

Introduced Galliforms As Seed Predators And Dispersers In Hawaiian Forests

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Abstract

In altered communities, novel species' interactions may critically impact ecosystem functioning. One key ecosystem process, seed dispersal, often requires mutualistic interactions between frugivores and fruiting plants, and functional traits, such as seed width, may affect interaction outcomes. Forests of the Hawaiian Islands have experienced high species turnover, and introduced galliforms, the largest of the extant avian frugivores, consume fruit from both native and non-native plants. We investigated the impact of two galliform species on seed dispersal processes in Hawaiian forests. Using captive Kalij Pheasants (*Lophura leucomelanos*) and Erckel's Francolins (*Pternistis erckelii*), we measured the probability of seed survival during gut passage and seed germination following gut passage. We also examined which seeds are being dispersed in forests on the islands of O'ahu and Hawai'i. We found that galliforms are major seed predators for both native and non-native plants, with less than 5% of seeds surviving gut passage for all plants tested and in both bird species. Gut passage by Kalij Pheasants significantly reduced the probability of seeds germinating, especially for the native plants. Further, larger-seeded plants were both less likely to survive gut passage and to germinate. In the wild, galliforms dispersed native and non-native seeds at similar rates. Overall, our results suggest the introduced galliforms are a double-edged sword in conservation efforts; they may help reduce the spread of non-native plants, but they also reduce seed dispersal of native plants. Broadly, we show mutualism breakdown may occur following high species turnover, and that functional traits can be useful for predicting outcomes from novel species' interactions.

Introduction

Ecosystems can be subject to abrupt changes in species assemblages following disruption by human activities (Steffen et al. 2011, Kueffer 2017), especially on oceanic islands (Fernández-Palacios et al. 2021). Species requiring mutualisms may be particularly vulnerable to the loss and gain of species (Christian 2001). For instance, the loss of mutualistic partners may cause reduced fitness of partners, mutualism breakdown, and even coextinction of native species (Chomicki and Renner 2017). The gain of species, on the other hand, can potentially benefit native species if non-native species substitute mutualistic partners that have gone extinct (Chimera and Drake 2010, Aslan et al. 2012). However, non-native species are often more likely to form mutualisms with one another, which can accelerate invasions, intensify negative impacts to the ecosystem, and ultimately result in invasional meltdown (Simberloff and Von Holle 1999, Simberloff 2006).

Seed dispersal is a key ecosystem process that often depends on mutualisms between fruit-eating animals (hereafter frugivores) and fruiting plants (Howe and Smallwood 1982). Fruiting plants are generally adapted for dispersal by many frugivore species through diffuse coevolution (Herrera 1982), yet frugivores vary in their effectiveness as dispersers for different plant species (Schupp 1993, Perea et al. 2013, Draxler and Kissling 2022). For instance, some frugivore species reduce seed survival during fruit handling and/or gut passage, such as those with powerful gizzards or chiseling teeth, while in other species, the probability of germination may increase following gut passage (Traveset 1998, Schupp 1993,

Larios et al. 2017). The impact of a frugivore species on seed dispersal depends not only on traits of the frugivore, but also on traits of the plant species, with seed size often being one of the most important functional traits (Galetti et al. 2013, Sperry et al. 2021, Vizentin-Bugoni et al. 2021). Seed size affects not only the probability of consumption by frugivores (e.g., birds typically do not consume fruits with seeds larger than the gape width of their bill, Wheelwright 1985), it may also impact rates of seed survival during gut passage and the probability of seed germination following gut passage (Dehling et al. 2016, Kleyheeg et al. 2018). Whether seed size positively or negatively affects survival during gut passage is variable and dependent on the frugivore species (Traveset et al. 2001). Thus, in altered communities, outcomes of novel plant-frugivore interactions are expected to vary with frugivore species and the seed size of plants, and overall impacts may differ for native and non-native plant species (Sperry et al. 2021, Martin-Albarracin et al. 2018).

