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Channel Island foxes (*Urocyon littoralis*) are viable seed dispersal agents of toyon (*Heteromeles arbutifolia*)

Savannah L. Bartel[1,*], Juliann T. Schamel[2], Bridget A. Parrino[2], Melissa K. Marshall[2], and John L. Orrock[1]

[1]*University of Wisconsin–Madison, Department of Integrative Biology, 363 Birge Hall, 430 Lincoln Dr., Madison, WI 53706*
[2]*Channel Islands National Park, 1901 Spinnaker Dr., Ventura, CA 93001*

Abstract.—Mammals that consume fleshy fruit and deposit viable seeds in their scat can be important agents of seed dispersal for plants. Despite the knowledge that the island fox (*Urocyon littoralis*) consumes large quantities of fleshy fruits, it is unknown whether seeds survive digestion by island foxes and are able to germinate. In order to evaluate whether island foxes are agents of viable seed dispersal on the Channel Islands, we collected island fox scat on Santa Cruz Island in February 2021 and conducted germination assays on digested seeds found in scat. We compared the germinability and germination rates of 200 toyon (*Heteromeles arbutifolia*) seeds digested by island foxes with that of 100 undigested seeds that were manually removed from toyon fruit collected in the same location and time period as scat collection. Over the course of 25 d, 32% of the seeds digested by island foxes germinated, and 61% of the undigested seeds germinated. Seeds digested by foxes germinated at slower rates than undigested seeds, and there was a 21.4% wider range of germination times for digested seeds than for undigested seeds. There was also substantial variation in the probability of seed germination among scat samples, ranging from 0% to 100%, indicating that the quality of dispersal by island foxes may depend upon individual fox traits or an individual fox's environment. These results show that island foxes are effective dispersal agents of toyon seeds, but the benefits of being dispersed by foxes come at a cost of reduced germination. Environmental changes on the Channel Islands that modify the diet and space use of island foxes could therefore affect dispersal and recruitment of island plants.

Resumen.—Los mamíferos que consumen frutos carnosos y dejan semillas viables en sus excrementos pueden ser importantes agentes de dispersión de semillas de plantas. A pesar de que, se sabe que el zorro isleño (*Urocyon littoralis*) consume grandes cantidades de frutos carnosos, se desconoce si las semillas sobreviven al proceso de digestión y son capaces de germinar. Para evaluar si los zorros isleños son agentes de dispersión de semillas viables en las Islas del Canal (Channel Islands), recolectamos excremento de zorros isleños en la isla Santa Cruz en febrero de 2021 y llevamos a cabo análisis de germinación en las semillas digeridas que se encontraron en los excrementos. Comparamos la germinabilidad y las tasas de germinación de 200 semillas de toyon (*Heteromeles arbutifolia*) digeridas por zorros isleños con las de 100 semillas no digeridas que se extrajeron manualmente de la fruta de toyon recolectada en el mismo lugar y período de tiempo que la recolección de excrementos. Durante el transcurso de 25 días, germinaron el 32% de las semillas digeridas por los zorros isleños y el 61% de las semillas sin digerir. Las semillas digeridas por los zorros germinaron a un ritmo más lento que las semillas sin digerir, y se detectó un intervalo de tiempo de germinación de 21.4% más amplio en las semillas digeridas que en las semillas sin digerir. También se encontró una variación sustancial en la probabilidad de germinación de semillas entre las muestras de excrementos, que van del 0% al 100%, lo que indica que la calidad de la dispersión por parte de los zorros isleños podría depender de las características individuales del zorro o del entorno de un zorro individual. Estos resultados indican que los zorros isleños son agentes eficaces de dispersión de semillas de toyon, aunque la germinación es reducida. Por lo tanto, los cambios ambientales en las Islas del Canal que modifican la dieta y el uso del espacio de los zorros de las islas podrían afectar la dispersión y el reclutamiento de plantas de las islas.

