

Opposing forces of seed dispersal and seed predation by mammals for an invasive
cactus in East Africa

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Introduction

Biological invasions cause many economic and conservation problems, and rank as the second leading driver of biodiversity loss across the globe (Lowe *et al.* 2000; Simberloff *et al.* 2013). Invasive species can disrupt native mutualisms and food web dynamics (Mack *et al.* 2000; Theoharides & Dukes, 2007; Traveset & Richardson, 2014), may compete with native species (Mack *et al.* 2000; Clavero *et al.* 2009), and can alter soil and nutrient cycling (Mack *et al.* 2000; Rout & Chrzanowski, 2009). These alterations can result in a loss of rangeland productivity and consequent economic losses (Strum, Stirling & Mutunga, 2014; Traveset & Richardson, 2014). While expensive, eradication efforts often are unsuccessful, so the extent to which land managers can rely on natural (non-human) agents to limit invasive species offers a desirable alternative or complement to targeted interventions (Mack *et al.* 2000). Introduced organisms experience an array of potential competitors, pathogens, and predators with which they have no prior exposure, leading to a potential suite of interactions distinct from those in their native ranges (Mack *et al.* 2000; Theoharides & Dukes, 2007).

In addition to escaping such enemies in its introduced range, interactions between invasive and native species can also disrupt mutualism networks (Traveset & Richardson, 2014). The results are often simultaneously beneficial to populations of the invasive species and detrimental to native populations (Mitchell *et al.* 2006; Theoharides & Dukes, 2007). For example, if an invasive plant is more attractive to pollinators than a native species, the invasive species will disrupt the native plant-pollinator mutualism (Traveset & Richardson, 2014).

The prickly pear cactus (*Opuntia stricta*) is ranked in the top 100 of the world's worst invasive alien species (Lowe *et al.* 2000), and it has become invasive in many regions around the world including: Australia, the Canary Islands, South Africa, the Mediterranean and Iberian

Peninsula, and St. Kitts and Nevis (Weber 2003; Novoa *et al.* 2015; Strum *et al.* 2015). This arid-adapted species can thrive in very low resource conditions, allowing it to outcompete native species during droughts. In addition, interactions with native seed dispersers can increase *O. stricta's* rate of establishment and spread in areas to which it has been introduced (Padrón *et al.* 2011). The cactus bears fruits throughout the year, encouraging consumption by native species, produces seeds that are viable for up to 15 years, and can also reproduce clonally, making it well-adapted for establishment after introduction (Dodd, 1940; Mandujno *et al.* 2001).

In the 1940s, *O. stricta* was introduced to Kenya, and its subsequent establishment and spread has had devastating effects on rangeland quality and native plant communities (Snyman *et al.* 2006; Strum *et al.* 2015). *Opuntia stricta* seeds are commonly dispersed by olive baboons (*Papio anubis*) through ingestion of its fleshy fruits and subsequent defecation of seeds (Fig. 1a; Foxcroft *et al.* 2004; Foxcroft & Rejmanek, 2007; Strum *et al.* 2015). Seed dispersal by baboons increases germination rates and the likelihood of seedling survival for other plant species (Kunz & Linsenmair, 2008; Lieberman *et al.* 1979).

Rodents forage in the feces deposited by larger mammals (Vander Wall & Longland, 2004), allowing for further manipulation of dispersed seeds. Thus, the fate of dispersed seeds is often uncertain. Seed predation functions as a strong selective pressure, especially during early succession dispersal activities (Orrock *et al.* 2006). Seed predators limit spread of plant populations by consuming seeds before germination (Fig. 1b). Preferences exhibited by seed predators also influence changes in plant community composition and diversity (Brown & Heske, 1990; Howe & Brown, 2000). Previously, there has been no investigation of whether the presence of baboon feces encourages seed predation on *O. stricta*.

Here we investigated the post-dispersal fate of *O. stricta* seeds that have been consumed by baboons. We investigated whether *O. stricta* seeds are removed from baboon feces by secondary seed dispersers, consumed by seed predators, or remain undisturbed in baboon feces. Specifically, does the presence of fecal material influence use by seed dispersers or seed predators? If it does, we expect organisms to prefer seeds within fecal piles to piles of bare seeds in controlled paired trials, as evidenced by shorter latency to consumption (“time to use”) for seeds in fecal piles relative to controls.

Materials and Methods

Our study was conducted at the Mpala Research Centre (MRC), in Laikipia County, located in the highlands of central Kenya (0°17'N, 37° 52'E, 1600-m elevation). The MRC experiences a mean annual rainfall of approximately 500mm (Ford & Goheen, 2015). The local habitat is a semi-arid savanna characterized by red sandy loam resulting from metamorphic basement rock, with a vegetation overstory of *Acacia* spp. (Goheen *et al.* 2013; Ford & Goheen, 2015).

