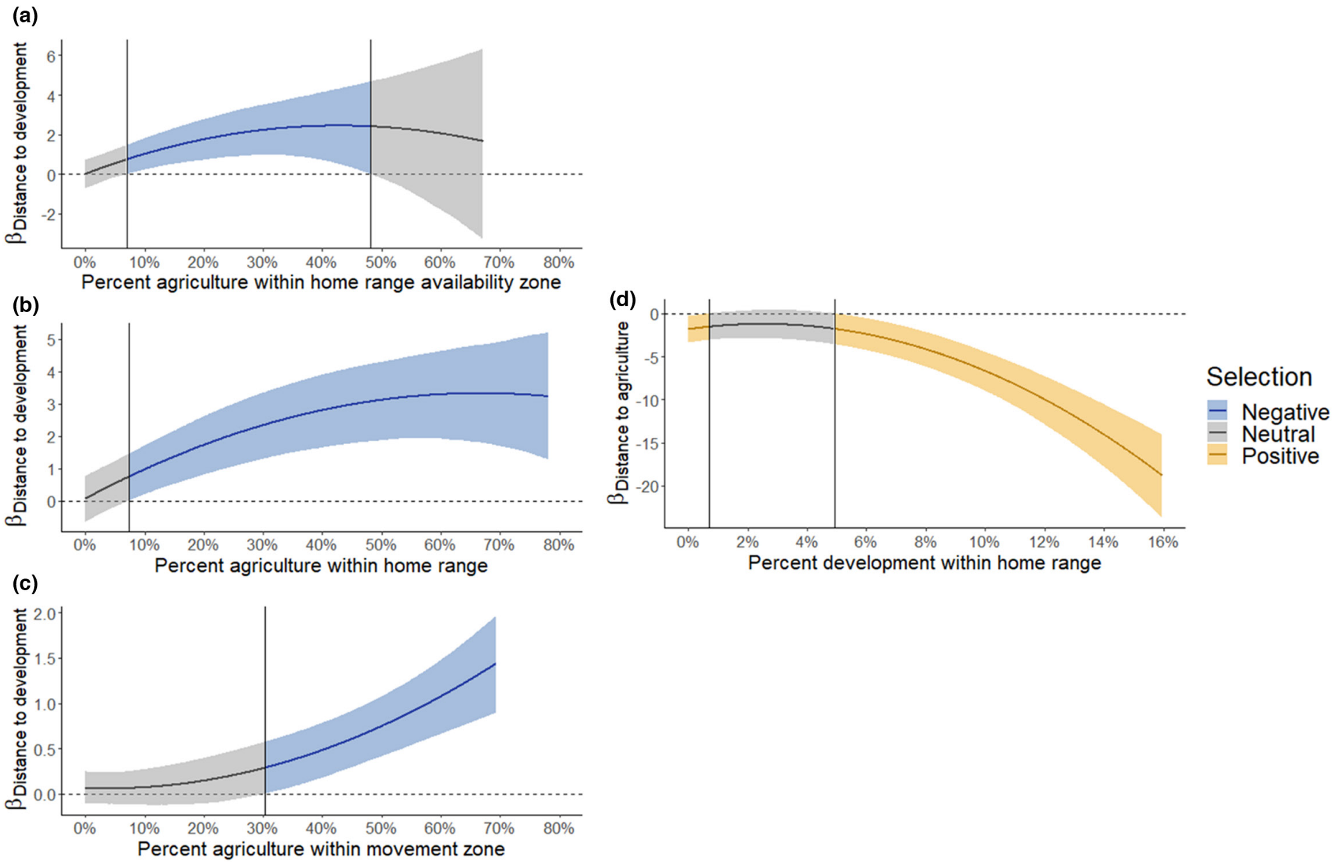

FIGURE 3 Level-specific functional responses (mean ± 95% CI) in elk *Cervus canadensis* winter habitat selection for development relation to irrigated agriculture (a = second order, b = third order, c = movement path) and selection for irrigated agriculture in relation to development (d = third order); solid vertical lines identify thresholds associated with shifts in selection, which are defined by availability values where the 95% CI does not overlap zero, Greater Yellowstone Ecosystem, 2002–2020. Note that the *y*-axis differs for each panel.

affect seasonal range use and that avoidance thresholds might be broadly similar for mule deer and elk. However, gaps in knowledge remain on avoidance thresholds of other species and a better understanding of how these habitat selection patterns can scale up to affect population-level processes. Additionally, we took an undifferentiated approach to identifying human disturbance using remotely sensed data, but questions remain regarding differential habitat selection patterns and avoidance thresholds of specific disturbance types such as buildings, roads and fences, the presence of humans, types of crop, livestock presence and response to predation risk from carnivores. It is also important to note that our estimated avoidance thresholds are likely partially a function of data collection locations; most of the elk included in this analysis were not collared in highly developed areas either because of trapping restrictions or because of the goals of the initial study. Thus, investigating elk habitat use in areas with greater development intensity than was included in this study is an area for future research.