Mammalian biodiversity is rapidly disappearing throughout the globe (Tilman et al. 2017, Brodie et al. 2021). Such changes in the distribution and abundance of mammals may be particularly impactful because mammalian species play critical roles in ecosystems (Estes et al. 2011, Peres et al. 2016, Kelt et al. 2019, Brodie et al. 2021). For example, the loss of large, seed-dispersing mammals may affect the viability of plant populations in the tropics (Beck et al. 2013, Terborgh

*Corresponding author: bartel2@wisc.edu

SLB orcid.org/0000-0001-5735-262X JLO orcid.org/0000-0003-07768-7389

2013, Peres et al. 2016, Bagchi et al. 2018). Importantly, the vast majority of research on mammal-mediated seed dispersal has focused on taxa outside of the order Carnivora (Draper et al. 2022), despite the potential for many carnivorous mammals to be effective agents of seed dispersal (Herrera 1989, Willson 1993, Draper et al. 2022). This lacuna is critical because carnivorous mammals are declining across the globe as a result of myriad human-induced environmental changes (e.g., harvesting, habitat loss, and habitat fragmentation; Estes et al. 2011, Ripple et al. 2014), and carnivore declines may have unrecognized effects on seed dispersal (e.g., Fedriani et al. 2020). Reduction of mammal-mediated seed dispersal may be particularly important in island ecosystems because these ecosystems are often highly imperiled and contain unique plant and animal species. Moreover, the introduction of nonnative mammals to island ecosystems may, in some cases, lead to invasional meltdown when nonnative mammals facilitate seed dispersal of introduced plants (Bourgeois et al. 2005, Traveset and Richardson 2014). Despite a wealth of research illustrating how nonnative mammals may be agents of seed dispersal for both native and nonnative plants in island ecosystems (Traveset 1995, Bourgeois et al. 2005, Heleno et al. 2011, Traveset et al. 2012, Nogales et al. 2015, Muñoz-Gallego et al. 2019, Draper et al. 2022, Fricke et al. 2022), the functional role of native insular mammals as agents of seed dispersal for native plants remains poorly understood.

The island fox (*Urocyon littoralis*) is an endemic mammalian species on the California Channel Islands. The island fox is highly omnivorous and often relies heavily on plant material, with 20%–40% of the annual diet containing fruit material (Crooks and Van Vuren 1995, Moore and Collins 1995, Cypher et al. 2014). This substantial reliance on fruit suggests that the island fox has the potential to play an important role in dispersing seeds, a role that may be further modified by significant changes in fox abundance and behavior generated by changes in introduced species, resource availability, and social interactions (Delibes-Mateos et al. 2008, Selwyn et al. 2020, Bartel and Orrock 2022, Burgos et al. 2022). Although the only published research (to our knowledge) evaluating seed dispersal by terrestrial vertebrates on the Channel Islands documented secondary seed dispersal by scatter-hoarding Island Scrub-Jays (*Aphelocoma canabis*; Pesendorfer et al. 2016, 2018), there are a number of omnivorous bird species that consume fleshy fruit on the Channel Islands and may also be agents of seed dispersal (e.g., *Callipepla californica, Catharus guttatus, Ixoreus naevius, Turdus migratorius, Mimus polyglottos, Sturnus vulgaris, Bombycilla cedrorum,* and *Pipilo maculatus*; Beal 1907a, 1907b, Bent 1949, Collins 2011). Since the island fox is the most abundant (and often the only) midsized mammalian omnivore on the Channel Islands, it may often be the sole mammalian agent of seed dispersal. However, much of the research on the potential ecological roles of the island fox has focused on predation and competition (Roemer et al. 2002, Phillips et al. 2007, Coonan et al. 2010a, 2010b, Orrock 2010, Orrock and Fletcher 2014, Bolas et al. 2022). Despite the potential for island foxes to provide important seed dispersal services, it is still unclear whether island foxes disperse the seeds of island plants. Specifically, it is unknown whether seeds digested by island foxes are viable or whether digestion by island foxes affects the speed at which seeds germinate.

