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Beyond use versus availability: behaviour-explicit resource selection

Ryan R. Wilson, Lynne Gilbert-Norton & Eric M. Gese

Resource selection studies are common in the wildlife ecology literature and typically rely on the comparison of locations used by wildlife and locations assumed to be available for use but where use was not observed. While standard use-availability designs are helpful for establishing general patterns of species occurrence, they are limited in their ability to help researchers understand the underlying behavioural mechanisms that lead to observed space-use patterns. Based on spatially-explicit behavioural observations from coyotes *Canis latrans* in Yellowstone National Park, Wyoming, we estimated resource selection for specific behaviours (i.e. predatory, laying and travelling) and for all used locations irrespective of behaviour, to test whether resource selection is behaviour-specific and not generalizable across behaviours. Behaviour-specific models differed significantly from the model not partitioned by behaviour. In particular, the predatory model identified selection for mesic-meadows which have previously been documented to have high small-mammal abundance. The non-partitioned model, however, showed avoidance of this vegetation type. Our results show that resource selection differs between behaviours and suggest that standard techniques for estimation of resource selection might be of limited use for understanding the underlying behavioural mechanisms of space use. Future research should continue to improve on methods for partitioning fine-scale movement data obtained from telemetry collars into discrete movement bouts representative of different behaviours.

Key words: behaviour, coyote, resource selection, study design, use-availability

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Understanding space use by animals and how it relates to features in the environment is considered a prerequisite for most management actions directed at a population (Aarts et al. 2008). Estimates of resource selection are especially important for assessing and predicting the impacts of management actions or disturbances to the habitat of a population (Johnson et al. 2005, Doherty et al. 2008, Bleich et al. 2010). Obtaining these estimates is also important for identifying areas of potential habitat for translocating species (e.g. O'Brien et al. 2005) and for anticipating potential changes to the distribution of species or populations as a result of global climate change (e.g. Sharma et al. 2009).

Assessment of resource selection by wildlife has a long history in the ecological literature and as a result, considerable research has been directed at determining the best set of statistical methods for its measurement and estimation (Manly et al. 2002). Recently, however, greater research emphasis has been given to increasing the level of inference that can be gained through resource selection studies (Hebblewhite & Merrill 2008, Beyer et al. 2010, McLoughlin et al. 2010, Matthiopoulos et al. 2011). In particular, there is a desire to better understand the behavioural mechanisms underpinning habitat use (Beyer et al. 2010). By understanding how resource selection varies among behaviours, one can better

predict what impacts environmental perturbations will have on population space-use patterns (Beyer et al. 2010). Additionally, many researchers have highlighted the importance of linking resource selection with an individual's fitness (Aldridge & Boyce 2007, Arlt & Pärt 2007). Estimating resource selection for individual behaviours may help address this by identifying areas on the landscape selected for behaviours that have a greater bearing on fitness. Thus, understanding variation in selection by behaviour can help make management efforts more effective.

Studies comparing landscape characteristics at used sites (regardless of behaviour) to those at random sites are informative but provide limited information on the underlying behaviour leading to the observed space-use patterns. Indeed, these studies are appropriate when the purpose is to understand general patterns of species occurrence in the landscape, but given that some behaviours are performed by animals more frequently than others, results of resource-selection studies could be biased towards more frequent behaviours. Even when the goal of the study is to understand general patterns affecting the occurrence of a species in the landscape, the temporal or spatial scale at which the analysis is conducted can dramatically change the results (Mayor et al. 2009). Given that behaviours occur at different spatial and temporal scales it is important to know how resource selection differs between behaviours if we want to understand behavioural mechanisms underlying space use.

