



## Featured Article

# Caribou Use of Habitat Near Energy Development in Arctic Alaska

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**ABSTRACT** Increasing demands for energy have generated interest in expanding oil and gas production on the North Slope of Alaska, USA, raising questions about the resilience of barren-ground caribou (*Rangifer tarandus*) populations to new development. Although the amount of habitat lost directly to energy development in the Arctic will likely be relatively small, there are significant concerns about habitat that may be indirectly affected because of caribou avoidance behaviors. Behavioral responses to energy development for wildlife have been documented, but such responses are often assumed to dissipate over time, despite scant information on the ability of animals to habituate. To understand the long-term effects of energy development on barren-ground caribou, we investigated the behavior of the Central Arctic Herd in northern Alaska, which has been exposed to oil development on its summer range for approximately 40 years. Using recent (2015–2017) location data from global positioning system (GPS)-collared females, we conducted a zone of influence analysis to assess whether caribou reduced their use of habitat near energy development, and if so, the distance the effects attenuated. We conducted this analysis for the calving, post-calving, and mosquito harassment periods when caribou exhibit distinct resource selection patterns, and contrasted our results to past research that investigated the responses of the Central Arctic Herd immediately following the construction of the oil fields. Despite the long-term presence of energy development within the Central Arctic Herd summer range, we found that female caribou exhibited avoidance responses to infrastructure during all time periods, although the effects waned across the summer. Caribou reduced their use of habitat within 5 km of development during the calving period, within 2 km during the post-calving period, and within 1 km during the mosquito harassment period; these areas were predicted to overlap 12%, 15%, and 17% of important calving, post-calving, and mosquito period habitat, respectively. During the calving period, the indirect effects we observed were similar to those observed in past research, whereas during the post-calving and mosquito periods, we detected avoidance responses that had not been previously reported. These findings corroborate a growing body of evidence suggesting that habituation to industrial development in caribou in the Arctic is likely to be weak or absent, and emphasizes the value of minimizing the footprint of infrastructure within important seasonal habitat to reduce behavioral effects to barren-ground caribou. © 2019 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

**KEY WORDS** barren-ground caribou, Central Arctic Herd, coastal plain, energy infrastructure, human disturbance, *Rangifer tarandus*, resource selection, zone of influence.

As the global demand for energy increases, infrastructure and activities related to oil and gas production are expanding (International Energy Agency 2015), with subsequent effects

on some wildlife populations (Northrup and Wittemyer 2013). The composition of energy development infrastructure is variable in different locations but often includes the construction of roads, wells, well pads, pipelines, and various support facilities, and associated activities (i.e., drilling, vehicle traffic). Although new infrastructure causes habitat loss and fragmentation, the area directly affected is often small relative to habitat that can be indirectly affected because of animal avoidance of development and related activities. Indeed, animals exhibit a variety of behaviors in response to development including large-scale displacement (Sawyer et al. 2006), altered patterns of movement (Dyer et al. 2002, Sawyer et al. 2013), and changes in habitat use

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and selection (Holloran et al. 2010, Beckmann et al. 2012, Northrup et al. 2015).

Although there is a growing body of literature on the behavioral responses of wildlife to energy development, little is known about how such behaviors may change over time. Often, there is an assumption that animals display the strongest response to development right after construction, gradually minimizing their reaction over time with subsequent exposure (Sawyer et al. 2017). Although such patterns of habituation have been observed for some species and development types (Thompson and Henderson 1998, Madsen and Boertmann 2008), investigators have also reported that habituation responses can be species-specific, weak, or even absent (Conomy et al. 1998, Côté et al. 2013). For example, Sawyer et al. (2017) reported that mule deer (*Odocoileus hemionus*) avoided energy infrastructure even after 17 years of exposure, exhibiting a stronger response to development at the end of the study period than they did during the initial construction phase. With energy infrastructure and activities continuing to expand into undeveloped landscapes, it is becoming increasingly important to quantify their effects on wildlife populations, and how such effects may vary across time.

As energy production increases in the United States, there is great interest in expanding oil and gas development on the North Slope of Alaska (Meier et al. 2014), raising significant concerns about the potential effects on barren-ground caribou (*Rangifer tarandus*). Caribou have high ecological, recreational, and economic value, and are a particularly important subsistence resource for Alaskans (Fall 2016). On the North Slope, caribou use coastal areas in the summer for calving, foraging, and as refuge from insects (White et al. 1975, Griffith et al. 2002, Wilson et al. 2012), the same areas targeted by industry for energy production (National Academy of Sciences 2003). Although caribou populations widely fluctuate in size, recent declines in 3 of 4 Alaska Arctic herds (Central Arctic, Teshekpuk, and Western Arctic herds have declined; Porcupine Herd has increased) have heightened interest in factors influencing their trends, and renewed questions about the resilience of caribou to expanding human disturbance. Currently, substantial development exists only within the summer range of the Central Arctic Herd (CAH), but new projects are currently being initiated and proposed within the summer ranges of the adjacent Teshekpuk and Porcupine caribou herds (Bureau of Land Management 2018a, b). Although habitat lost directly to energy infrastructure has been, and will likely continue to be, relatively small, wildlife managers and conservation practitioners are concerned about indirect habitat loss, displacement of caribou from important areas (e.g., calving grounds), the reduced ability of caribou to move between foraging areas and insect-relief habitat, and ultimately, their cumulative effects on caribou populations (Nellemann and Cameron 1998, Griffith et al. 2002, Cameron et al. 2005).