Toyon (*Heteromeles arbutifolia*) is among the most common native woody species on the Channel Islands (Schoenherr et al. 1999), and toyon berries are common items in island fox diets (Crooks and Van Vuren 1995, Cypher et al. 2014). While toyon berries are found in island fox diets year round, they are most common in island fox diets in the winter; frequencies in winter diets range from 29.6% on Santa Rosa Island to 87.9% on Santa Catalina Island (Cypher et al. 2014). In southern California, toyon berries mature in late fall and winter, and berries remain on the plants into January (Meyer 2008). An individual plant can produce tens to hundreds of thousands of fruits per year (Aslan 2011). A single toyon berry will have 2–3 seeds, and seed mass can vary geographically between 5.5 and 36 mg (Meyer 2008). While no published research (to our knowledge) has measured toyon fruit removal on the Channel Islands, past work estimated that as much as 94% of toyon fruits are removed by birds on mainland northern California (where island foxes are absent; Aslan 2011). Digestion by mainland mammals, including coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*), has also been shown to be a primary means of toyon seed dispersal (McMurray 1990, Wilson 1998, Silverstein 2005); however, the potential role of endemic island foxes as dispersers of toyon remains unknown because it is not known whether consumption by island foxes affects toyon germination. We evaluated the potential for island foxes to serve as agents of seed dispersal by comparing the germinability (i.e., proportion of seeds that germinate) and germination rates of toyon seeds digested by island foxes with those same rates of seeds that were manually removed from fruits and not digested by island foxes.

METHODS

Field Collection

We collected toyon seeds from Santa Cruz Island in February 2021. Island foxes are common on Santa Cruz Island (Schoenherr et al. 1999), and in 2009, toyon constituted 30.6% of the island fox's annual diet on Santa Cruz (Cypher et al. 2014). Island foxes and island spotted skunks (*Spilogale gracilis amphiala*) are the only midsize mammalian omnivores on the island, but past work comparing the annual diets of the 2 species on the island found that island spotted skunks do not consume fruits (Crooks and Van Vuren 1995). The importance of toyon as a dietary item for island foxes was also supported by our field observations (29 of 30 seed-containing scats collected during preliminary field collection contained toyon seeds). In order to acquire toyon seeds digested by island foxes, we collected island fox scat within the Channel Islands National Park area of Santa Cruz Island in early February 2021. Scat collection in this area was permitted by the National Park Service (NPS) under permit #CHIS-2019-SCI-0022. Scat was collected over a 1.5-km^2 area around the NPS Scorpion Canyon campground (latitude 34.04832440, longitude −119.56166670) and also around a 0.1-km^2 area that was <2 km southwest of the campground in Scorpion Canyon within an NPS live-trapping grid for island foxes. Ninety-five percent of the scat samples we used for germination assays were collected in the campground site. The campground site was characterized by grassland vegetation, mature *Eucalyptus* trees, a shrub community of toyon and lemonade berry (*Rhus integrifolia*), and relatively high densities of humans. The sampled campground site is estimated to fall within the home range of at least 35 individual island foxes (unpublished NPS data). All scat collected was <3 months old. The age of the scat was determined based on visual observations of moisture content (i.e., dry scat was not collected). Upon collection, each scat was weighed and individually stored. In order to acquire toyon seeds that were not consumed and subsequently digested by island foxes, we collected ripe toyon fruit from 10 individual toyon plants naturally occurring within the same locations and time frame as scat collection.