Numerous methods currently exist for partitioning animal movement paths into discrete movement types from which behaviour is inferred (Johnson et al. 2002, Jonsen et al. 2005, Barraquand & Benhamou 2008, Löttker et al. 2009, Moorter et al. 2010, Hanks et al. 2011). Based on these partitions, researchers have determined how resource selection differs between movement types (e.g. Johnson et al. 2002, Frair et al. 2005). These studies tend to find differences in resource selection between movement types but often assume what behaviour the movement type represents (e.g. foraging and migration). Given that most movement data are collected remotely, it is typically not possible to know if a movement type is correctly classified as a given behaviour, or the rates that movement types are misclassified as a given behaviour. Thus, to adequately show how results of resource selection studies differ when data are partitioned by behaviour, we require spatially-explicit behavioural observations.

Given that different resources are likely required

for the fulfilment of different behaviours, one would expect selection for habitat attributes to differ between behaviours (Beyer et al. 2010). Thus, we determined if resource selection is behaviour-specific and not generalizable across behaviours based on a set of spatially-explicit behavioural observations from coyotes *Canis latrans* (Gese et al. 1996a,b). This is important for understanding the limitations of standard approaches to estimating resource selection especially when attempting to improve our understanding of the behavioural mechanisms underlying space-use patterns of populations and their link to individual fitness.

Methods

We used spatially-explicit behavioural observations of coyotes in the Lamar Valley of Yellowstone National Park, Wyoming, collected during 1991-1993 (Gese et al. 1996a,b). We made observations from a vehicle or observation points on hills overlooking coyote territories during daylight hours with a 15x30 spotting scope. Based on these observations, we identified on a topographic map their location to within 10 m and then determined their respective UTM coordinates. We observed individually marked coyotes (i.e. using radio-collars and ear tags) or distinguishable adult coyotes (N = 28) based on physical markings, so observations are specific to individuals. For a more detailed description of the observation methods see Gese et al. (1996a,b).

We restricted our analysis to observations obtained during gestation (i.e. 16 February - 15 April) within each pack's respective territory. We delimited territory boundaries based on the location of behavioural observations consistent with defence of territorial borders as described in Shivik & Gese (2000). We also only used data from four of five coyote packs in the Lamar Valley because observations obtained from the fifth pack were biased towards one side of their territory due to unequal visibility. We classified observations into five general behavioural categories: predatory, travelling, marking, laying and other. In this analysis, we restrict observations classified as predatory, laying or travelling only. Based on the definitions of Gese et al. (1996a) we defined the three behaviours as follows: laying as any time a coyote was laying on its side with its head up and alert, or with its head down; travelling as any time a coyote was walking, trotting or running, even if occasionally stopping to check its sur-

roundings; and finally, we defined predatory behaviour as any pursuit of a prey item, including orienting, stalking, searching, chasing or capturing a prey, but not including the time spent travelling between predation attempts.

We generated 10 random locations per observed location, restricted to within the territory in which the observed point was located. We restricted used and random locations to within territory boundaries because the majority of coyote activity is restricted to within territories, and it is difficult to objectively define what area is 'available' to coyote outside their territory boundaries. We used the same random locations for all models.

Although all of the models we analysed are in a use-availability framework, for simplicity we refer to the model that does not partition used locations by behaviour as the use-availability model and all other models as behaviour-specific models. For all models, we extracted the vegetation type, elevation (available at: <http://ned.usgs.gov/>) and distance to roads. We reclassified the LANDFIRE vegetation map (available at: <http://landfire.cr.usgs.gov/>) for Lamar Valley into seven vegetation types (i.e. forest, grassland, road, sagebrush, mesic shrub-meadow, riparian and mesic-meadow) to match the types used by Gese et al. (1996a,b). We used forest as the reference vegetation class for the analysis. We made sure our sample of available points adequately captured the availability of each variable across the study area by calculating 'species-area' and observing that each reached an asymptote.