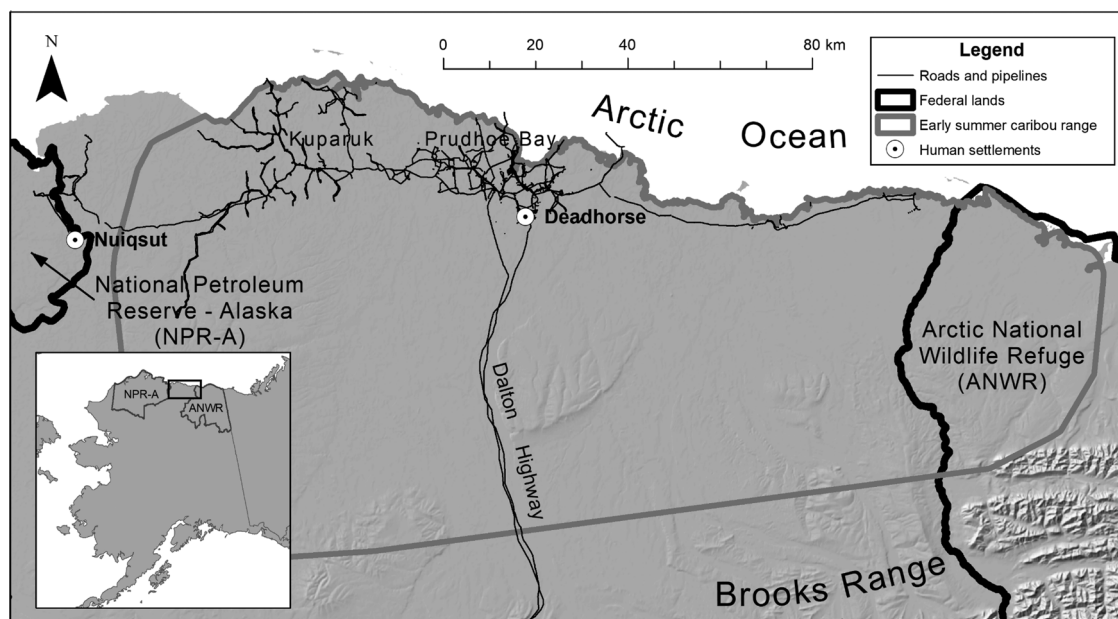
Within the CAH summer range, the above-ground footprint of oil development rapidly expanded in the 1970s and 1980s, with only modest increases during more recent years as a result of advances in directional drilling. Data collected in the late 1970s to early 1990s indicated that densities of calving caribou declined near infrastructure and as a

function of road density, calving grounds shifted away from infrastructure, and movements between foraging and insect-relief areas were inhibited by roads and pipelines (Smith and Cameron 1985; Dau and Cameron 1986; Cameron et al. 1992, 2005; Nellemann and Cameron 1998). Subsequent studies concluded, however, that caribou used elevated roads and well pads for insect relief (Pollard et al. 1996), and that summer caribou distributions were not strongly affected by energy infrastructure (Cronin et al. 1998, Noel et al. 2004). These conflicting reports have generated uncertainty about the long-term effects of energy development on caribou behavior and the ability of caribou to habituate to infrastructure in the Arctic, key issues for federal agencies analyzing the potential effects of new development projects (Bureau of Land Management 2018a, b).

To understand the long-term behavioral responses of barren-ground caribou to energy development, we examined summer habitat use patterns of caribou in the CAH relative to energy infrastructure after approximately 40 years of exposure. Our specific research objective was to determine whether caribou reduce their use of habitat near energy development, and if so, by what distance. Earlier studies of CAH behavior were largely based on aerial or road surveys, limiting the frequency (for aerial surveys) and spatial distribution (for road surveys) of data collection, and potentially inducing bias (Joly et al. 2006). To address these shortcomings, we conducted a zone of influence (ZOI) analysis (White and Gregovich 2017, Plante et al. 2018) using recent (2015–2017), fine-scale location data from global positioning system (GPS)-collared animals. Our analysis provides a contemporary snapshot of caribou responses to development and enabled us to evaluate those responses relative to past CAH research.

## STUDY AREA

The CAH early summer range occurs on the Arctic coastal plain, on the North Slope of Alaska (Fig. 1; 15,973 km<sup>2</sup>). The plain gradually rises from sea level along the coast to approximately 250 m at the edge of the foothills of the Brooks Range. The coastal plain is largely covered by thaw lakes and wetlands interspersed with ice-wedge polygons. The primary vegetation communities are wet and moist graminoid tundra, dominated by water sedge (*Carex aquatilis*) and cottongrass (*Eriophorum* spp.) with mosses and dwarf shrubs typically on hummocks. Summers are generally characterized as short, cool and moist, whereas winters are long, cold and dry, with annual precipitation averaging approximately 103 mm (<http://climate.gi.alaska.edu/Climate/Normals>, accessed 25 Oct 2019). Between 2010 and 2017, the average temperature in July (the warmest month) was 9.1°C and in February (the coolest month) was –24.2°C (Deadhorse weather station; [http://climate.gi.alaska.edu/acis\\_data](http://climate.gi.alaska.edu/acis_data), accessed 25 Oct 2019). The area is generally snow-free from June through September. Caribou are the dominant large herbivore on the coastal plain, although moose (*Alces alces*) and muskox (*Ovibos moschatus*) also occur in low densities. The primary predators of caribou are brown bears (*Ursus arctos*), wolves (*Canis lupus*), and golden eagles (*Aquila chrysaetos*). Lands used by



**Figure 1.** Central Arctic Caribou Herd early summer (1 Jun–15 Jul) range in northern Alaska, USA, based on a 100% minimum convex polygon of caribou collar locations, 2015–2017. Outside the federal land parcels, land is owned and managed by the State of Alaska.

CAH during early summer are primarily owned and managed by the State of Alaska and the United States Fish and Wildlife Service Arctic National Wildlife Refuge (Fig. 1).

In May, female caribou in the CAH typically migrate north from the Brooks Range to their calving grounds on the Arctic coastal plain. After calving in early June, they continue to move north towards the coast during the mid-summer period of mosquito (Family Culicidae) harassment, and then shift south towards the foothills of the Brooks Range later in the summer (White et al. 1975, Arthur and Del Vecchio 2009, Nicholson et al. 2016). In mid-September, caribou in the CAH migrate to winter ranges on the south side of the Brooks Range or remain on the coastal plain (Nicholson et al. 2016). Regular monitoring of caribou abundance in the CAH began in 1978 when the herd was estimated to be 5,000 animals. Abundance gradually increased until it was about 68,000 in 2010, and subsequently declined to about 28,000 in 2017 (Alaska Department of Fish and Game [ADFG] 2017, 2018).

Oil infrastructure within the CAH summer range is concentrated within approximately 25 km of the Arctic Ocean (Fig. 1) and consists of a network of roads, pipelines, well pads, processing stations and support facilities primarily operated by BP and ConocoPhillips. In addition to the oil fields, the CAH summer range is bisected by the Trans-Alaska Pipeline and Dalton highway (Fig. 1).