Germination Assay

Between 20 and 21 February 2021, we manually removed seeds from scat and stored them in a dry container at room temperature. Digested seeds were extracted from scats with forceps while we rinsed the scat with water, and we then counted the total number of seeds extracted from each scat sample. Undigested seeds were separated from toyon fruit pulp with forceps and rinsed with water. All seeds were visually inspected under a dissecting microscope so that only undamaged seeds would be used for germination assays. Twenty-nine of the 30 processed scat samples contained toyon seeds. One of the samples contained seeds of toyon as well as lemonade berry and prickly pear (*Opuntia* spp.), and one of the scat samples contained only seeds of lemonade berry. These 2 scat samples containing additional seed species were not used for germination assays in order to control for the effects that different fruit species may have on gut retention times (e.g., Levey and Martínez del Rio 2001, Tewksbury et al. 2008). Among the 30 samples of scat collected and processed, 93% had >10 undamaged toyon seeds, and we randomly selected 20 scat samples from this subset for germination assays.

On 24 February 2021, we randomly placed 10 undamaged seeds from each scat sample in a sterile plastic petri dish (100 × 15 mm; Fisher brand) with a germination blotter (3.37 inches [8.57 cm] diameter; Anchor Paper, St. Paul, MN), amounting to 200 digested seeds across 20 independent scat replicates. Undigested seeds collected from individual plants were randomly placed in a petri dish with a germination blotter, amounting to 100 undigested seeds across 10 individual toyon plants. In order to kill fungi, all seeds were submerged in a 5% bleach solution for 20 s directly before they were placed in the petri dishes (Wilson 1998, Silverstein 2005). Petri dishes were randomly arranged along a single level in a Percival plant growth chamber (model E-41L2, Percival Scientific, Perry, IA) set at 13.7 °C, the mean temperature for the months of February and March on Santa Cruz

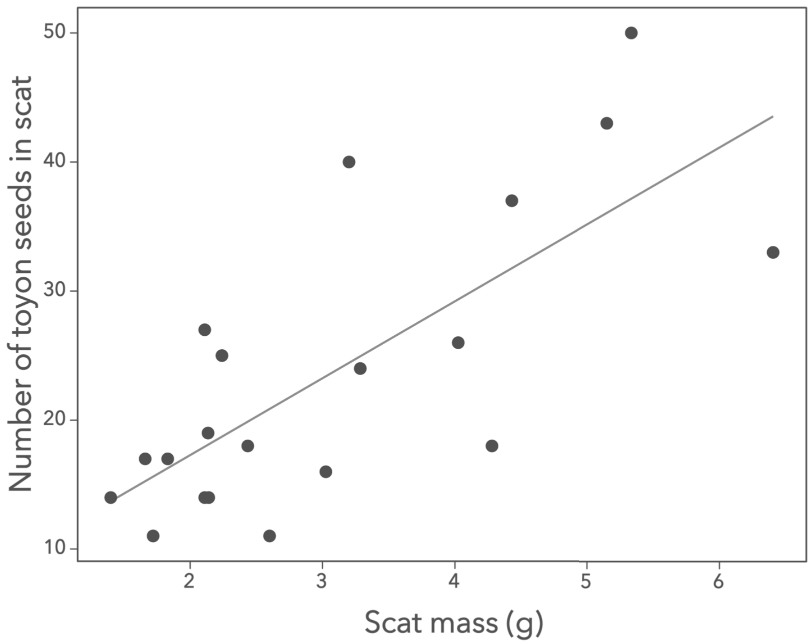

Fig. 1. Significantly positive correlation between the number of toyon (*Heteromeles arbutifolia*) seeds found per scat and scat mass ($r^2 = 0.55$, $t = 4.68$, $P < 0.001$).

Island from 2018 to 2020 (University of California Natural Reserve System Weather Station Database). Blotters in the petri dishes were saturated with deionized water. Seeds were checked daily, and deionized water was added as necessary to keep blotters saturated. We considered seeds to have germinated when the radicle was >1 mm in length. Upon germination, each seed was removed from the petri dish. We concluded the study on 22 March after 72 h had passed without any new germination events. This 25-d duration coincides with typical recommendations for germination trials with toyon seeds (20–28 d; Emery 1988, Meyer 2008, Everett 2012). This trial period should be sufficient for all viable seeds to germinate because toyon seeds are thought to be nondormant at dispersal (Emery 1988, Keeley 1991, Meyer 2008, Everett 2012).