Lacking any formally protected reserves, Laikipia is comprised entirely of cattle ranches and private mixed-use conservancies. Although local economies are based upon livestock production, the transition to community-based conservation and ecotourism has driven the local economy's recent adaptations to urban development and tourist demand. Traditional pastoral communities, however, face an ever-growing problem caused by *O. stricta*, as rangeland quality has decreased due to *O. stricta*'s ability to outcompete native plants (Strum *et al.* 2015).

Our study was conducted from May 2015 through July 2015. We collected dry baboon feces containing *O. stricta* seeds from baboon roost and forage sites across the MRC. Intact fecal samples were placed on the ground next to a known number of *O. stricta* seeds previously removed from feces. We then monitored both the feces and the seed piles using a motion-

triggered Reconyx RC45 cameras (Reconyx, Inc. Holmen, USA). The feces and cameras were left for three nights before collection. We sampled at five sites across the MRC, with three replicates (pairs of fecal and control seed piles) at each site. Seeds were evaluated for signs of seed predation by the presence of emptied seed hulls, and camera trap images were reviewed to identify mammalian visitors to species.

We evaluated whether rodents showed a preference for the seeds within feces or bare seeds by recording “time to use,” which is the latency between trial initiation at sunset (1900h) and first image capture of an individual consuming seeds. Multiple observers verified species identifications independently, and photographs featuring ambiguously identified species were not included in the analysis. Multiple detections of a single species within 60 minutes of one another were treated as a single observation (Hodge & Arbogast, 2015). Data was analyzed in R (version 2.3.2; R Core Team 2015) using a Cox proportional hazards model to determine whether seed treatment (feces or control) predicted the latency to consumption.

Results

Three species were identified from the camera trap photos: unlined ground squirrel (*Xerus rutilus*, n=2), superb starling (*Lamprotornis superbus*, n=1), and fringe-tailed gerbil (*Gerbilliscus robustus*, n=17).

All *G. robustus* visits occurred within a 12-hour period, from sunset to sunrise (approximately 1900-700h). The Cox proportional hazard model showed that *G. robustus* demonstrated a shorter time to use for the seeds within feces than for the bare control seeds ($p < 0.001$; $\beta = -1.98 \pm 0.58$; Fig. 2). Empty seed hulls were found at 100% of the sites that had been visited by *G. robustus*.

Discussion

Gerbilliscus robustus functions as a seed predator for the invasive *Opuntia stricta* in central Kenya. *O. stricta* seeds in feces piles were removed and consumed at higher rates than bare seeds, suggesting that the presence of fecal material influences seed predation by *G. robustus*. Our results are consistent with other studies in which seed predators associate the scent of feces with a food source (Hulme, 1994; Janzen, 1982b). For example, seed rich feces are favored over seed poor feces by seed predators (Janzen, 1982a). One difference between our study design and that of previous studies is that we used dry, rather than wet, feces. If odor is the signal that attracted rodents to the seed piles, as presumed by previous studies, our experiment shows that even dry, aged feces can be detected and sought out by rodents. Therefore our results may be a conservative estimate of seed predation from mammalian fecal deposits, as fresh feces may prove an even stronger attractant to rodents.

Baboons can deposit large quantities of seeds within a single defecation event. In our study plots, an average baboon feces weighs 8.62 grams and contains 259 seeds (standard error = 27.15). In comparison a dropped whole fruit from *O. stricta* contains 60-120 seeds. Thus, fecal deposits can be a relatively rich source of food for *G. robustus* and other seed predators. Rodents may also have learned to associate baboon roost sites with numerous, seed-rich feces piles as abundant food sources (Janzen, 1982b).

While some seeds may escape seed predation, the majority of seeds in our experiment were consumed. Previous studies, however, found that the majority of seeds were consumed from feces when discovered by seed predators (Janzen, 1982a; LoGiudice & Ostfeld, 2002). The presence of alternative food sources may decrease the rates of seed predation on a given species (LoGiudice & Ostfeld, 2002). Our study was conducted during the dry season in a water limited system, and results could have varied greatly if data had been collected during the wet season