Following human arrival (~800 years ago), forest ecosystems of the Hawaiian Islands have been transformed by high rates of both extinction and invasion (Lockwood 2006, Barton et al. 2021). While most woody native Hawaiian plants are adapted for dispersal by fruit-eating birds, nearly all frugivores native to the islands have gone extinct as a result of human activities (Boyer 2008, Case and Tarwater 2020). Many non-native species of fruiting plant and frugivore have become established, and novel seed dispersal networks have developed with non-native frugivores consuming and dispersing seeds primarily of non-native plants (Vizentin-Bugoni et al. 2019). In particular, the loss of large-bodied birds with large gapes, including terrestrial waterfowl (Anatidae) and corvids (Corvidae), may be causing dispersal-limitation in large-seeded plants (Chimera and Drake 2010, Culliney et al. 2012, Case and Tarwater 2020). For example, the smaller-gaped modern, mostly non-native bird assemblage, has not been documented dispersing plants with seeds wider than 8.1 mm (Sperry et al. 2021, Case and Tarwater 2020).

The largest birds in Hawaiian forests are now non-native galliforms, which were introduced for recreational hunting in the mid-twentieth century (Lewin and Lewin 1984). Owing to their larger body sizes and gape widths, galliforms have the potential to offer substitutive roles in dispersal of native plants, including species with larger seeds (Case and Tarwater 2020). There is some evidence of native and non-native plants being dispersed by one of the common galliforms, Kalij Pheasants (*Lophura leucomelanos*) on Hawai'i (Lewin and Lewin 1984) and both Kalij Pheasants and Erckel's Francolins (*Pternistis erckelii*) on O'ahu (Vizentin-Bugoni et al. 2021). Nevertheless, galliforms have powerful gizzards, which have the potential to destroy seeds during digestion (Carpenter et al. 2020, Santamaría and Franco 2000). The extent to which galliforms depredate seeds and whether this varies with seed width is uncertain. Kalij Pheasants and Erckel's Francolins occupy a large range of forested habitat across the Hawaiian Archipelago, where a large percentage of threatened and endangered plant species occur (Lewin and Lewin 1984, Carpenter et al. 2020, Case and Tarwater 2020). Given that galliforms have the potential to ingest and disperse many seeds, including those of large-seeded plants, it is critical to determine how they impact seed dispersal and seed predation, and whether they are aiding in or impeding the spread of native or non-native plants, or neither. Here, we tested the impact of galliforms on seed dispersal and the role of seed width by testing the probability of seed survival and germination following

gut passage using captive Kalij Pheasants and Erckel's Francolins. Lastly, we examined which seeds are being dispersed in the wild by these bird species in novel forests of O'ahu and Hawai'i.

Methods

Study areas

For this study, we combined data from two distinct investigations of seed dispersal by non-native galliforms, one on the island of Hawai'i occurring from 2004–2005 and the other on the island of O'ahu occurring from 2019–2021. On Hawai'i, we studied seed dispersal by Kalij Pheasants at two adjacent sites in Hawai'i Volcanoes National Park (HAVO), including Kīpuka Puauulu (19°26'21.21"N 155°18'11.21"W, hereafter PUA) and the 'Ōla'a Tract (19°27'33.75"N 155°12'20.31"W, hereafter OLA). Both PUA and OLA are mesic to wet forest at approximately 1,200 m asl. Although these sites were dominated by native plant species during the study, many non-native plant species had established populations within these areas. Captive Kalij Pheasants on Hawai'i were held in an aviary at Kilauea Field Station in HAVO.

On O'ahu, we studied seed dispersal by Kalij Pheasants and Erckel's Francolins at two adjacent sites in the northern Waiānae Range, including Kahanāiki Management Unit (21°32'12.55"N 158°11'35.40"W, hereafter KAH) and Pahole Natural Area Reserve (21°32'11.30"N 158°10'47.64"W, hereafter PAH). Both sites are mesic rainforest at elevations of 667 m for KAH and 594 m for PAH. Forests within KAH and PAH were composed of a mix of native and non-native plant species, with 40.2% and 30.4% of plant species dispersed by frugivores being non-native at KAH and PAH, respectively (details on O'ahu sites provided in Vizentin-Bugoni et al. 2019). Captive Kalij Pheasants and Erckel's Francolins on O'ahu were held at an aviary located at Waimea Valley Botanical Gardens.

Plant traits

Fruits were collected from study areas or other forested areas within each respective island. For all plant species tested in seed survival and germination experiments, we recorded seed width and the number of seeds per fruit, measured to estimate the total number of seeds ingested from fruits consumed in trials. Most measurements were taken from Sperry et al. (2021), who collected and measured seeds and fruits on O'ahu. For plant species not already measured (42.3% of plant species examined, N = 52), we measured them from fresh samples using the same protocol as Sperry et al. (2021). In brief, the width of the seed (or other diaspore, such as a hard achene or endocarp) was measured as the second-longest axis of each seed using digital calipers, and a mean value was calculated for each plant species from measures of 10 seeds per species. We measured seed width, as opposed to seed length (longest axis), because width imposes the greatest constraint on frugivores' ability to swallow a seed (Wheelwright 1985). The number of seeds per fruit was estimated for each plant species by counting all seeds within a fruit from 5–18 fruits per species (median = 10). For both measurements, fruits were collected from multiple individual plants to account for any potential individual variation in traits. Lastly, seeds were

photographed and/or kept as voucher specimens to assist with species identification of gut-passed seeds.