Data Analysis

We used a linear model to evaluate whether the mass of each scat was significantly related to the total number of toyon seeds found in the scat. We used a generalized linear model with a binomial error distribution and logit link function to evaluate whether digestion by island foxes affected the proportion of seeds that germinated during the experiment. Digestion by island foxes was treated as a fixed effect. We used a Cox mixed-effects model to evaluate whether digestion by foxes affected the seed germination rate. Digestion by island foxes was treated as a fixed effect, and collection sample ID (i.e., individual scat ID or individual plant ID) was treated as a random effect. Linear models were constructed using the *stats* package in R version 3.6.1 (R Core Development Team 2019). The Cox mixed-effects model was constructed using the *coxme* package (Therneau 2019) in R version 3.6.1 (R Core Development Team 2019).

RESULTS

We found a significantly positive relationship between scat mass and the total number of toyon seeds contained in the scat ($r^2 = 0.55$, $t = 4.68$, $P < 0.001$; Fig. 1). Over the course of 25 d, 64 out of 200 (32%) digested seeds germinated and 59 out of 100 (59%) undigested seeds germinated. There was a significant effect of digestion by island foxes on the probability of seed germination ($\beta = -1.12$, SE = 0.25, $\chi^2 = 20.00$, $P < 0.001$) such that seeds digested by foxes were less likely to germinate than seeds manually removed from pulp (Fig. 2A). Seeds digested by foxes germinated at slower rates than seeds manually

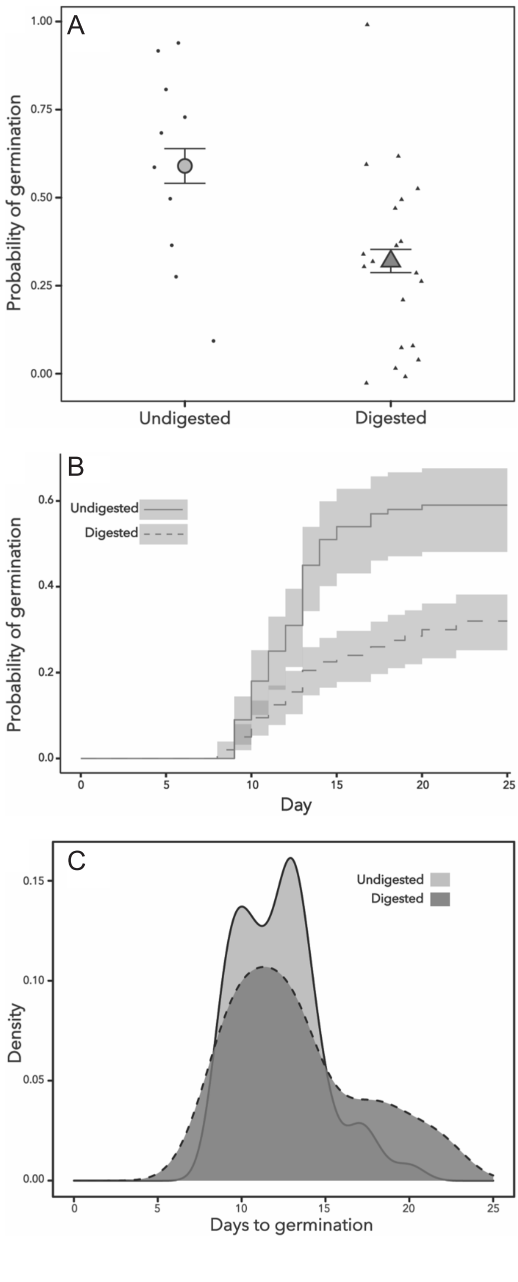

Fig. 2. ***A*,** Toyon (*Heteromeles arburtifolia*) seeds digested by island foxes (i.e., removed from scat) were significantly less likely to germinate than undigested seeds (i.e., manually removed from fruit pulp; $\beta = -1.12$, SE = 0.25, $\chi^2 = 20.00$, $P < 0.001$). Notably, we found substantial variation in seed germination among scat samples, ranging from 0 to 1.0 germination probability. ***B*,** We used a mixed-model survival analysis to examine the rate at which seeds germinated. Digested seeds germinated at slower rates than undigested seeds ($\beta = -0.96$, SE = 0.39, $\chi^2 = 5.89$, $P = 0.015$). ***C*,** Kernel density plots show that the distribution of germination time for seeds digested by island foxes was wider than the distribution of germination time for undigested seeds.