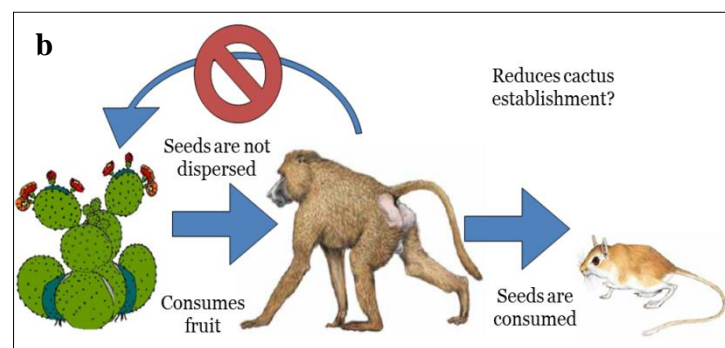
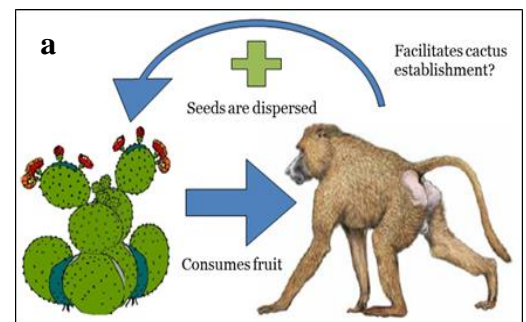
when food resources are more available. It is unclear how alternative food sources would affect consumption of *O. stricta* seeds by *G. robustus*. A previous study in Laikipia, however, demonstrated that *O. stricta* seeds are preferred for consumption in comparison to native seeds by *G. robustus* (Bernard *et al.* 2014).

Although many factors influence the spread and abundance of *O. stricta*, seed predators, such as *G. robustus*, may influence and disrupt dispersal (LoGiudice & Ostfeld, 2002). Seed predators are capable of inhibiting seed survival and dispersal, as well as influencing plant community and composition (Whelan *et al.* 1991). A long-term exclosure of large herbivores at the MRC, was found to result in an increase in rodent densities (Goheen *et al.* 2013), indicating that rodent populations are suppressed by large herbivores. *Opuntia stricta* abundance is highest across areas in which large herbivores are tolerated, such as wildlife conservancies, and lowest in areas where large herbivores are absent (Hodge in prep; Bernard *et al.* 2014). Future studies should examine whether declines in populations of large herbivores increase rates of seed predation on *O. stricta*, affecting its rate of reproduction and spread.

Figures

Figure 1. a) Schematic of seed dispersal hypothesis. *Opuntia stricta* establishment is facilitated by baboon consumption of fruit and subsequent defecation of seeds. b) Schematic of seed predation hypothesis. *Opuntia stricta* establishment is

decreased due to seed predation on *O. stricta* seeds after defecation via baboon.



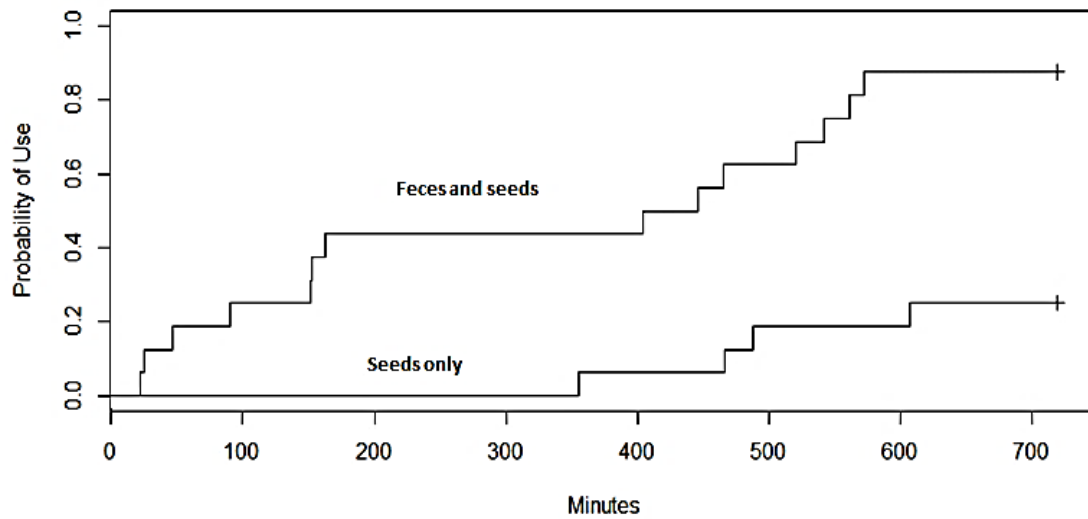


Figure 2. Cumulative probability of overnight use of seed piles by *Gerbilliscus robustus* (n=18 visitations). Probability of use increases with the presence of baboon feces ($\beta = -1.98 \pm 0.58$; $p < 0.001$).

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