Seed survival

On Hawai'i, two Kalij Pheasants, one male and one female, were kept in a single cage, and on O'ahu, one male Kalij Pheasant and four Erckel's Francolins (including two males, one female, and one of unknown sex) were kept in separate open-air cages. Birds were fed a diet of cracked corn, a feed manufactured to meet nutritional requirements for galliforms, and occasional mealworms, peanuts, produce, and/or hard-boiled eggs. Further, small stones were provided within cages to serve as available gizzard grit to birds.

Overall, we conducted 194 gut passage trials in which birds consumed fruits (and seeds), comprising 172 trials with 49 plant species tested with Kalij Pheasants and 22 trials with 12 plant species tested with Erckel's Francolins. Across all plant species tested, 35 were native and 18 were non-native. A t-test showed that native and non-native plant species tested did not significantly differ in seed width (mean for native = 2.6 ± 1.8 S.D. mm, mean for non-native = 2.6 ± 1.2 S.D. mm, p-value = 0.908). For each trial, fruits were offered to birds at the beginning of each day and removed before the end of each day, with the exception of 16 Kalij Pheasant trials where fruits were offered continuously and overnight, during which frugivory was monitored and confirmed using a motion-activated game camera. The number of fruits offered per trial varied (range = 1–100) depending on the availability of fruit at collection sites, the size of fruits, and number of seeds per fruit (more fruits were offered when fruits contained fewer seeds). All fruits were counted at the start and end of each trial to determine how many fruits were consumed. The median number of consumed fruits was 15 (range = 1–100). Plant species trials were often repeated if no fruits were consumed. When at least one fruit was consumed, we waited a minimum of 5 days between the detection of an intact seed of the tested plant species and the start of the next trial with the same bird(s) and plant species, thus minimizing potential overlap in gut passage time between trials. Across all trials, the maximum gut passage time ranged from <1 to 53 days (median = 5 days, Appendix Fig. 1). Cages were thoroughly searched for feces each morning, before the start of feeding trials. Feces were collected from cages everyday while birds were in captivity. All collected feces were carefully sieved and examined. All intact seeds we detected were identified to species using a dissecting microscope, with reference to seed photographs and/or voucher collections. A seed was considered intact if there was no apparent damage to the exterior of seed coats or embryos. Most seed predation events were obvious (e.g. the seed was cracked or broken in half, Fig. 1), but if we encountered uncertainty, seeds were dissected beneath a microscope using a scalpel to determine whether embryos were intact, suggesting that the seed is potentially viable (Frischie et al. 2020).

The number of fruits consumed per trial was multiplied by the mean number of seeds per fruit for each plant species to estimate the total number of seeds consumed per trial. The number of intact seeds detected in feces was divided by the total number of seeds consumed to estimate the proportion of seeds surviving gut passage for each trial.

Seed germination

We compared germinability in seeds that were ingested by Kalij Pheasants and seeds that were not ingested (control). Overall, we tested seeds from 20 plant species: 6 non-native and 14 native. We selected these species because they occurred frequently in the Kalij Pheasant diet and/or seeds were available from wild plants at our sites. A t-test showed that native and non-native plant species examined did not significantly differ in seed width (mean for native = 1.8 ± 1.3 S.D. mm, mean for non-native = 2.0 ± 1.0 S.D. mm, p -value = 0.268). Ingested seeds were extracted from Kalij Pheasant feces collected in the wild, or fruits were fed to aviary birds and seeds were extracted from feces collected in the aviary. Only intact and seemingly fresh feces were collected from the wild, and because we were interested in the proportion of seeds germinated, rather than the speed of germination, the exact age of collected samples was unimportant for our research objectives. Seeds were extracted and identified from feces on the same day of collection. Control seeds were collected from at least five individual plants growing at the same site where the feces were collected. Fruit pulp was manually removed from control seeds. We had 358 replicates in total, comprising 5–10 replicates for each species treatment. Each replicate had its own Petri dish of 10–19 planted seeds (median = 10). All seeds were soaked in water for 24 hours immediately before planting. After soaking, seeds were placed in Petri dishes containing moist, sterile sand. Petri dishes were placed under timed full spectrum lights in a heated laboratory at HAVO (8–10 hours sunlight/day). Seeds were considered germinated upon the emergence of the radicle. After germinating, seeds were removed from Petri dishes so as not to interfere with germination of other seeds. Ingested and control seeds were monitored at least three times a week for 24 months.

