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Influence of Invasive European Beachgrass on Mesopredator Activity in the Coastal Dunes of Northern California

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Abstract.—Invasive species impact local flora and fauna directly and indirectly. The coastal dunes of Northern California have been altered by the introduction of the European Beachgrass *Ammophila arenaria*. Previous studies have shown that rodent abundance is higher in areas where the beachgrass dominates. This direct impact could prompt an indirect response in mesopredators that prey upon the rodents, but this hypothesis has not yet been examined in coastal dunes. We used camera traps to examine the activity of mesopredators in invaded dunes with very high density of beachgrass and in restored dunes with very low density of beachgrass, from March to September 2013. Our results indicate that the activity of the mesopredators was significantly higher in the restored habitat. Mesopredators may be more active in this area because of other available food and because the high cover of the beachgrass in the invaded habitat may render prey less accessible than in the more diverse and open restored area.

Influencia de la Hierba Invasora Barrón en la Actividad de los Meso-depredadores en las Dunas Costeras del Norte de California

Resumen.–Especies invasoras impactan la flora y fauna local en forma directa e indirecta. Las dunas costeras del Norte de California han sido alteradas por la introducción de la hierba barrón *Ammophila arenaria*. Estudios anteriores han demostrado que la abundancia de roedores es más alta en areas donde predomina el barrón. Esta interacción podría afectar indirectamente a los meso-depredadores que se alimentan de roedores locales; sin embargo, esta hipótesis aún no ha sido examinada en la dunas costeras. Usamos cámaras de visión nocturna para examinar la actividad de los meso-depredadores en dunas invadidas con alta densidad de barrón y en dunas restauradas con baja densidad de barrón de Marzo a Setiembre del 2013. Nuestros resultados indican que la actividad de los meso-depredadores fue significativamente mayor en el habitat restaurada. Los meso-depredadores podrían mantenerse más activos en el area restaurada ya que podría haber otro tipo de alimento disponible, y porque la alta densidad del barrón en las dunas invadidas les dificultaría el acceso a su presa.

Key Words.—Ammophila arenaria; competition; dunes; Gray Fox; mesocarnivore; predation; rodents; Striped Skunk

Introduction

Ecosystem functions have been shown to be directly associated with biodiversity (Chapin et al. 2000; Cardinale et al. 2006; Duffy et al. 2007). In the last decades, habitat loss and invasive species have been considered among the main causes for the loss of species (Wilcove et al. 1998). Invasive species can alter entire habitats, modify the abundance of species, and affect food webs which can lead to a cascade of indirect effects (Vitousek et al. 1996; Mooney and Cleland 2001). In the coastal dunes of Northern California, the ecosystem has been altered by the presence of the invasive European Beachgrass (*Ammophila arenaria*). European Beachgrass, hereafter beachgrass, is a rhizomatous grass that was introduced in California in the mid-1800s to stabilize the coastal dunes, and it competes with native dune plants (Pickert 2013). This invasion has not only impacted native plants (Buell et al. 1995) but also other creatures such as the threatened Western Snowy Plover (*Charadrius alexandrinus nivosus*: U.S. Fish and Wildlife Service 1993, Muir and Colwell 2010). However, relatively little research has examined its effects on other vertebrates.

The most common rodents in the coastal dunes of Northern California are the North American Deermouse (*Peromyscus maniculatus*), Western Harvest Mouse (*Reithrodontomys megalotis*), and California Vole (*Microtus californicus*). The presence of the beachgrass has provided a new habitat for these rodents, and mark-recapture analysis of data suggest they are more abundant in habitat invaded by beachgrass than in native dune habitat (Daniel Barton and Justin Brice, unpubl. data). Moreover, artificial food tray analyses suggest rodents perceive less predation risk due to the extra cover of beachgrass, which can grow to over one meter in height (Johnson and De León 2015).

Mesopredators are small to mid-sized generalist carnivores. Their diets include a broad variety of prey, and they far outnumber specialist carnivores in abundance (Prugh et al. 2009; Roemer et al. 2009). Mesopredators play a critical role in many ecosystems and previous studies suggest that they are capable of suppressing small mammal populations in fragmented landscapes (Eagan et al. 2011). In the coastal dunes of Humboldt Bay, Gray Foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), feral cats (*Felis catus*), and Striped Skunks (*Mephitis mephitis*) are nocturnal mesopredators that prey on rodents, so the impacts of beachgrass on rodent abundance and perceived risk of predation could trigger effects in the activity of mesocarnivores as well.