removed from pulp ($\beta = -0.96$, SE = 0.39, $\chi^2 = 5.89$, $P = 0.015$; Fig. 2B), and the range in germination time for digested seeds (14 d) was 21.4% wider than the range of germination time for seeds removed from pulp (11 d, Fig. 2C).

DISCUSSION

Our study's finding that 32% of seeds digested by island foxes are able to germinate within 25 d shows that island foxes can be viable seed dispersal agents of toyon. Digestion of toyon fruit by island foxes provides an effective means to separate seeds from the pulp; however, the proportion of seeds that germinate after digestion is significantly lower than that of seeds manually removed from pulp (Fig. 2A). These findings indicate that dispersal by island foxes comes at a substantial cost: only a fraction of the seeds consumed by foxes have the potential to germinate. The efficacy of a seed dispersal agent can be estimated by evaluating the quantity of seeds dispersed and the quality of that dispersal (i.e., the quality of seed treatment during handling/digestion and probability of postdispersal survival; Schupp 1993, Schupp et al. 2010). Past work shows that toyon can constitute the majority of island fox diets when it is seasonally available (Crooks and Van Vuren 1995, Cypher et al. 2014), and we found that a single scat deposit can disperse as many as 62 toyon seeds. These findings indicate that island foxes have the potential to disperse large quantities of toyon seeds and may be highly effective seed dispersal agents from the quantitative perspective. However, island foxes are likely relatively low-quality seed dispersal agents given the low proportion of digested seeds that germinate. We acknowledge that some of the digested seeds that did not germinate during our 25-d trial may have been viable and could have germinated if the trial had continued for a longer period. However, we expect that the trial period was sufficient for all viable seeds to germinate because toyon seeds are thought to be nondormant at dispersal (Emery 1988, Keeley 1991, Meyer 2008, Everett 2012). This trial period is also the recommended duration for germination trials with toyon (Emery 1988, Meyer 2008, Everett 2012).

Past work on California's mainland gray foxes (*Urocyon cinereoargenteus*) found that digestion by gray foxes did not significantly affect probability of toyon seed germination or the timing of germination (Wilson 1998), indicating that island foxes are slightly less effective dispersal agents, from the dispersal-quality perspective, than their mainland counterparts. It is possible that this variation in dispersal quality is due to differences in seed traits between island and mainland toyon populations (Soltani et al. 2018). Future research is needed to determine whether toyon seed traits differ significantly between mainland and island populations and whether these traits mediate the effects of fox digestion. We also expect that this variation may result from differences in morphology between island foxes and gray foxes. Island foxes are substantially smaller than gray foxes, and gut retention time—a determinant for how long seeds are exposed to digestive enzymes—scales with body size in carnivore species (Draper et al. 2022). The difference in the effect of digestion by island foxes and gray foxes is unsurprising when considering the well-documented variation in the effects of vertebrate digestion on seed germinability, which can be specific to the species pair (i.e., the same seed species may be affected differently by digestion in different vertebrate species, and vice versa; Traveset and Willson 1997, Rubalcava-Castillo et al. 2020, Draper et al. 2022). Interestingly, a recent review on the effects of carnivorous vertebrates as seed dispersal agents found that seed viability was not negatively affected by carnivore digestion in 70.6% of the reviewed cases (defined as each seed–carnivore pair; Draper et al. 2022). This review also found substantial variation in the effects of carnivore digestion on seed germination timing: 49% of the cases found accelerated germination with digestion, and 13.7% of the cases found delayed germination (Draper et al. 2022). Our study provides evidence that the island fox may be the more rare case in which digestion by a carnivore leads to decreased germinability and delayed germination rate of toyon seeds. However, since the effects of digestion can be species-pair specific (Traveset and Willson 1997, Rubalcava-Castillo et al. 2020, Draper et al. 2022), it is possible that the effects of island fox digestion on other seed species may be substantially different than its effects on toyon.