Seed dispersal in the wild

Across study areas, feces were periodically collected from the ground in locations where birds were known to occur. Owing to their large size and coating of white urate, feces were easily identifiable as galliforms. On Hawai'i, Kalij Pheasants were the only galliform species established in our study areas, and thus, we did not need to use additional techniques to determine bird species. To distinguish between potential galliform species at our sites on O'ahu, we used DNA metabarcoding of fecal samples. Specifically, a small amount of each fecal sample was sequenced to determine the bird species prior to sorting through samples for seeds.

In total, we collected fecal samples on Hawai'i from January 2004 to December 2005, including 1588 samples from PUA and 845 samples from OLA. Fecal samples on O'ahu were collected from February 2017 to December 2018, and comprised 10 samples for Kalij Pheasants and 48 samples for Erckel's Francolins at PAH and 17 samples for Kalij Pheasants and 43 samples for Erckel's Francolins at KAH. Samples were kept in a freezer until sorting for seeds. Samples were sorted using a sieve, and intact seeds were counted and identified to species using a stereo microscope and a reference seed collection.

Statistical analyses

All data analyses were conducted using statistical software R version 4.1.1 (R Core Team 2020). Plant species was included as a random effect in all models. Our gut passage experiments were designed to test the effects of each predictor of interest, and thus each single term predictor was retained in all

models. However, we used AIC model selection to determine whether interactions between predictors should be retained in gut passage models, and a top model was chosen based on the lowest AIC value (Appendix, Table 1). For our dispersal models, we did not conduct model selection because our objective was simply to compare dispersal patterns based on bird species, study site, and plant origin (native or non-native).

Gut passage effects on seed survival. To examine the effect of gut passage on seed survival, data from Kalij Pheasants and Erckel's Francolins were pooled between study areas. After testing for non-linearity and finding none (using a generalized additive mixed model, GAMM), we used a generalized linear mixed effects model (GLMM) with a Beta error distribution. Our response variable was the proportion of seeds surviving gut passage (detected intact) from all seeds consumed by birds per trial. In our global model, we examined the predictor variables of bird species, seed width, plant origin, and two-way interactions between bird species and the other two predictors.

Gut passage effects on seed germination. We used a GAMM with a quasibinomial error distribution to test the effect of Kalij Pheasant gut passage on seed germination. For this analysis, we used a GAMM because the relationship between seed width and germination was non-linear (estimated degrees of freedom, or e.d.f. >1). Our response variable was the proportion of seeds that germinated from all seeds planted per treatment. Our global model included seed width (allowed to vary nonlinearly), plant origin, treatment (control or ingested), and two-way interactions between treatment and the other predictors.

Seed dispersal in the wild. To explore whether galliforms were more likely to disperse native versus non-native seeds and how dispersal varied between bird species and island, we used GLMMs with a Beta error distribution. Each island was modelled separately because our O'ahu sites had both bird species, whereas our Hawai'i sites had just Kalij Pheasants. Further, the islands differ in the extent of native and non-native plant species and in sample size. In each island-specific model, our response variable was the proportion of fecal samples that contained viable seeds of a particular plant species out of all fecal samples collected per site. We used this approach, as opposed to the number of seeds per species within fecal samples, because plant species vary in the number of seeds per fruit and in dispersal outcomes (e.g., germination rates). In the O'ahu model, predictor variables were plant origin, site, bird species, and an interaction between plant origin and bird species. In the Hawai'i model, plant origin and site were included as predictor variables.