The coastal dunes of Manila, Humboldt County, California are owned by private and public bodies with different land management practices and histories, resulting in marked differences in habitat on adjacent properties. This allows wildlife communities to be compared on habitats that have been invaded by *Ammophila* versus those that have been restored to a native plant community (e.g., Johnson and De León 2015). Here, we examine the effect of European Beachgrass on mesopredator activity in these coastal dunes. Previous work has shown that relative abundance of rodent prey was on average over four times higher on trapping grids in the invaded than in the restored habitat (Daniel Barton and Justin Brice, unpubl. data). A strong difference in prey density could affect foraging mesopredators (Abrams and Ginzburg 2000), therefore, we hypothesized that mesopredators would be more frequently detected in invaded habitat. Using remote cameras, we tested the prediction that the detection frequency of mesopredators is higher in invaded habitat than in restored habitat in our study area.

Methods

Study area.—The coastal dunes of Northern California are one of the most diverse dune systems in the West coast and support endemic plant species such as Pink Sand Verbena (*Abronia umbellata brevifolia*), Humboldt Bay Owl's Clover (*Castilleja ambigua humboldtiensis*), Dark-eyed Gilia (*Gilia millefoliata*), American Glehnia (Glehnia littoralis leiocarpa), Humboldt Bay Wallflower (*Erysimum menziesii eurekensii*), and Beach Layia (*Layia carnosa*; U.S. Fish and Wildlife Service 2015. Humboldt Bay homepage. Avaialble at http://www.fws.gov/refuge/humboldt_bay/. [Accessed 22 August 2015]). The study was conducted from March to September 2013 in coastal habitat in Humboldt County in northwestern California on two adjacent properties managed by the Friends of the Dunes (FOD) and the Bureau of Land Management's (BLM) Ma-le'l Dunes cooperative management area. The beachgrass-invaded area was located on FOD property, which is a non-profit organization created in 1982 focused on the ecology of coastal dunes. The FOD area was dominated by a very dense population of beachgrass during our study (Fig. 1). The area with low beachgrass density (restored) was located on adjacent BLM property. The BLM partnered with the California Conservation Corps for 14 y (1997–2010) to successfully remove the invasive beachgrass. The BLM site is dominated by native plant species and the density of the beachgrass is very low (Johnson and De León 2015). We conducted our study on a single 2.1 km transect that spanned the border separated these two habitats.

Figure 1. Habitat invaded and dominated by European Beachgrass, *Ammophila arenaria* (top), and restored habitat with higher plant diversity and lower vegetative cover (bottom). (Photographed by Matthew D. Johnson).

Data collection.—With one exception, we collected data for six consecutive days the last week of each month (every 28 d) from March through September of 2013, for a total of 41 sampling nights. September was sampled for only five nights and at an interval of 35 d due to the federal government shutdown on 2 October during our last night of data collection. We used this interval to largely control for moonphase in this study (mean lunar illumination ± 1 SE = 70.7 ± 8.1%), and preliminary analyses indicated it was not a significant predictor of mesopredator activity. We used camera trapping due to its low invasiveness, and because it is a viable method for detecting mammals at different scales (Rowcliffe et al. 2008; Thorn et al. 2009). We deployed 20 night vision cameras (Trophy Cam®, Bushnell Outdoor Products, Overland Park, Kansas) at 1900 (± 30 min) and retrieved them at 0700 (± 30 min) the following morning. We placed 20 cameras along a line transect laid parallel to the foredune (60–80 m from the ocean's waveslope), 10 in the area with beachgrass (FOD property) and 10 in the restored habitat (BLM). We distributed cameras at 100 m intervals, with a 100 m buffer zone between the two adjacent habitats, making a total transect length of 2.1 km (including the buffer zone). We mounted each camera on 2-m wooden pole (0.5 m buried in the sand and 1.5

m above sand level). Cameras were set on photograph mode (three shots per perceived detection) with a 1 min recovery period before the next detection. People setting up the cameras always left the station walking across the camera to make sure it was, in fact, working properly.

We baited each camera station with a 260 g can of Valley Fresh® 100% natural chicken breast in water (Hormel Foods, Austin, Minnesota) placed roughly 3 m away from the base of the wooden pole. We placed baits in patches with low vegetation and with field of view of 5 × 6 m. Cans remained unopened and we made five holes (approximately 0.5 cm diameter) on the top to release the scent of the chicken, and we staked each can firmly into the sand with a 20 cm tent spike driven through the container. Cans remained in place for each 6-d sampling period per month, and we used new cans each month. We trained cameras directly at the bait cans with a field of view approximately 8-10 m wide. Bait cans were not obscured by grass or other vegetation. Cameras never failed to detect field workers setting up or checking the stations, and all detections of mesopredators included multiple photographs during a given visit to a bait station. Animals as small as rodents were successfully detected by the cameras, and the most frequently detected mesopredator species were not the largest (see Results), so we assume there was no size bias to detection. Therefore, we assume that our detection rate (probability of obtaining a detection if the animal actually visited the bait station) was nearly 100% and did not vary between habitats.