## METHODS

### Caribou Data

During 2015–2017, we captured adult female caribou in the CAH ( $\geq 2$  yr old) via net gun (Barrett et al. 1982) following protocols approved by ADFG's institutional animal care and use committee (protocols 2015-06, 2016-30, and 0019-2017-19). We conducted captures in April in 2015 and

2017, and late June in 2016, and attempted to mark a representative sample of female caribou in the herd. We fit caribou with GPS-satellite collars (Telonics, Mesa, AZ, USA) programmed to collect a location every 2 hours during summer (ADFG managed GPS-collar data).

For our analyses, we opted to use collar locations collected between 1 June and 15 July because this was when caribou in the CAH were commonly located within 20 km of development (Fig. S1, available online in Supporting Information), well within the distance they would be expected to exhibit any responses to development based on past research (Dau and Cameron 1986; Cameron et al. 1992, 2005). Additionally, this time frame encapsulated 3 different periods recognized by management agencies where caribou exhibit distinct behavioral patterns: calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul; Person et al. 2007, Wilson et al. 2012). All collared individuals in our analysis appeared to be exposed to energy infrastructure during early summer; the 100% minimum convex polygons (MCP) for each collared female each year (1 Jun–15 Jul) overlapped infrastructure.

We screened all locations to remove gross errors (i.e., outside Alaska) and faulty timestamps, which comprised  $<0.2\%$  of the data. We excluded data from a collared caribou in 2015 and another in 2017 that left the CAH and joined adjacent herds. In 2016, we collared 16 caribou at the start of the mosquito period; we excluded locations from the first week those animals were collared to reduce any capture-related effects.

### Characterizing Caribou Habitat and Energy Development

We assessed caribou responses in the CAH to different habitat variables irrespective of energy development, quantifying their selection for distance to the coast, topography

(i.e., elevation, aspect, slope), vegetation, and water. These factors have been associated with caribou resource use in previous studies (Walsh et al. 1992, Parrett 2007, Wilson et al. 2012) and depict general patterns in habitat conditions on the Arctic coastal plain. We characterized use and availability of different habitat covariates within 1-km<sup>2</sup> circular buffers of locations to account for landscape-scale selection, the high movement rates of caribou during summer (Person et al. 2007), and the large extent of the study area (Fig. 1; 15,973 km<sup>2</sup>).

Caribou often move towards the coast during periods of intense mosquito harassment because cooler, windier weather along the Arctic Ocean provides insect relief (White et al. 1975). We calculated the Euclidean distance (km) between the coast and the center of each buffer (corresponding to the location; Alaska State Geo-Spatial Data Clearinghouse; <http://www.asgdc.state.ak.us/?#2974>; 1:63,360 scale, accessed 1 Sep 2017). To characterize topography, we acquired elevation data from the United States Geological Survey (USGS) National Elevation Dataset (<http://www.usgs.gov>, accessed 23 Aug 2017; 25-m resolution), and derived slope and aspect (aspect was categorical: north, east, south, west, flat). We calculated the average elevation and slope within each buffer, and the dominant aspect class. To quantify spatial variation in the proportion of different vegetation communities, which represent forage opportunities in the vicinity, we used the coarse landcover classification developed by the Alaska Center for Conservation Science (Boggs et al. 2016; 30-m resolution). Within our study area there were 14 different classes; we combined bare ground and sparse vegetation into a single sparse category, and dwarf shrub and dwarf shrub-lichen into a single dwarf shrub category. For vegetation types that comprised  $\geq 4\%$  of the study area (dwarf shrub, herbaceous marsh, herbaceous mesic, herbaceous wet, low shrub, sparse, and tussock tundra; Table S1, available online in Supporting Information), we calculated the proportion of each type within the buffer around each location. Additionally, we used the Alaska Center for Conservation Science landcover classification to delineate pixels (100-m resolution) categorized as water (binary; 1 = water) because lakes are abundant along the coast and not generally used by caribou (Wilson et al. 2012).

To depict the footprint of energy development within the CAH summer range, we compiled digital spatial data from oil companies (BP, ConocoPhillips) and the Alaska government (Alaska State Geospatial Data Clearinghouse) detailing the locations of roads, pipelines, well pads, processing stations, and support facilities. We used the World Imagery base map from ArcMap 10.5 (Esri, Redlands, CA, USA) to manually digitize infrastructure around Point Thomson because digital spatial data were unavailable for that area. We excluded pads that had no recent activity (considered inactive; identified as being overgrown with vegetation and devoid of any equipment) from further consideration. These abandoned pads (10% of all pads) were primarily related to exploratory activities when the oil fields were initially developed in the 1970s and 1980s. Around all

active infrastructure ( $\sim 48.8$  km<sup>2</sup>, comprising 0.3% of the study area), we created nested concentric 1-km buffers ranging from 1 km to 20 km, to be employed in our ZOI analysis.

### Resource Selection Modeling

To conduct our analysis, we first developed and validated resource selection function (RSF) models (Manly et al. 2002, Koper and Manseau 2012) to predict caribou use based solely on ecological covariates not related to energy development. Habitat selection of Arctic caribou during the early summer (1 Jun–15 Jul) is dynamic (Fig. S1), shifting in response to calving, mosquito harassment, and forage conditions (Griffith et al. 2002, Parrett 2007, Wilson et al. 2012). To account for this variation, we modeled caribou selection separately for the calving, post-calving, and mosquito periods. For each period, we quantified population-level patterns of resource selection (second order; individual selection within the population range; Meyer and Thuiller 2006) using a use-availability design (Manly et al. 2002). We delineated available habitat for all periods as the 100% MCP around caribou locations collected from 1 June to 15 July (Fig. 1). We used a consistent area of availability to enable comparisons in resource selection across periods and because caribou are highly mobile and can easily travel within this area during early summer (Arthur and Del Vecchio 2009, Nicholson et al. 2016). We removed areas within the MCP that overlapped with the Arctic Ocean (bounding the north end of the study area). Within the population-level MCP, we randomly selected locations using a 1:10 ratio of those that were used to those considered available (Koper and Manseau 2012). We attributed habitat covariates to all used and available locations.

