COASTAL VEGETATION COMMUNITIES AFFECT MESOCARNIVORE ACTIVITY IN NORTHERN CALIFORNIA DUNE ECOSYSTEMS

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Abstract.—Dune restoration (i.e., removing invasive plant species) may influence mesocarnivore activity on the coastal dunes of Northern California. A previous study suggested mesocarnivores preferred restored areas where European Beachgrass (Ammophila arenaria) was removed over areas heavily vegetated with this invasive plant, but that study may have been confounded by distance to coastal forest. The aim of our study was to examine the effects of proximity to coastal forest and cover types on mesocarnivore activity in the coastal dunes. We deployed 20 motion-sensitive cameras for four weeks within the Ma-le’l Dunes Cooperative Management Area in Humboldt County, California, along transects that varied in local habitat composition and distance to nearby coastal forest. We treated photographs of the same species of mesocarnivore as separate detections if they were separated in time by at least 60 min, and we used the detection rate (total number of detections per number of viable camera checks) as an index of mesocarnivore activity. Model selection results indicate that both distance to forest and amount of Beach Pine (Pinus contorta contorta) habitat near a camera were important factors in mesocarnivore detection rates. We found a negative correlation between distance to forest and detection rate of mesocarnivores. Mesocarnivores may build their dens within the forest and enter the dunes to forage, thus their activity is likely highest close to the forest. Beach Pine stands may serve as cover for mesocarnivores as they forage within the dunes. By understanding these relationships, dune managers in this area can better evaluate management practices and invasive species removal.

Key Words.—Ammophila arenaria; camera traps; coastal dunes; European beachgrass; habitat use; Northern California; mesocarnivores

INTRODUCTION

Habitat and prey availability are factors that influence mesocarnivore habitat use (Ross et al. 2012). Invasive plants may change rodent predator avoidance behaviors and have influences up the trophic web (Johnson and De León 2015). In an experiment using artificial food trays, Johnson and De León (2015) showed that rodents may perceive less predation risk due to the cover provided by European Beachgrass (Ammophila arenaria, hereafter beachgrass), which can grow up to a meter in height.

Indeed, Delgado de la Flor and Johnson (2015) found that despite lower small mammal abundance in areas where invasive beachgrass had been removed, mesocarnivore activity was significantly higher in these areas, suggesting that habitat restoration could benefit the mesocarnivore community. However, the spatial extent of their study was constrained to make use of ongoing beachgrass removal, and they acknowledged that their results could have been confounded by the fact that the restored area was closer to coastal forest (Delgado de la Flor and Johnson 2015). Moreover, the dune landscape is a mosaic of several habitats, including small dense patches of Beach Pine (Pinus contorta contorta), dune mat (low-growing vegetation), and shrubs. Forests and densely vegetated habitats can provide important cover for mesocarnivores and could thereby affect their use of nearby open habitats, such as those in coastal dunes. Forest cover, type, and proximity are known to impact mesocarnivore habitat use in other areas (Lesmeister et al. 2015).

The term mesocarnivores refers to small to mid-sized mammalian carnivores (Roemer et al. 2009). Their diets typically include a broad variety of prey, and they far outnumber large specialist carnivores in abundance (Prugh et al. 2009; Roemer et al. 2009; Delgado de la Flor and Johnson 2015). They exhibit tremendous variation among species in terms of primary food, foraging style, and habitat associations. Within our study area in the coastal dunes of Humboldt Bay, Gray Foxes (Urocyon cinereoargenteus), North American Raccoons (Procyon lotor), and Striped Skunks (Mephitis mephitis) are common nocturnal mesocarnivores that prey on rodents (Delgado de la Flor and Johnson 2015). Feral Cats (Felis catus) are also a common introduced mesocarnivore to this area.

We examined the hypothesis that mesocarnivore activity in coastal dunes is positively influenced by forest habitats. We tested the predictions that mesocarnivore detection rates at camera traps decrease with increasing distance from coastal forest edge, and increase with increasing proportion of Beach Pine habitat within 50 m of cameras. We also sought to provide managers with an index of mesocarnivore species presence, including both native species and invasive Feral Cats. Understanding the mechanisms for apparent responses of mesocarnivores to habitat is valuable for biologists, conservationists, and managers who are concerned with habitat selection...
and quality, the long-term protection of this area, and continuing efforts to remove beachgrass and conserve native wildlife.