Data analysis.–We used the number of detections of each species per month as index of activity. We considered each photograph of a mesopredator at a camera station as one detection as long as it was at least 60 min from the previous photograph of that species at that station. Multiple detections of the same individual animals were possible even on the same night, and almost certainly occurred within the week and among the seven months of the study. Therefore, our detection rate provided an index of mesopredator activity, rather than a measure of local abundance. For the analysis, we checked for temporal autocorrelation in the number of mesopredator detections among months. Finding none (see Results), we analyzed the data in Program R with the numbers of detections as our response variable in linear mixed effects Poisson models to test for the effects of habitat, month, and their interaction on mesocarnivore activity. We performed analyses on all mesopredator species pooled, and species-specific analyses for skunk and raccoon (the two most commonly detected species, see Results). For each response variable, we created five a priori candidate models with various combinations of predictor variables, with habitat and month as fixed terms, and station as a random effect. 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; models within two AICc were considered competitive with the best models.

Results

We recorded 188 mesopredator detections of five species (Table 1). Western striped skunk was the most commonly detected species with 93 detections (49.5%), followed by 62 detections of gray fox (33%), 21 of feral cat (11.2%), eight of opossum (4.3%), and four of raccoon (2.1%), with numbers varying between habitats (Table 1). There was little evidence of temporal autocorrelation from one month to the next, with autocorrelation values ranging from -0.08 to 0.52 (all $P > 0.25$) depending on species and habitat. Therefore, we subsequently treated month as a fixed effect. There were strong effects of habitat, month, and their interaction on the number of total mesopredator detections. Model selection indicated the full model was better supported than simpler models (ΔAIC > 4), though a model with habitat and month as additive rather than interactive terms was also competitive (ΔAIC = 0.81; Table 2). Mesopredator activity was significantly higher in the restored habitat, with 132 detections in the restored habitat and 56 detections in the invaded habitat (Table 1, Fig. 2). Activity peaked in mid to late summer in the restored habitat, while in the invaded habitat it peaked in the early summer (Fig. 2).

The activity of skunks and foxes each showed effects of habitat and month. For skunks, there were strong effects of habitat, month, and their interaction, though once again an additive model with month and habitat was competitive (Table 2). Skunks were detected more in the restored than the invaded habitat, and this difference was especially pronounced in mid to late summer months (Fig. 3a). For gray foxes, the top model included habitat and month as additive effects (Table 2). Foxes were

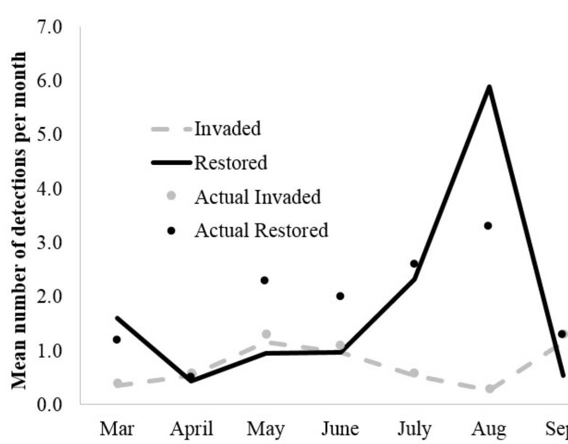

Figure 2. Detections per month of all mesocarnivores in coastal dune habitats of Northern California that were dominated by the invasive grass *Ammophila arenaria* (gray) or restored to native vegetation (black), March-September 2013. Observed data are indicated by points, model predicted patterns (see Table 2) are indicated by lines.

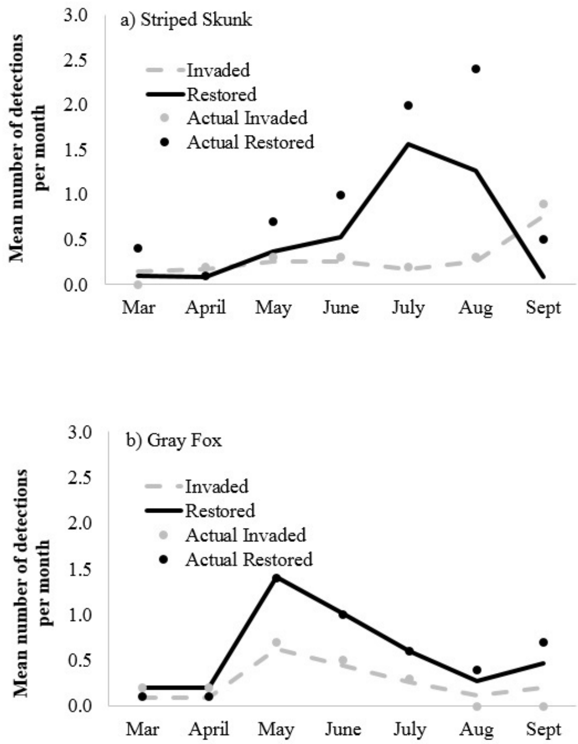

Figure 3. Detections per month of all Striped Skunks (a; *Mephitis mephitis*) and Gray Foxes (b; *Urocyon cinereoargenteus*) in coastal dune habitats of Northern California that were dominated by the invasive grass *Ammophila arenaria* (gray) or restored to native vegetation (black), March-September 2013. Observed data are indicated by points, model predicted patterns (see Table 2) are indicated by lines.