We developed RSF models (Manly et al. 2002) for each period using covariates representing distance to coast, topography, proportions of different vegetation types, and the presence of water. We used generalized linear mixed models (GLMMs; Bolker et al. 2009) with a logit-link function to accommodate our use-availability design. All models included a random effect for each animal-year data set (Gillies et al. 2006). Although the variance for the random effects in some post-calving and mosquito period models were estimated to be zero (indicating that they did not explain additional variation beyond that estimated by the residual variation), we retained the random effects structure in all models to facilitate model comparisons and reflect our study design. Prior to running models, we tested for multicollinearity among covariates using correlation coefficients ( $|r| \leq 0.6$ ) and variance inflation factors (VIFs;  $VIFs \leq 3$ ; Zuur et al. 2010). In all periods, elevation was correlated with slope and the proportion of tussock tundra ( $r \geq 0.63$ ), so we removed elevation from further analyses. The proportion of tussock tundra continued to have a high VIF ( $> 10$ ), so we also removed that variable from further consideration. After these removals, correlation coefficients were  $\leq 0.39$  and VIFs were  $\leq 2.24$ .

For each period, we tested all possible combinations of variables to determine the set of habitat factors that

exhibited the best model fit. Our habitat covariates included distance to coast, slope, aspect, the proportion of different vegetation types (models included either all vegetation types or none of them), and whether a pixel was classified as water. Our reference class for aspect (categorical variable) was north. For models with distance to coast or slope, we also tested models with quadratic terms for these variables to allow for nonlinear responses. We scaled continuous variables (all variables except aspect and water) to facilitate model convergence and the interpretation of relative effects (Schielzeth 2010). We used Akaike's Information Criterion (AIC) to score models, and identified the best performing model as having the lowest AIC score and highest model weight (Burnham and Anderson 2002). Because the top model for each period had an AIC value at least 6 units below the second-best model (and  $\geq 95\%$  of the model weight), we did not conduct model averaging. For modeling, we used the lme4 (Bates et al. 2015) and MuMIn (Barton 2016) packages in R version 3.5.2 (R Core Team 2018).

We validated the top model for each period using k-fold cross validation (Boyce et al. 2002), including all locations from each animal-year data set in either the model training or testing set (Koper and Manseau 2012). We used 5 folds and 10 bins, repeating the process 10 times to generate a mean Spearman correlation. For models with high predictive power (mean  $r_s \geq 0.70$ ), we calculated predicted probabilities of caribou resource selection across the study area (scaled between 0 to 1). We then used the contrast validation index (CVI; Hirzel et al. 2006, Fedy et al. 2014) to objectively determine an RSF probability threshold (in increments of 0.05, ranging between 0 and 1) for identifying habitats with high probabilities of use. This approach distinguishes an RSF threshold of the highest predicted probabilities of use that contain the maximum proportion of observed locations, while minimizing the proportion of the landscape that is included. We considered areas identified by the CVI during each period to be particularly important caribou habitat.

### Assessing the Influence of Energy Development on Caribou Behavior

We used coefficients from our top habitat selection models to generate spatial predictions of the relative probability of female caribou use during the calving, post-calving, and mosquito periods. For robust habitat models with high predictive power (i.e., mean  $r_s \geq 0.70$ ), these RSF predictions should be strongly correlated with patterns of observed caribou use in the absence of any development effects. Thus, we assessed patterns of observed and expected caribou use to determine whether the presence of development altered this expectation (White and Gregovich 2017, Plante et al. 2018). This approach is considered a quasi-treatment-control experiment given that caribou use in the absence of development can be estimated from patterns of habitat selection. We compared the proportion of observed caribou locations to those that would be expected from predictions of our habitat models within nested, concentric

1-km buffers that ranged from 0 to 20 km from infrastructure. We conducted calculations within 20 km of energy infrastructure because past research found that CAH responses to energy development occurred well within this distance (caribou densities declined within 4 km from development; Cameron et al. 1992, 2005).

For each 1-km buffer for each period, we calculated observed use as the number of used caribou locations within the buffer divided by the total number of used locations across all buffers (for that period). We calculated expected use as the summed relative probability of use (RSF volume) within each buffer divided by the total across all buffers (total RSF volume; period-specific), and then weighted by the animals' starting locations following White and Gregovich (2017). The weighting accounted for caribou exposure to development being dependent upon their general location and movement patterns within the study area (as development was patchily distributed). Within each period, for each animal-year data set, we determined the distance between an animal's starting location (their first location within the period) and all their other GPS locations. We then randomly simulated locations using those same distances from their starting location, but with random azimuths (i.e., radiating in random directions from the starting location), emulating animal-year-specific movement patterns. If a random point was generated outside the study area (i.e., in the Arctic Ocean), we regenerated the point. We calculated the distance to the nearest infrastructure for each random location and pooled those distances across individuals to estimate the proportion of locations within each 1-km buffer (0–20 km from infrastructure). We used the proportion of simulated locations within each buffer to weight the expected use value, such that expected use became a function of both habitat conditions and the likely distribution of caribou within the study area.

We then determined buffer-specific selection ratios (observed/expected use) for each period, where values  $< 1$  indicated that observed caribou use was less than expected, and values  $\geq 1$  indicated that use was equal or greater than expected. We used a non-parametric bootstrap approach to determine 95% confidence intervals for each selection ratio (Efron and Tibshirani 1993) based on randomly drawing (with replacement) used locations for each period. Bootstrapped selection ratios ( $n = 10,000/\text{period}$ ) were based on different samples of observed use, given the expected use. We considered the ZOI to be the distance from development where the selection ratios and 95% confidence intervals were consistently  $< 1$ . This approach is useful for quantifying specific thresholds in animal behavioral responses to habitat conditions, which can be difficult to identify directly from generalized linear models (Ficetola and Denoël 2009, Boulanger et al. 2012), even when disturbance covariates are incorporated (e.g., including a term for distance to disturbance in a GLMM). This approach also yielded results that could be evaluated in the context of earlier investigations of CAH densities within different 1-km distance intervals to development (Cameron et al. 1992, 2005; Cronin et al. 1998; Noel et al. 2004).