**Methods**

**Study site.**—We studied the mesocarnivore community in the Ma-le’l Dunes Cooperative Management Area (CMA) and the Lanphere Dunes of the Humboldt Bay National Wildlife Refuge located on the North Spit of Humboldt Bay near the town of Manila in Humboldt County, California, USA (Fig. 1). This area is managed by the U.S. Bureau of Land Management (BLM) and the U.S. Fish and Wildlife Service (USFWS). The dune landscape is a mosaic composed of six habitats. For the purpose of this study, we defined these unique habitats using information from Buell et al. (1995) and Pickart and Barbour (2007). From the ocean moving inland there are: (1) beach comprising the open strip of sand immediately adjacent to the ocean; (2) native foredune grassland comprising dunes running parallel to the beach with vegetated dune ridges dominated by the native grass *Elymus mollis mollis*; (3) dune mat habitat comprising a community of over 40 low-growing herbaceous and suffrutescents native plant species (Buell et al. 1995; Pickart 1988), including Coastal Sagewort (*Artemisia pycnocephala*), Beach Bur-sage (*Ambrosia chamissonis*), Pink Sand Verbena (*Abronia umbellata brevifolia*), and Beach Pea (*Lathyrus littoralis*; Sawyer et al. 2009; NatureServe 2005); (4) herbaceous wet swales that are dominated by Dune Sedge (*Carex obnupta*) and Pacific Silverweed (*Potentilla anserina*) and woody wet swales that are dominated by Coastal Willow (*Salix hookeriana*); (5) open dunes with little to no vegetation; and (6) dense forest stands dominated by Beach Pine, Sitka Spruce (*Picea sitchensis*), and Grand Fir (*Abies grandis*). To better understand the role of distance to forest as a confounding effect on mesocarnivore habitat use, our sampling design focused on mesocarnivore use of the dune mat habitat, which in some places is heavily invaded by beachgrass that commonly outcompete native plants. In the northern portion of the Ma-le’l Dunes CMA and Lanphere Dunes, beachgrass has been removed and the dune mat habitat restored. In this area, dune restoration has occurred and been maintained since the 1980s across more than 11.3 km of coastline in Humboldt and Del Norte counties (Pickart 2013; U.S. Fish and Wildlife Service. 2017. Dune Restoration - Humboldt Bay. Available at https://www.fws.gov/refuge/Humboldt_Bay/wildlife_and_habitat/DunesRestoration.html [Accessed 10 July 2017]).

**Sampling scheme.**—We deployed 20 cameras on two transects (10 cameras per transect) within our study area. The cameras varied in brand, with each brand present on each transect: StealthCam STC-G30NGK (StealthCam, Grand Prairie, Texas, USA); Trophy Cam® (Bushnell Outdoor Products, Overland Park, Kansas, USA); and Wild Game Innovations x4x (Wild Game Innovations, Grand Prairie, Texas, USA). The model type of each camera did not influence placement and we distributed model types haphazardly at the stations such that each camera model had a wide range of distance to forest and local habitat conditions. After deployment, we confirmed there were no differences in the distribution of camera models with respect to transect number, local habitat, or distance to forest. We set cameras to take three photos in a series, on high sensitivity, and to wait 60 s before the next series of photos. Transect 1 followed the crest of the foredune grassland and transect 2 was 100 m east of, and parallel to, transect 1. We placed cameras 200 m apart along each transect. We offset northing positions of camera stations in the two transects by 100 m to alternate the camera stations and minimize attracting an animal from one camera station to the next (Fig. 1). Although the two transects were parallel to each other, the meandering edge of the forest (dark green in Fig. 1) provided variation in distance from each camera station to the nearest forest edge both within and between the transects. The meandering edge of the forest also ensured that distance to forest was not simply the inverse of distance to shoreline, which is a straight edge parallel to the two transects. We measured the distance from each camera station to the nearest forest edge using images from Google Earth (Version 7.7.8.3036) and used these data to investigate the relationship between mesocarnivore activity and proximity to forest.

We avoided placing cameras near tall or thick vegetation to reduce false triggers. In the event that the proposed coordinates of a camera station were placed...
in thick vegetation, we moved the camera station to the closest open area within the dune mat. We mounted each camera on a rebar pole 0.5 m above the ground, facing north, and directed the camera at bait placed 3–6 m away. We baited each camera station with a 142 g can of chicken meat. We punched three holes into each can to attract mesocarnivores and we secured each can to the ground with four stakes.

We deployed cameras 28 September 2015 and retrieved them 30 October 2015. We checked all camera stations every 4 d over a period of four weeks. We exchanged memory cards and bait cans when checking cameras. In February 2016, we revisited each camera station location to assess the vegetation cover surrounding each station. We visually estimated the percentage cover of each of the six vegetation types (to nearest 10%) in each quadrant of a 50 m circle centered upon the camera station, then averaged the quadrants to yield the percentage cover within the 50 m radius.