While it is unclear why island foxes provide relatively low-quality seed dispersal for toyon, the overall effectiveness of a seed dispersal agent is determined both by the quantity and quality of seed dispersal (Schupp 1993, Jordano and Schupp 2000, Schupp et al. 2010). It is important to consider that island fox diets contain relatively more plant material than gray fox diets (Laughrin 1977, Coonan et al. 2010b), indicating that island foxes may disperse relatively greater quantities of seeds. We therefore suggest that island foxes have the potential to be highly effective seed dispersal agents for toyon when environmental conditions promote high rates of toyon consumption.

Importantly, toyon on the mainland is likely to be dispersed by many mammals (e.g., gray foxes, coyotes, and raccoons; McMurray 1990, Wilson 1998, Silverstein 2005, Meyer 2008) and at least 10 bird species (Aslan 2011). In contrast, toyon on the Channel Islands has fewer mammalian dispersal agents since island foxes are the only midsize omnivorous mammal that consumes it (Crooks and Van Vuren 1995). Hence, island foxes may be particularly important for the movement and persistence of toyon on the islands despite the negative effects of fox digestion on seed germination. While our work provides an important first step by quantifying postdispersal germinability, future studies that evaluate the dispersal effectiveness of the island fox in relation to other potential dispersers on the island (e.g., avian omnivores such as *Callipepla californica*, *Catharus guttatus*, *Ixoreus naevius*, *Mimus polyglottos*, *Turdus migratorius*, etc.; Beal 1907a, 1907b, Bent 1949, Collins 2011) will be essential for understanding the ecological role of this endemic carnivore.

While the benefits of island fox dispersal for toyon are unlikely to accrue because of decreased germination percentages and delayed germination, the consumption of toyon fruits by island foxes may still be highly valuable to toyon and other plants in several other ways. For example, previous work evaluating the benefits of seed dispersal by mainland coyotes (*Canis latrans*) indicates that rodents are less likely to consume seeds that are associated with canid scat (Bartel and Orrock 2021). Since island mice have been found to avoid island fox scat while foraging (Orrock 2010), we hypothesize that seeds may be at a lower risk of postdispersal predation when they are dispersed by island foxes. Moreover, the effects of island fox digestion on germination time may also have benefits. In contexts where precipitation patterns can be highly variable, delaying germination can help increase fitness by ensuring that plants do not germinate after small precipitation events followed by dry periods (Turkington et al. 2005, Orrock and Christopher 2010). Hence, the effects of island fox digestion on delayed seed germination may prevent toyon seeds from germinating during spurious rain events during southern California's dry season. However, past work in the inland United States (Provo, Utah) has shown that digestion of netleaf hackberry (*Celtis reticulata*) seeds by coyote (*Canis latrans*) decreased time to germination, producing seedlings that were 9.5% taller than seedlings grown from undigested seeds (Stevens et al. 2020). This past work suggests that delayed germination timing of toyon seeds digested by island foxes may limit seedling growth, but further research is needed to evaluate whether the timing of germination has a considerable effect on toyon seedling growth rates over the growing season on the Channel Islands.