## RESULTS

Across the 3 years of the study, we fit 56 adult female caribou with GPS-collars, collecting 87 animal-year data sets: 16 in 2015, 27 in 2016, and 44 in 2017. During the calving and post-calving periods, we collected 71 animal-year data sets, and during the mosquito period, we collected 87 (because 2016 captures occurred in late Jun). Between 1 June and 15 July, we obtained 34,041 caribou locations: 11,390 during calving, 6,472 during post-calving, and 16,179 during the mosquito period. Across all periods, collars had a median fix rate of 84%. When fix rates are <90% there is a concern that locations may be missed as a function of specific habitat features (i.e., dense overstory vegetation) and introduce bias in resource selection studies (Frair et al. 2010). We obtained 100% of our programmed fixes (between 1 Jun and 15 Jul) from collars that were recovered from the field, indicating that our missing fixes were a function of errors in the Argos uplink transmission, not due to specific habitat features. Indeed, the Arctic coastal plain is relatively flat, with limited topographic relief, and low-growing tundra vegetation. As a result, we considered missing fixes to be random with respect to habitat attributes.

### Resource Selection Modeling

The best performing models for all periods included all habitat variables, with quadratic terms for distance to coast and slope ( $\Delta AIC \geq 6.1$  for second-best models; Table 1; see Tables S2–S5, available online in Supporting Information, for coefficients of top models and all modeling results). During the calving period, caribou most strongly selected for areas that were at intermediate distances to the coast (~50 km; Fig. 2A), had low slopes (<5 degrees; Fig. 2B), and had southern and eastern aspects (Fig. 3). Female caribou also strongly selected for areas with higher proportions of herbaceous mesic vegetation, and avoided areas with low shrubs, sparse vegetation, and water (Fig. 3). During the post-calving period, areas selected by caribou shifted towards the coast (with areas ~30 km from the coast having the highest probabilities; Fig. 2A). They similarly selected areas that had low slopes (<5 degrees; Fig. 2B), southern and

eastern aspects, and higher proportions of herbaceous mesic vegetation, and avoided water (Fig. 3). Although caribou avoided sparse vegetation (i.e., sand and gravel bars) during the calving period, they selected sparse vegetation during the post-calving period, probably in response to some early mosquito harassment (Fig. 3). During the mosquito period, caribou selected areas directly adjacent to the coast, with minimal slopes (<1 degree; Fig. 2A,B). Although they still selected areas with higher proportions of herbaceous mesic vegetation, their selection for distinct vegetation types generally dampened (Fig. 3). Similar to the post-calving period, caribou selected for areas with sparse vegetation and avoided water. Whereas caribou selected most strongly for southern aspects during the calving and post-calving periods, they selected most strongly for eastern aspects during the mosquito period.

The top model for each summer period (Fig. 4) validated well with mean Spearman's rank correlations  $\geq 0.91$  (Table 1). The CVI analysis identified threshold RSF values of 0.15 for the calving period and 0.10 for the post-calving and mosquito periods. For each period, these threshold values delineated large portions of the study area (3,859–7,475 km<sup>2</sup>) that were required to encompass a majority of the observed caribou locations (68–93%; Table 2; Fig. S2, available online in Supporting Information).

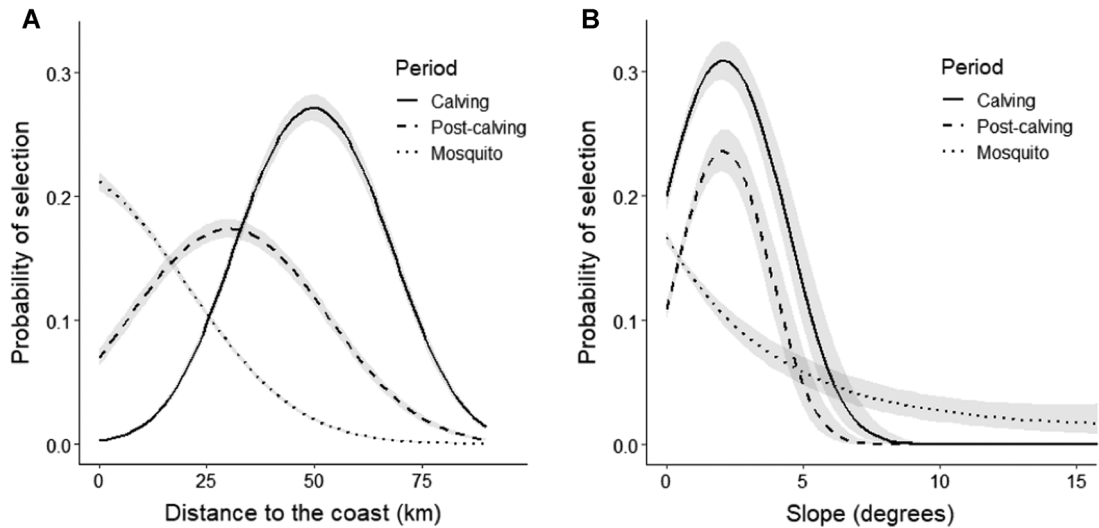
### Caribou Behavioral Responses to Energy Development

Based on buffer-specific selection ratios, the ZOI (where the selection ratios and their 95% CIs were consistently <1) was estimated to be 5 km during the calving period, 2 km during the post-calving period, and 1 km during the mosquito period (Table 2; Fig. 5; Table S6, available online in Supporting Information). Selection ratios for the mosquito period were high for distance intervals >12 km (Fig. 5C) where proportions of expected use were very small (<0.01). Based on the CVI analysis (Fig. S2), the ZOI during the calving period overlapped 12% of important calving habitat, the ZOI for the post-calving period overlapped 15% of important post-calving habitat, and the ZOI for the mosquito period overlapped 17% of important mosquito period habitat (Table 2).

**Table 1.** Model selection criteria for female caribou resource selection during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito periods (25 Jun–15 Jul) in the Central Arctic Herd, Alaska, USA, 2015–2017. Model covariates included distance to coast (coast), slope, aspect, water, and proportions of different vegetation types (veg; dwarf shrub, herbaceous marsh, herbaceous mesic, herbaceous wet, low shrub and sparse). We present the log-likelihood (LL), Akaike's Information Criterion (AIC), and weight for each model. We provide the top 2 models for each period; no other models had  $\Delta AIC$  values <10. We also include the mean cross validation correlation ( $r_s$ ) for each top model.