Analysis.—After each camera check, we sorted the photographs from each camera to determine mesocarnivore activity and distinguish false triggers from actual mesocarnivore captures. We treated photographs of the same species of mesocarnivore as separate detections if they were separated by at least 60 min, and we used the detection rate as an index of mesocarnivore activity. In a few cases (see Results), cameras malfunctioned, so we used the total number of detections per number of viable camera checks as our index of activity. We used linear regression to compare detection rates over time. We analyzed the data in Program R using detection rate as our response variable in linear correlation models to test for the effects of distance to forest and amount of local Beach Pine habitat on mesocarnivore activity (R Developmental Core Team 2008). We performed analyses on all mesocarnivore species pooled, and species-specific analyses for Feral Cat, Striped Skunk, and Gray Fox (the three most commonly detected species). For each response variable, we created four a priori candidate models: detection rate as a function of distance to forest, percentage Beach Pine within 50 m radius, both factors, or neither (intercept only). We compared models using Akaike’s Information Criterion corrected for small sample size (AICc) and selected the best model based on the lowest AICc value (Burnham and Anderson 2003).

Results

There were two instances (of 160 camera checks) in which cameras failed either due to battery loss or positioning error. We excluded these sampling sessions from our analyses. Therefore, our results are based on 158 viable camera checks. There were 253 mesocarnivore detections on the cameras of which 36.4% were Feral Cat, 36.0% were Striped Skunk, 23.3% were Gray Fox, 4.0% were Virginia Opossum (*Didelphis virginiana*), and 0.4% were North American Raccoon. There were also several non-carnivore species detected, such as Black-tailed Jackrabbits (*Lepus californicus*), Common Raven (*Corvus corax*), and a number of unidentified bird and mice species. Detection rate did not significantly increase or decrease over the 28-d study period (eight checks, $F_{1,7} = 3.78, P = 0.100$).

The highly irregular forest edge provided a wide range of distances to forest among the 20 camera stations (165–543 m; mean ± SD = 387.6 ± 114.0 m). The percentage cover values of each of the six vegetation types ranged from 0–65% cover (16.7 ± 12.58%). There was a negative correlation between detection rate of all mesocarnivores and distance to forest ($r = -0.484, t = -2.344, df = 19, P = 0.031$), and a positive correlation with percentage of Beach Pine habitat within a 50 m radius ($r = 0.488, t = 2.370, df = 19, P = 0.029$). Analysis of these factors using the detection rate of individual species yielded correlations in the same directions, but were only significant for distance to forest and skunk detection rate ($r = -0.476, t = -2.294, df = 19, P = 0.034$) and percentage of Beach Pine and Feral Cat detection rate ($r = 0.570, t = 2.945, df = 19, P = 0.009$). The percentage of Beach Pine and distance to forest were not significantly correlated with each other ($t = -1.759, df = 19, P = 0.096$).

Model selection results indicate that both distance to forest and percentage of Beach Pine are important factors in mesocarnivore detection rates (Table 1). Although the single best model for total mesocarnivore detection rate included only distance to forest (Fig. 2), the models with Beach Pine were also competitive (within 2 AICc), and all fit the data more strongly than did the null model. The top model explained 34.3% of the null deviance. Distance to forest was also the single best variable for predicting the detection rate of Striped Skunks and Gray Foxes, though other models were also competitive. Percentage of Beach Pine within 50 m was the best
predictor of Feral Cat detection rate, and this model was the most competitive among the candidate set.

**DISCUSSION**

We hypothesized that mesocarnivore activity in coastal dunes is affected by nearby forest habitats. Our findings support this hypothesis. There was significantly more activity of mesocarnivores closer to the forest and also in places with high percentages of Beach Pine habitat within 50 m. Results were strongest for skunks and distance to forest, and for Feral Cats and percentage of Beach Pine. However, it is important to note that our results are entirely correlative and cannot confirm or refute causation. Additional studies involving telemetry would better reveal how mesocarnivore foraging behavior varies with distance to forest and local habitat in this study system.

Mesocarnivores may be attracted to the coastal forest strip and to patches of Beach Pine habitat because they provide access to cover and potential denning sites (Pineda-Guerrera et al. 2015). These species may leave the core of their home ranges in forest and pine patches to forage for prey, such as small rodents, that are known to inhabit the dunes (Elbroch and Allen 2013; Delgado de la Flor and Johnson 2015). The open dune habitat offers few if any denning sites, and most mesocarnivores probably rely on the forest for cover and dens. Because skunks have smaller home ranges than foxes, raccoons, and cats (Tucker 1988; Beasley et al. 2007; Horn et al. 2011; Rosatte et al. 2011), they may be less likely to travel farther from their core use areas in cover when foraging, which could explain why the effect of distance to forest was strongest for skunks in our study. Different microclimates within the habitats may also influence species habitat usage (Červinka et al. 2011).