We used mixed-effects logistic regression, with a random intercept for pack to estimate how vegetation, elevation and distance-to-road related to the relative probability of use, or relative probability of a behaviour occurring. For the use-availability model, our sample of used points was all coyote observations irrespective of behaviour. For behaviour-specific models, we only used locations classified as a given behaviour as our sample of used locations for the model. We tested between inclusion of an additional intercept term for individuals or individuals nested within packs. Neither improved model fit based on Akaike Information Criteria (AIC; Burnham & Anderson 2002) as the majority of the variation was between packs and not individuals. Thus, we only report results from models with a random intercept for packs. We standardized elevation and distance to road covariates to aid in model convergence (Zuur et al. 2009). We also estimated variance inflation factors (VIF) for elevation and distance to

road and ensured that there was no evidence of collinearity (i.e. $VIF < 3$; Zuur et al. 2009). We estimated selection functions with the lmer function in the lme4 package (Bates 2007) in R (R Development Core Team 2010) and used AIC to select the most parsimonious model. Because the goal of our study was not to find the best models describing coyote resource selection, but rather to highlight differences in results when used points are partitioned by behaviour, we did not perform model validation (e.g. k-fold cross validation) on our models.

Results

Of the 1,246 coyote locations obtained during gestation and used in this analysis, 378 were classified as predatory, 431 as laying and 437 as travelling. We obtained an average of 45 (SD = 44) observations from each coyote and 312 (SD = 107) for each pack.

The best use-availability model (Table 1) retained all covariates, however, not all coefficients for vegetation type differed from selection of forest patches (Table 2). Only patches of sagebrush and road had coefficients different from forest patches, with both being avoided (see Table 2). The model also indicated avoidance of high elevation areas and areas closer to the road through Lamar Valley (see Table 2).

The best predatory model retained all variables in the final model except distance to road (see Table 2), although the full model was marginally competitive (i.e. $\Delta AIC < 2.0$; see Table 1). All but two types of vegetation patches were selected at the same level as forest patches. Selection for road was significantly lower than for forest, but patches of mesic-meadow had significantly higher selection for predatory behaviour (see Table 2). Additionally, higher elevation sites were avoided.

The best model for laying behaviour was the full model. There was negative selection for high elevation sites and areas close to road for laying (see Table 2). Patches of mesic-meadow, riparian, road and sagebrush were selected at levels significantly lower than patches of forest, whereas all other vegetation types had equal selection as forest.

Finally, the best model for travelling behaviour did not include vegetation type as a model covariate unlike all other models. The only variables retained in the final model were elevation and distance to road, indicating avoidance of high elevation sites and areas closer to the road (see Table 2).

Table 1. Model selection scores for all resource selection models considered in analysis, including AIC weights (w) based on data from coyotes in Lamar Valley, Yellowstone National Park, during 1991-1993. Variables included are distance to road (Road), elevation (Elev) and vegetation type (Veg). The use-availability model contained all used locations, whereas the behavioural models (i.e. predatory, laying and travelling) only contained used locations classified as a given behaviour.

Parameters	Model											
	Use-availability			Predatory			Laying			Travelling		
	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w	AIC	ΔAIC	w
Road + Elev+ Veg	7037.6	0.0	1.0	2034.4	1.6	0.3	2443.3	0.0	0.9	2563.1	2.5	0.2
Road + Elev	7057.2	19.6	0.0	2046.5	13.7	0.0	2447.1	3.8	0.1	2560.6	0.0	0.8
Elev + Veg	7067.6	30.0	0.0	2032.8	0.0	0.7	2452.9	9.6	0.0	2589.4	28.9	0.0
Elev	7078.6	41.0	0.0	2044.5	11.7	0.0	2453.3	10.0	0.0	2586.4	25.8	0.0
Road + Veg	7669.7	632.1	0.0	2294.0	261.2	0.0	2685.0	241.7	0.0	2701.6	141.1	0.0
Road	7879.5	841.9	0.0	2421.1	388.2	0.0	2727.4	284.1	0.0	2757.9	197.3	0.0
Veg	7915.9	878.3	0.0	2358.8	326.0	0.0	2777.1	333.8	0.0	2795.7	235.1	0.0
Null	8354.7	1317.1	0.0	2537.4	504.5	0.0	2892.6	449.2	0.0	2932.8	372.2	0.0