Model	<i>n</i>	Groups <sup>a</sup>	df	LL	AIC	$\Delta AIC$	Weight	$\bar{x}$ $r_s$
Calving								
Coast+coast <sup>2</sup> +slope+slope <sup>2</sup> +aspect+water+veg	125,290	71	17	-27,880.0	55,794.0	0.0	1.00	0.91
Coast+coast <sup>2</sup> +slope+aspect+water+veg	125,290	71	16	-27,951.3	55,934.5	140.5	0.00	
Post-calving								
Coast+coast <sup>2</sup> +slope+slope <sup>2</sup> +aspect+water+veg	71,192	71	17	-18,228.4	36,490.8	0.0	1.00	0.98
Coast+coast <sup>2</sup> +slope+slope <sup>2</sup> +aspect+veg	71,192	71	16	-18,292.6	36,617.2	126.4	0.00	
Mosquito								
Coast+coast <sup>2</sup> +slope+slope <sup>2</sup> +aspect+water+veg	177,969	87	17	-44,957.8	89,949.6	0.0	0.95	0.97
Coast+coast <sup>2</sup> +slope+aspect+water+veg	177,969	87	16	-44,961.8	89,955.7	6.1	0.05	

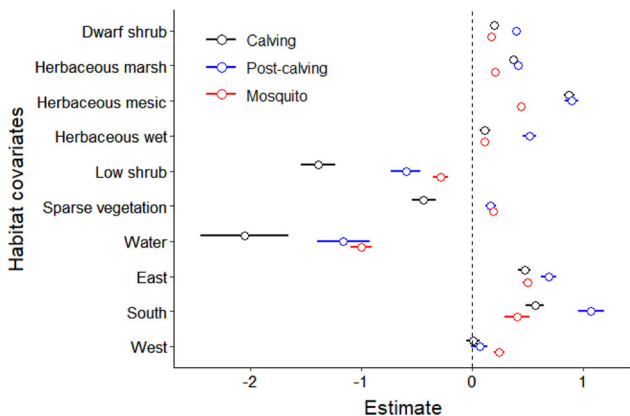
<sup>a</sup> The number of animal-year data sets included in the modeling.



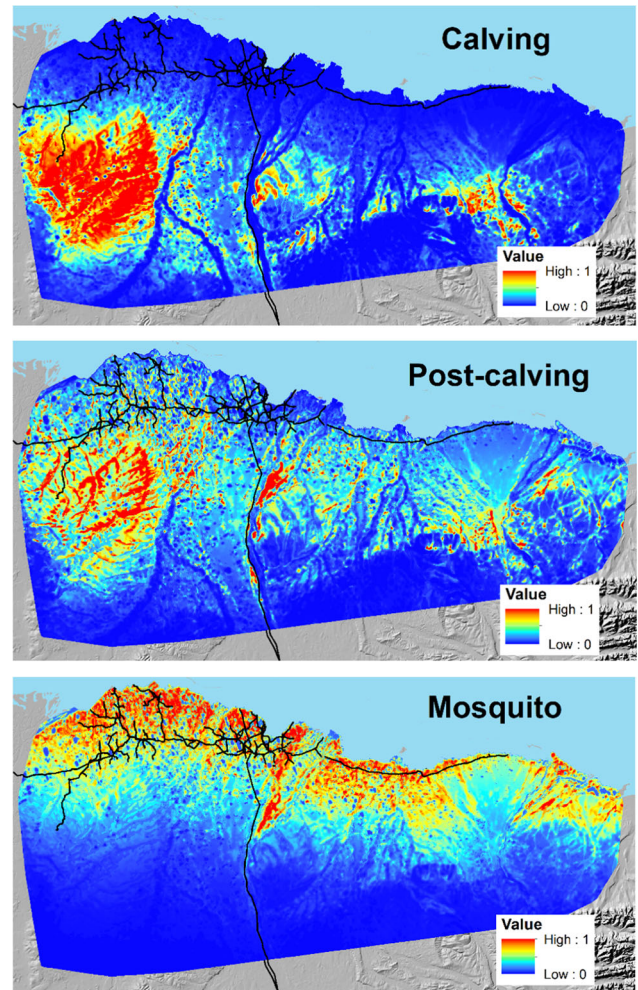
**Figure 2.** Female caribou relative probability of selection (and 95% CIs) for distance to the coast (A) and slope (B) during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. We held all other covariates from the top models at their mean values for used locations.

## DISCUSSION

Despite the long-term presence of energy development within the CAH summer range, female caribou reduced their use of habitat near infrastructure during all the time periods we examined, although the effects waned across the summer. Caribou avoidance of infrastructure was strongest during the calving period, and similar to results from past studies conducted immediately post-construction. For example, in the years following the initial development of the Kuparuk oil field (1982–1987), helicopter transect surveys were conducted during the calving season to assess caribou densities within different 1-km intervals from infrastructure. Investigators reported that densities were less than expected within 4 km of infrastructure (Cameron et al. 1992, 2005). Approximately 30 years later, calving females reduced their use of habitat within 5 km of infrastructure, with observed use being, on average, about half of what was expected (Fig. 5A; Table S6).



**Figure 3.** Coefficients and 95% confidence intervals (where visible) for female caribou selection of different proportions of vegetation types, water (binary), and aspects (categorical, with north as the reference class) during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. We standardized values for proportions of vegetation types.



**Figure 4.** Predicted resource selection probabilities (based on habitat attributes not related to energy development) for female caribou during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. Black lines depict infrastructure associated with energy development (e.g., roads, pipelines, pads).

**Table 2.** Summary statistics for each caribou period including the zone of influence (ZOI) of energy development estimated for female caribou, the number of observed locations used to calculate the ZOI, the resource selection function (RSF) threshold value used to identify important seasonal caribou habitat, the area encompassed by the threshold value, the proportion of caribou locations contained by the threshold, and the proportion of important seasonal habitat within the ZOI. We provide statistics for the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito periods (25 Jun–15 Jul) in the Central Arctic Herd, Alaska, USA, based on collar data collected during 2015–2017.