Delgado de la Flor and Johnson (2015) concluded that restoring dune mat habitat by removing beachgrass likely increases mesocarnivore activity. However, our results suggest that some of their findings may be influenced by their study area, where restored dunes tended to be closer to forest habitats than unrestored and invaded habitats. Thus, we recommend future studies seek to further resolve this complexity, perhaps by using telemetry to track individual animals and determine their home range, habitat use, and visitation to cover habitats and dune mat vegetation.

Our intent was to obtain an index of activity, rather than estimate abundance or occupancy. Our camera stations were relatively close to each other (about 200 m), they were baited, and they were checked frequently (every 4 d) over a short time period (28 d). Therefore,

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**Table 1.** Model selection results for generalized linear models of remote camera detection rates for all mesocarnivores and individual mesocarnivore species as predicted by distance to coastal forest and the percent of Beach Pine habitat within 50-m radius of a camera. Data were collected from 28 September to 30 October 2015 in Ma-le’l Dunes Cooperative Management Area, Humboldt County, California, USA. First entries are top models in a candidate set, though in several cases other models were also competitive (within 2 AICc).

<table>
<thead>
<tr>
<th>Model</th>
<th>Deviance</th>
<th>AICc</th>
<th>wt</th>
<th>$r^2$</th>
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<tr>
<td>All mesocarnivores</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to forest</td>
<td>23.764</td>
<td>67.706</td>
<td>0.146</td>
<td>0.241</td>
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<td>Percent Beach Pine</td>
<td>23.998</td>
<td>67.902</td>
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<td>0.234</td>
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<td>Distance forest + Beach Pine</td>
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<td>67.982</td>
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<td>0.343</td>
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<td>Null (intercept only)</td>
<td>31.309</td>
<td>70.427</td>
<td>0.003</td>
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</tr>
<tr>
<td>Striped Skunk</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to forest</td>
<td>4.450</td>
<td>34.199</td>
<td>0.417</td>
<td>0.225</td>
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<tr>
<td>Distance forest + Beach Pine</td>
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<td>35.506</td>
<td>0.217</td>
<td>0.294</td>
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<tr>
<td>Percent Beach Pine</td>
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<td>35.342</td>
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<tr>
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<td>36.512</td>
<td>0.131</td>
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<tr>
<td>Feral Cat</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent Beach Pine</td>
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<td>33.754</td>
<td>0.706</td>
<td>0.327</td>
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<tr>
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<tr>
<td>Distance to forest</td>
<td>5.697</td>
<td>39.141</td>
<td>0.048</td>
<td>0.119</td>
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<tr>
<td>Gray Fox</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Distance to forest</td>
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<tr>
<td>Percent Beach Pine</td>
<td>2.567</td>
<td>23.200</td>
<td>0.113</td>
<td>0.023</td>
</tr>
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</table>
although our data structure is technically appropriate for an occupancy analysis, such an analysis is not informative because all stations were occupied (detected one or more mesocarnivores) and it is likely that the same individual carnivore was detected at more than one station. We could make better use of the data by analyzing variation in the number of detections, with the assumption that higher detection rates indicate greater mesocarnivore activity. With our design, it is possible that opportunistic individual animals cued into the array of baited camera stations. However, we detected no statistically significant trend in the detection rate over time.

Our results should only be interpreted within the limited spatial and temporal extent of our study. Different camera models may have introduced heterogeneity based upon different sensitivities between camera types. Our cameras were relatively close together, and in most cases, we could not identify individual animals. However, in one case we identified the same cat visiting multiple camera stations during our study. Therefore, our detection rate does not provide a measure of mesocarnivore abundance; rather, it serves as an index of mesocarnivore activity.

Mesocarnivores hold important ecological roles within plant and animal communities (Roemer et al. 2009). These species can have major influences on population sizes of birds, rodents, and other prey species, and understanding these relationships provides critical information for conservation planning (Cervinka et al. 2011). Our relatively high number of Feral Cat detections (36.4% of total mesocarnivore detections; although likely only a few individuals because a single animal likely visited multiple stations in a single night) is also noteworthy and was markedly higher than the recent study (only 11% of all detections; Delgado de la Flor and Johnson 2015). Along with Striped Skunk, detections of Feral Cats were the most numerous in our study. Our camera stations were at least 2.2 km from the nearest residential area suggesting that Feral Cats may penetrate into coastal dunes, or they may live there permanently. These cats likely influence numerous prey communities, rodents and especially ground-nesting birds. Future work should be aimed at understanding effects of this introduced predator in this system.

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