We anticipate that toyon is not the only plant species that benefits from dispersal by island foxes. Past work evaluating the diet composition of island foxes across the 6 Channel Islands that contain foxes revealed that the seeds of several native plants are commonly found in fox scat: prickly pear (*Opuntia* spp.), manzanita (*Arctostaphylos* spp.), summer holly (*Comarostaphylis diversifolia*), island redberry (*Rhamnus pirifolia*), and lemonade berry (Cypher et al. 2014). Since this work also found that the seeds of nonnative plants such as ice plant (*Carpobrotus* spp., *Mesembryanthemum crystallinum*) and Australian saltbush (*Atriplex semibaccata*) were also common in island fox scat (Cypher et al. 2014), island foxes may also play a currently unrecognized role in facilitating plant invasions on the Channel Islands.

Interestingly, we found substantial variation among individual scat samples in the probability of seed germination, ranging from 0% to 100% (Fig. 2A). It is possible that these differences in seed germinability among scat samples may be a result of differences in the seasonal timing of scat deposition. For example, scat samples with lower seed germinability may have been deposited earlier in the season, thus increasing the likelihood of seed exposure to desiccation or low temperatures, which can inhibit seed germination (Borchert and Tyler 2011, Wawrzyniak et al. 2020). Alternatively, these findings also indicate that the quality of dispersal by island foxes might vary as a result of individual fox traits or an individual fox's environment. Since we collected scat in an area estimated to contain at least 35 individual foxes (unpublished NPS data), we expect that the majority of our independent scat samples came from distinct individuals. It is therefore possible that between-sample variation in seed germination may reflect individual-level variation in seed dispersal quality by island foxes (Zwolak 2018, Zwolak and Sih 2020, Bartel and Orrock 2022). For example, scat samples with low probabilities of seed germination may have been deposited by individual foxes that consumed and hence digested greater amounts of unripened berries with seeds that were not fully mature. It is possible that socially subordinate foxes consume greater amounts of unripened berries if ripened berries are readily depleted by socially dominant foxes (Bartel and Orrock 2022). Moreover, an individual fox's size and diet can affect gut retention time, which may be a source of variation in seed germination between scat samples (Zwolak 2018, Zwolak and Sih 2020).

Future Directions

In finding that island foxes can be viable agents of seed dispersal for toyon, our results illustrate that variation in fox resource selection and space use may explain spatial patterns in seed movement and recruitment of fox-dispersed plant species on the Channel Islands. For example, recent work found that island fox populations exhibit a high degree of individualized diet specialization (Page et al. 2021), suggesting that the quantity of seed dispersal services provided by individual foxes may be highly variable. Considering both the results of Page et al. (2021) and our results, evidence suggests that island foxes may exhibit substantial individual-level variation in seed dispersal effectiveness. Future research examining potential endogenous and exogenous predictors of individual diet and germinability of digested seeds (e.g., individual social status, personality, or resource availability within the home range) may illuminate how individual-level variation in seed dispersal effectiveness by omnivorous mammals can contribute to spatial patterns in plant populations. Importantly, island foxes are known to consume substantial quantities of invasive plants (e.g., iceplant) and animals (e.g., deer and elk) on invaded islands (Cypher et al. 2014). Since increased consumption of nonnative food items may result in decreased consumption of native fruits, it is possible that the introduction of nonnative species to the islands may disrupt seed dispersal services to native plants by island foxes. Moreover, island fox movement and microhabitat use can affect seed dispersal distance as well as the likelihood of postdispersal seed survival (Schupp et al. 2010). Since food subsidies supplied by humans and individual fox social status are known to affect space use of other omnivorous fox species (Cancio et al. 2017, Dorning and Harris 2017, 2019), it is possible that human recreation on the Channel Islands and changes in island fox social structure could modify spatial patterns in seed movement and plant recruitment. Past work has indeed found that island foxes had smaller home ranges and consumed more anthropogenic foods near urban areas on human-inhabited San Clemente Island (Gould and Andelt 2013). It is therefore likely that human activities may alter the quantity and distance of seed dispersed by island foxes. Future research that tracks changes in individual fox behavior in response to environmental changes on the islands (e.g., human recreation or introduction of nonnative species), while explicitly measuring the quantity and quality of seed dispersal services by individual foxes, may reveal major gains or losses in seed dispersal for island plants.

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