Season	ZOI (km)	Number of observed locations <sup>a</sup>	RSF threshold value	Area within threshold (km <sup>2</sup> )	Proportion of locations contained	Proportion of important habitat within ZOI
Calving	5	6,474	0.15	3,859	0.82	0.12
Post-calving	2	4,810	0.10	4,627	0.68	0.15
Mosquito	1	14,825	0.10	7,475	0.93	0.17

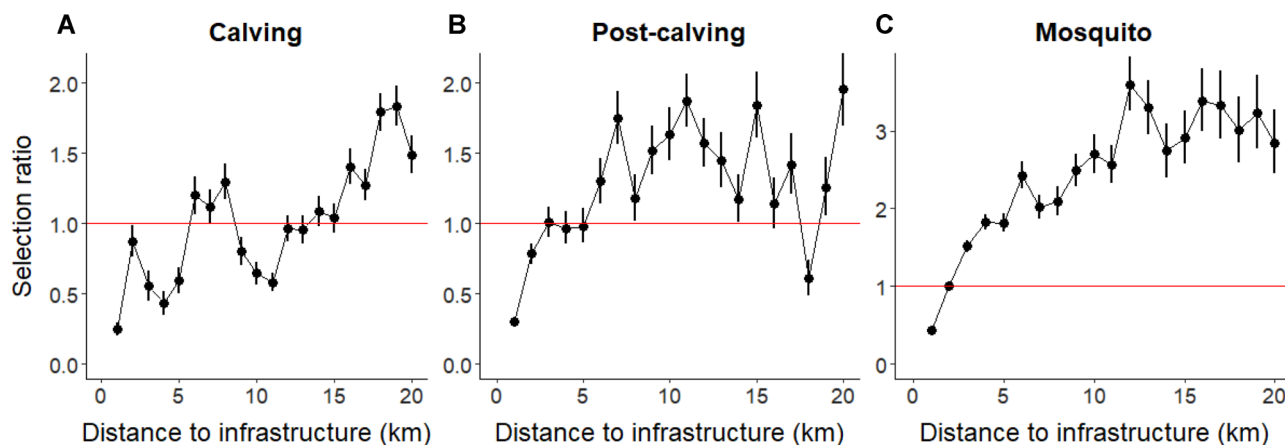
<sup>a</sup> Number of observed locations within 20 km of energy development.

Habituation occurs when there is a waning of a behavioral response over time as a result of repeated stimulation (Thorpe 1963), a process that does not appear to have occurred for caribou in the CAH during the calving period. These results are consistent with findings from other Arctic caribou herds, where habituation to anthropogenic development has been weak or absent (Boulanger et al. 2012, Johnson and Russell 2014). Although some ungulate populations have exhibited stronger avoidance responses to energy development over time (Sawyer et al. 2017), we suspect that the slight increase we observed from past studies partially reflects a shift in the calving distribution (Cameron et al. 1992). In the early 1980s, caribou largely calved in areas close to the coast that were subsequently developed (Cameron et al. 2005). As development expanded, the distribution of calving females shifted inland, reducing the number of calving caribou close to infrastructure (Noel et al. 2004). Such abandonment of habitat close to energy development has been similarly observed for pronghorn (*Antilocapra americana*; Beckmann et al. 2012) and mule deer (Sawyer et al. 2006) on their winter ranges.

Although caribou also reduced their use of habitat near infrastructure during post-calving and mosquito periods, their responses were weaker (2 km and 1 km, respectively) than during the calving period, likely because of increasing mosquito harassment. Mosquito harassment largely drives caribou behavior during mid-summer when caribou increase

their movement rates and travel to cooler, windier areas along the coast for relief (White et al. 1975, Cameron et al. 1995, Pollard et al. 1996), areas that also happen to be close to energy development (Fig. 4). In the past, mosquito harassment typically began during late June, although earlier spring phenology in the Arctic is causing mosquitoes to hatch earlier (Culler et al. 2015) such that harassment now begins during the post-calving period in some years. As the severity of mosquito harassment increases across the summer, we suspect that caribou cannot afford to be strongly risk averse (Frid and Dill 2002); they must traverse the oil fields to access insect-relief habitat near the ocean (Fig. 4). As our findings demonstrate, however, caribou use of developed landscapes does not imply that infrastructure has no influence on their behavior, just that the distance it appears to alter their behavior is reduced. Similar patterns have been observed in bison (*Bison bison*) and mule deer, where avoidance of human activity or infrastructure declines during late winter or severe winters, when animals are presumed to be experiencing additional stress (Hayward et al. 2015, Sawyer et al. 2017). Responses of female caribou to development may also have waned across the summer as a function of their calves getting older. Stankowich (2008) reported that female ungulates with more vulnerable offspring were most sensitive to disturbance.

Although our work corroborates research on caribou responses to development during the calving period, it



**Figure 5.** Selection ratios (and 95% CIs where visible) of female caribou (observed/expected use) within 1-km distance intervals from energy infrastructure during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. The red lines indicate the value where observed caribou use equals expected use. Note that during the mosquito harassment period, intervals  $\geq 8$  km from development had very low proportions of expected use ( $<0.02$ ).



contradicts past studies conducted during the post-calving and mosquito periods. For example, Cronin et al. (1998) modeled summer (mid-Jun to mid-Aug) caribou numbers as a function of distance to infrastructure and other covariates and concluded that caribou distributions were not influenced by the presence of development. They failed to detect significant relationships between caribou distributions and any covariate, even distance to coast, despite its known importance in predicting summer habitat use (White et al. 1975, Pollard et al. 1996). Similarly, Noel et al. (2004) reported no influence of roads on caribou densities during late June through mid-August (although they failed to account for new development within their study area; Joly et al. 2006). We suggest that the results of these studies were likely confounded by their analysis periods. Both studies evaluated caribou locations collected across a 6–8-week period when their use of different areas is highly dynamic, as caribou move between coastal insect-relief areas and inland foraging areas (Figs. 2–4, S1; White et al. 1975, Parrett 2007, Wilson et al. 2012). Furthermore, both studies failed to account for spatial heterogeneity in habitat conditions relative to energy development, and how it shifts across the summer (Fig. 4). We suspect that these shortcomings diminished the ability of these studies to accurately estimate caribou responses to infrastructure, emphasizing the importance of quantifying caribou responses within periods when behavior is relatively consistent and after accounting for spatial variation in habitat quality.