As predicted, we found that elk exhibited a functional response in habitat use in relation to irrigated agriculture, with selection for irrigated agriculture at low to moderate levels of availability regardless of what level of selection we considered. Although we focused on analysis on the winter months, which are not the growing season for many crops in this region, agriculture fields still represent an important winter habitat for elk and other ungulates (Anderson et al., 2012; Brennan et al., 2015). Irrigated agriculture is a source of nutritious forage for elk (Barker et al., 2019) and, therefore, can act as a spatial nutritional subsidy, even in the winter. However, the use of agricultural areas also increases the potential for conflict with landowners (Hegel et al., 2009) and increases the risk of disease transmission to livestock (Rayl et al., 2019).Therefore, elk are likely able to benefit the most from irrigated agriculture at intermediate availability levels with nearby non-agriculture areas serving as refuges. Neutral selection for agriculture at the highest levels of availability likely occurs because the benefits of using these areas no longer outweigh the costs.

Our results indicate a complex interplay between development and irrigated agriculture, with elk exhibiting the strongest selection for agriculture when their home ranges had more development. Areas with higher development likely have less natural forage for elk, which in turn leads to a higher reliance on agricultural food sources. Although irrigated agriculture might allow elk to persist in developed areas where they might otherwise be extirpated, the reliance on agricultural food subsidies might result increase human-wildlife conflict because of crop damage (Hegel et al., 2009). Therefore, a better understanding of the spatial patterns of elk-landowner conflict related to landscape composition of agriculture and development could prove beneficial.

4.1 | Conservation implications

Of particular importance to conservation planning are the low thresholds of human development that result in elk avoidance of areas. Although much of the GYE falls within protected areas, the majority of elk herds in this system, including many that summer in parks and wilderness areas, rely on private lands, especially in their winter ranges (Gigliotti et al., 2022). Private lands in this system are vulnerable to future human development (Gude et al., 2006; Hansen & Phillips, 2018), given that many areas of the GYE do not have any zoning regulations in place (Gigliotti et al., 2022) and coupled with the fact that the Covid-19 pandemic has at least partially resulted in more people moving to this part of the country (Dimke et al., 2021). Because elk exhibit such a low avoidance threshold to human development, conservation measures, whether regulatory (i.e. restrictions on future development) or voluntary (e.g., conservation easements or habitat leasing), could prioritize areas that are still below the development avoidance thresholds. For example, zoning regulations that restrict development in undeveloped parts of the landscape and instead encourage new development in areas that have already been modified could be beneficial for elk populations.

Conversely, some agency and conservation groups seek to maintain or limit elk abundance in specific areas. In these situations, knowing thresholds of agriculture and human development where elk use or avoid areas could be useful in creating management plans. Finally, our finding that selection and functional responses are strongest at the second order suggests that conservation actions might be most impactful when they are chosen based on information about the overall landscape structure, rather than just information on a more localized level. For example, localized habitat improvements such as fence modifications or road crossing structures might only be beneficial for elk if the larger landscape contains ample suitable habitat.

Our research highlights the importance of understanding variability in wildlife habitat selection at multiple levels, particularly in relation to anthropogenic land uses. Although previous research has focused on various ways human development and agriculture might be affecting wildlife, quantifying specific avoidance thresholds can provide valuable information for land managers and can help inform future land-use planning. Given the on-going land-use conversion worldwide, knowledge of explicit avoidance thresholds is beneficial to wildlife in systems globally.

AUTHOR CONTRIBUTIONS

Laura C. Gigliotti and Arthur D. Middleton conceived the ideas; M. Paul Atwood, Eric K. Cole, Alyson Courtemanch, Sarah Dewey, Justin A. Gude, Mark Hurley, Matthew Kauffman, Kailin Kroetz, Bryan Leonard, Daniel R. MacNulty, Eric Maichak, Douglas McWhirter, Tony W. Mong, Kelly Proffitt, Brandon Scurlock and Daniel R. Stahler collected the data or contributed to the interpretation of results; Laura C. Gigliotti analysed the data and led the writing of the manuscript; all authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.cvdncjt7x (Gigliotti et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Sample sizes of individual elk within 21 elk herds included in the analyses and mean days monitored per herd, Greater Yellowstone Ecosystem, 2002–2020. See Figure S1 for mapped locations of the included herds.

Table S2: Average 95% quantile distance between yearly herd centroids and all GPS locations within a given herd, and the average percent of home range availability zones covered by an individual home range, Greater Yellowstone Ecosystem, 2002–2020.

Table S3: Model selection results for elk winter functional response models for development in relation to irrigated agriculture and for irrigated agriculture in relation to development, Greater Yellowstone Ecosystem, 2002–2020.

Figure S1: Map of winter ranges of 21 elk herds included in the analyses within inset map indicating the location of the GYE in crosshatching, Greater Yellowstone Ecosystem, 2002–2020. Basemap sources are Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS user community.

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