None of the behavioural models indicated selection or avoidance for all of the variables in the use-availability model (see Table 2). The predatory model indicated stronger avoidance of high elevation areas than the use-availability model, and distance-to-road was not an important explanatory variable for where predatory behaviour occurred. Selection of vegetation types also differed between the predatory and use-availability models. The predatory model indicated significantly greater selection for mesic-meadows than forest whereas the use-availability model indicated mesic-meadows selected at similar levels to forest (see Table 2). Additionally, in the predatory model, selection for sage did not differ from forest, whereas in the use-availability model it was avoided (see Table 2).

The model for laying behaviour had similar coefficient estimates for elevation and distance-to-road as the use-availability model, but differed in a number of vegetation coefficient estimates (see Table 2). The

laying model indicated that riparian and mesic-meadow patches were selected significantly less than forest patches, whereas the use-availability model indicated no difference in selection (see Table 2).

The model for travelling behaviour differed most from the use-availability model with no selection or avoidance of particular vegetation types. Additionally, the travelling behaviour model showed lower avoidance of high elevation sites, and greater avoidance of areas close to the road compared to the use-availability model (see Table 2).

Discussion

Our results support the contention that resource selection differs between behaviours. All of the behaviour-specific models showed different patterns of resource selection than the use-availability model rather than simply changes in the magnitude of coef-

Table 2. Mixed effects logistic regression results for data from coyotes in Lamar Valley, Yellowstone National Park, during 1991-1993. The use-availability model contained all used locations, whereas the behavioural models (i.e. predatory, laying and travelling) only contained used locations classified as a given behaviour. All models used the same sample of available points.

Variable	Model											
	Use-availability			Predatory			Laying			Travelling		
	β	SE	P-value	β	SE	P-value	β	SE	P-value	β	SE	P-value
Intercept	-3.69	0.29	< 0.001	-4.95	0.54	< 0.001	-3.64	0.33	< 0.001	-3.29	0.20	< 0.001
Grassland	-0.11	0.24	0.639	0.06	0.46	0.896	-0.49	0.43	0.260	NA	NA	NA
Mesic meadow	0.02	0.13	0.890	0.67	0.25	0.009	-0.53	0.26	0.038	NA	NA	NA
Mesic shrub	-0.05	0.24	0.830	-0.00	0.49	0.993	0.16	0.38	0.665	NA	NA	NA
Riparian	-0.17	0.11	0.111	0.07	0.22	0.744	-0.50	0.17	0.004	NA	NA	NA
Road	-1.06	0.25	< 0.001	-1.42	0.62	0.023	-1.12	0.39	0.004	NA	NA	NA
Sagebrush	-0.34	0.11	0.001	-0.15	0.23	0.518	-0.42	0.17	0.014	NA	NA	NA
Elevation	-3.09	0.17	< 0.001	-5.16	0.43	< 0.001	-3.32	0.30	< 0.001	-1.96	0.19	< 0.001
Distance-to-road	-0.26	0.05	< 0.001	NA	NA	NA	-0.28	0.08	< 0.001	-0.41	0.08	< 0.001

ficient estimates. These results indicate that use-availability models not partitioned by behaviour are insufficient for understanding the underlying behavioural mechanisms of space use and can produce results opposite to those obtained specifically for those behaviours. This should not come as a surprise given that others have shown differences in the distribution of behaviour (Marzluff et al. 2001) and selection of different landscape attributes for different behaviours across home ranges (Willems & Hill 2009).