detected more frequently in the restored than the invaded habitat, and detections peaked in early summer, but there was little evidence for an interaction between habitat and month (Fig. 3b).

Discussion

We hypothesized that higher prey abundance in the invaded habitat than in the restored habitat would correspond with higher mesopredator activity. Our findings were contrary to this hypothesis. Although local studies have shown that prey is more abundant in the invaded areas (Daniel Barton and Justin Brice, unpubl. data), mesopredators may spend more time in the restored habitat because prey there are more exposed and vulnerable to attack, which has been found for other canids (Thibault and Ouellet 2005; van der Meer et al. 2014). Results from a study of rodent foraging in our study system also suggests that rodents perceive greater predation risk in the more open restored habitat (Johnson and De León 2015).

Another point to consider is the proximity of the habitat to a nearby forest. Nocturnal mesopredators may seek refuge in more forested habitats during the day, and move into the dunes for nocturnal foraging. In our study, there is a mixed coastal forest closer to the restored area than to the invaded area, so it is possible this proximity is partly responsible for the higher mesopredator activity we observed. Because we had no site replication, we cannot distinguish the effect of this confounding variable from apparent effects of invasive grass in our study. Nevertheless, the rate of mesopredator detections in the restored area did not increase with proximity to forest. Future research should focus on replicating our study in two or more locations and should examine the influence of adjacent forested habitats on mesopredators.

Our study did not examine the influence of abiotic factors such as temperature and precipitation. The spatial extent of our study was small enough (2.1 km) that these factors likely affected the restored and invaded habitats similarly, though we cannot exclude the possibility of an interaction between habitat and temperature or precipitation (e.g., temperature affects mesopredator activity in the invaded but not the restored habitat). We collected our data approximately every 28 d to largely control for possible confounding effects of moonlight (see Methods). However, rodents and their predators are known to respond to moonphase (Perea et al. 2011; Prugh and Golden 2014; Johnson and De León 2015), so future researchers may wish to examine variation in predator activity and moonphase in this system.

Previous studies have documented the negative effects of invasive beachgrass on native plants in our study area (Pickert 2013). Although the dense beachgrass may provide habitat for native rodents, our results suggest that at these sites the beachgrass negatively influences

Table 1. The number of mesopredator detections from March to September 2013 in the coastal dunes of Northern California that were dominated by the invasive grass *Ammophila arenaria* or restored to native vegetation.

Species		Number of detections	
		Invaded	Restored
Striped Skunk	*Mephitis mephitis*	22	71
Gray Fox	*Urocyon cinereoargenteus*	19	43
Feral Cat	*Felis catus*	11	10
Virginia Opossum	*Didelphis virginiana*	2	6
North American Raccoon	*Procyon lotor*	2	2
Total		56	132

Table 2. Generalized linear mixed-effect models and AICc values for the number of detections of Striped Skunks (*Mephitis mephitis*), Gray Foxes (*Urocyon cinereoargenteus*), and all mesocarnivores pooled in coastal dunes of Northern California. Station (20 camera stations) was a random effect, while habitat (invaded by *Ammophila arenaria* or restored) and month (March to September 2013) were fixed effects.

Model		Mesocarnivores		Skunks		Foxes	
	df	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc
detections ~ 1 + (1|Station)	2	468.89	11.66	331.32	24.00	261.90	15.81
detections ~ Habitat + (1|Station)	3	464.46	7.23	327.66	20.34	257.82	11.73
detections ~ Month + (1|Station)	8	462.16	4.93	311.81	4.49	249.86	3.77
detections ~ Habitat + Month + (1|Station)	9	458.04	0.81	308.46	1.14	246.09	0.00
detections ~ Habitat * Month + (1|Station)	15	457.23	0.00	307.32	0.00	254.64	8.55

the use of dunes by skunks, and foxes. Even though our detection rate of feral cats was low (11% of all detections), the number of detections was similar between the two habitats, suggesting this non-native predator may be more resilient to the effect of the invasive beachgrass, at least at our study site. We conclude that the restoration of coastal dunes in this system likely benefits mesocarnivores, which can stabilize ecosystem processes.

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