Caribou selection for different habitat covariates (i.e., distance to coast, topography, vegetation, and water) was dynamic across the 3 periods we evaluated (Figs. 2–4). Some of the patterns we observed were similar to past research on caribou herds in Arctic Alaska, and some patterns were unique. Comparable to past research on the CAH and the neighboring Teshekpuk Herd, caribou moved towards the coast during mid-summer when insect harassment was high (Fig. 2; White et al. 1975, Pollard et al. 1996, Wilson et al. 2012). This behavior is different from caribou in the nearby Porcupine Herd, which typically move up into the foothills and mountains of the Brooks Range for insect relief (Walsh et al. 1992, Russell et al. 1993), likely because of their proximity to higher elevations relative to other herds. Whereas monitoring data collected on the CAH in the early 1980s reported that calving grounds were located adjacent to the coast (Cameron et al. 2005), our results mirrored patterns in more recent studies where calving grounds were located inland, south of the oil fields (Fig. 4; Arthur and Del Vecchio 2009, Nicholson et al. 2016). Similar to the Teshekpuk and Porcupine caribou herds, caribou in the CAH selected for herbaceous mesic vegetation during the calving period (Fancy and Whitten 1991, Wilson et al. 2012), and reduced their selection for wetter vegetation types during the mosquito harassment period (Walsh et al. 1992, Parrett 2007, Wilson et al. 2012). Caribou in the CAH also increased their selection for sparse vegetation during the post-calving and mosquito periods, presumably in response to greater insect harassment, whereas caribou in the Teshekpuk Herd avoided that land cover type until later

in the summer (Wilson et al. 2012). Disparities between the CAH and other caribou herds may be partly due to different compositions and juxtapositions of land cover types within their respective ranges.

Investigators have raised concerns that indirect losses of habitat could reduce access to key foraging areas, and ultimately, have demographic consequences for the CAH (Nellemann and Cameron 1998, Cameron et al. 2005). During the short Arctic summer, caribou must regain and amass body stores that can be used for the subsequent winter and reproductive season (Barboza and Parker 2008, Taillon et al. 2013). As a result, White (1983) suggested that even minor declines in nutrients could have multiplier effects on body condition, survival and reproductive success. Recent research reported that nitrogen, which is likely limiting for caribou (Barboza et al. 2018), is highest early in the summer on the coastal plain, emphasizing the importance of this area for early summer foraging (Barboza et al. 2018, Johnson et al. 2018). Depending on the period, we found that caribou use was reduced in significant portions of important habitat areas; the ZOI overlapped with 12% of important calving habitat (based on our CVI analysis), 15% of post-calving habitat, and 17% of mosquito habitat, respectively. Despite these potential reductions in forage accessibility, major changes in the population size of CAH appear unrelated to changes in development. For example, when energy development expanded around Prudhoe Bay during the 1980s and 1990s, the CAH population increased from about 5,000 to approximately 28,000 individuals (Cameron et al. 2005). Recently, the CAH population declined from approximately 68,000 in 2010 to about 28,000 in 2017 (ADFG 2018), years when energy infrastructure and activities were relatively consistent. These patterns suggest that non-development factors (e.g., forage quality, weather, emigration) have been the primary drivers of major population trends, even though other studies have demonstrated that development appears to have some measurable effects. For example, Cameron et al. (2005) reported that between 1988 and 1994 parturition rates were lower and reproductive pauses higher for females in the western portion of the CAH summer range where development was concentrated, compared to the eastern portion of the range where development was minimal. Lenart (2015), however, reported no significant differences in parturition rates between the 2 areas using data collected between 1997 and 2014. Arthur and Del Vecchio (2009) also compared caribou calving parameters between western and eastern portions of the CAH range and reported that calves in the west (with increased development) were smaller and lighter than those born in the east but that survival rates did not significantly differ. These studies indicate that additional fitness investigations of the CAH may be warranted, particularly given that the influence of energy development may be dependent on variation in environmental conditions or herd density (e.g., reduced forage accessibility may be important only when herd abundance is high). Indeed, anthropogenic effects on wildlife populations can be weak or variable (Hansen et al. 2005, Harju et al. 2010) and an

increasing number of studies have linked expanding energy infrastructure to reduced vital rates and abundance in ungulate populations (Christie et al. 2015, Johnson et al. 2017, Sawyer et al. 2017, Peterson et al. 2018).

Our study quantified broad-scale avoidance responses of female caribou to energy development, but there were key limitations of our analyses that are important to recognize. For example, we combined all types of infrastructure (e.g., roads, pads, pipelines) into a single footprint of development, and thus were unable to discriminate fine-scale responses of caribou within the oil fields. Murphy and Curatolo (1987) reported that caribou were more likely to cross a single structure (pipeline or road) than multiple adjacent structures (e.g., pipelines situated adjacent to roads), and Cameron et al. (1995) noted that pipelines constructed <1.0 m above the ground were largely barriers to caribou movement, whereas those elevated to a height of >1.5 m could allow movement. Given these observations, different infrastructure designs likely elicit distinct behavioral responses from caribou, which may be mediated by the surrounding habitat conditions. Because the spatial extent of our analysis was so large (encompassing all of the early summer range; Fig. 1) and distances to different development types were highly correlated within this area, our analytical approach was not appropriate for estimating infrastructure-specific responses. This is an important need for future work. Furthermore, our inferences are based on a recent snapshot of 3 years of caribou GPS-collar data, when the size of the herd had substantially declined (~28,000). It will be useful to investigate this issue for different herd sizes and foraging conditions in the future with additional years of data.

## MANAGEMENT IMPLICATIONS

Our work suggests that habituation to industrial development by Arctic caribou is likely to be weak or absent. Minimizing the influence of energy development on caribou behavior may be accomplished by reducing the overall footprint of development within key seasonal habitat areas and movement corridors. The long-term indirect effects of energy infrastructure are poorly understood but deserve additional study because they could reduce the carrying capacity of important seasonal ranges and potentially have demographic effects. Finally, given the dynamic nature of caribou resource selection across summer, our work highlights the importance of assessing behavioral patterns for distinct life-history periods, as animal responses could otherwise be masked.

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