The differences in the results obtained from the predatory model and the use-availability model are especially compelling. The predatory model identified mesic-meadow as an important vegetation type for hunting whereas the use-availability model showed the opposite result. Interestingly, another study of coyotes in Lamar Valley identified mesic-grasslands as having the highest small mammal prey biomass (Moorcroft et al. 2006). Thus, our model of predatory behaviour correctly identified important small mammal hunting areas for coyotes. Had we simply relied on the use-availability model to infer importance of areas for coyotes, we would have entirely missed the importance of mesic-grasslands for hunting by coyote packs in the area. It should be acknowledged, however, that selection for hunting grounds likely differs depending on the type of species pursued (e.g. Lingle 2002); thus selection estimates for predatory behaviour may differ if broken down further by species.

Our study highlights the potential for mismanagement of wildlife populations to occur if landscape factors selected or avoided for specific behaviours are not considered. Others have encountered similar situations where ignoring behaviour-specific space-use patterns could be detrimental to populations. In their study of potential mitigation measures for destruction of spotted owl *Strix occidentalis* habitat, Bingham & Noon (1997) suggested that conservation of owl core areas would be sufficient to mitigate the destruction of other owl habitat because it was the area receiving the highest use. As Buchanan et al. (1998) correctly acknowledged, however, this could lead to serious mismanagement of the population because core areas do not necessarily encompass all of the 'important' areas for owls to perform their life history tasks. That is, without knowing where animals selected to perform all of their important behaviours (i.e. most influential to their fitness), simply relying on where animals most frequently occurred was insufficient to guide habitat conservation measures.

Numerous studies have documented the usually erroneous assumption that the intensity of habitat use is proportional to the importance of that area for wildlife (e.g. Van Horne 1983, Garshelis 2000, Beyer et al. 2010). As Garshelis (2000) noted, activities that require much time (e.g. resting) may be less important to an animal's fitness than activities of shorter duration (e.g. drinking). Problems with inferring importance from typical resource selection studies can be partially overcome by looking at behaviour-specific selection (Garshelis 2000, Beyer et al. 2010). Instead of identifying areas where animals are most likely to occur (which could be biased towards less important behaviours), behaviour-specific selection estimates can be used to locate areas with the highest probability of a given behaviour occurring. When coupled with the method introduced by Matthiopoulos et al. (2011) which allows for the estimation of selection with differing levels of availability, one could begin to understand thresholds required for specific behaviours to occur. Additionally, by understanding which features of the landscape individuals select to perform behaviours that have a large impact on their fitness (i.e. hunting vs laying), we can better grasp which environmental attributes are most directly linked to an individual's fitness.

We understand that obtaining spatially-explicit behavioural data suitable for behaviour-specific resource selection is likely difficult in most field settings. Even when individuals can be readily observed, obtaining a sufficient number of observations from a large enough sample of individuals is an extremely labour-intensive process. Therefore, we are not suggesting that everyone have spatially-explicit behavioural observations, but rather showing that a greater mechanistic understanding of space use can be obtained when behaviour is considered (Beyer et al. 2010). As noted earlier, numerous methods exist to partition fine-scale movement data into different movement types (e.g. Johnson et al. 2002, Barraquand & Benhamou 2008, Moorter et al. 2010). These techniques provide the best opportunity yet to help integrate behaviour into selection studies. Our results support the increased use of these methods even though some can be analytically challenging to implement.

Our study should encourage researchers to justify that results from a use-availability design are adequate for the questions being asked and level of inference desired. Future research should continue to improve on methods for partitioning fine-scale movement data into discrete movement bouts repre-

sentative of different behaviours, especially by combining movement data with other sources of behavioural information to ensure that behavioural classifications for movement types are accurate (e.g. activity sensors; Moorter et al. 2010). Future research should also focus on linking behaviour-specific selection to individual fitness. One could potentially relate individual survival or fecundity to how much area of high value habitat for important behaviours (e.g. predation) is available within individual territories. This could help better guide decisions on how to best manage the population. Finally, validation of behaviours derived from movement patterns is needed (Löttker et al. 2009), but should not discourage researchers from estimating resource selection for specific movement types when there is clear biological rationale for their use.

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