Results

Gut passage effects on seed survival

Both galliforms were largely seed predators, with the predicted percentage of seeds surviving per trial ranging from 0.7–4.6%. However, Kalij Pheasants destroyed a significantly smaller percentage of ingested seeds (predicted mean = 3.5% of consumed seeds survived per trial, 95% CI = 2.0–6.2%) than Erckel's Francolins (predicted mean = 1.05% of consumed seeds survived per trial, 95% CI = 0.5–2.4%,

Fig. 2). Plant origin did not significantly affect seed survival (Table 1), suggesting that neither native nor non-native seeds are more likely to survive gut passage from plant species tested. Further, we detected a significant negative relationship between seed width and seed survival (Table 1). Specifically, larger seeds were less likely to survive gut passage than smaller seeds (Fig. 2). Our top model, with the lowest AIC, had no interactions, contained 35.8% of the model weight, and $R^2 = 0.64$ (Table 1, Appendix Table 1).

Gut passage effects on seed germination

Seeds that were in the control treatments (not gut passed) had a higher probability of germination, with 28.3% (95% CI = 12.3–52.3%, based on predicted output from the model) of planted seeds germinated, compared to seeds that passed through the gut of a Kalij Pheasant. Gut passed seeds had a 11.3% probability of germination (95% CI = 3.7–26.9%). Plant origin significantly affected germination, with native plant species less likely to germinate compared to non-native plant species, based on the plant species examined (Fig. 3A, Table 1, Appendix Table 2). Similar to our results for survival during gut passage, seed germination rates decreased with seed size (Fig. 3B, Table 1). Our top model with the lowest AIC contained 98.3% of the model weight and $R^2 = 0.37$ and included seed width, plant origin, and an interaction between the two (Table 1, Appendix Table 1).

Seed dispersal in the wild

Across all sites, 66.6% of fecal samples contained intact seeds, and 82.9% of fecal samples contained seed fragments (N = 1579 fecal samples). At our two sites on O'ahu, we detected five viable seeds from one native plant species and 3150 viable seeds from four non-native plant species in the feces of Erckel's Francolins (N = 91 fecal samples, Appendix Table 3). From Kalij Pheasant samples on O'ahu, we detected 50 viable seeds from four native plant species and 207 viable seeds from three non-native plant species (N = 27 fecal samples, Appendix Table 3). At our two sites on Hawai'i, we detected 37816 viable seeds from at least 18 native plant species and 15973 viable seeds from 10 non-native plant species in the feces of Kalij Pheasants (N = 2433 fecal samples, Appendix Table 3).

On both islands, plant origin did not significantly influence the probability of detecting seeds from a given plant species within feces (Table 1, Fig. 4). Further, bird species did not significantly differ in dispersal of native versus non-native seeds on O'ahu (Fig. 4). On O'ahu, study area influenced seed dispersal, with seeds of particular plant species at PAH being more likely to occur in a greater number of feces compared to those at KAH. In contrast, there were no differences detected on Hawai'i based on plant origin or study site (Table 1).

Discussion

In communities altered by extinction or invasion, the loss or gain of species may affect mutualisms, with cascading effects on ecosystem processes (Palmer et al. 2008, Traveset and Richardson 2014, Galetti et al. 2013). In the Hawaiian Islands, we show that non-native galliforms were largely seed predators for fruiting plants, with less than 5% of seeds surviving gut passage across all plant species examined.

Further, gut passage by galliforms reduced germinability of ingested seeds, particularly for native plants. We also found that larger seeds were less likely to survive gut passage and to germinate following gut passage. In the wild, we found that galliforms were equally as likely to disperse seeds from native versus non-native plants, with variation between sites. Collectively, these findings suggest that non-native galliforms are poor dispersers, with the majority of ingested seeds not surviving gut passage or germination. They may act as a double-edged sword in Hawaiian forests – reducing the spread of non-native plants, but also reducing the dispersal of native plants. Galliforms are now the largest birds in Hawaiian forests, and their larger gape widths (16.7 mm for Kalij Pheasants and 15.1 mm for Erckel's Francolins, Case and Tarwater 2020) suggest the potential to fill substitutive roles in dispersal of large-seeded plants. However, our results suggest an opposite scenario, by which gut passage by non-native galliforms reduces both seed survival and germination in large-seeded plant species. Hence, these birds may be replacing extinct native seed predators, rather than extinct native seed dispersers (Carpenter et al. 2020).

Galliforms are known to be major seed predators worldwide, likely due to their powerful gizzards. For instance, the Salvin's Currawong (*Mitu salvinii*) is highly frugivorous in its native range within the Amazon rainforest, but it destroys most of the seeds it consumes (Santamaría and Franco 2000). Destruction of non-native seeds is a potential conservation benefit of galliform introductions, and fruit removal by galliforms could reduce availability of invasive seeds and dispersal by other frugivores in the system. However, predation on native seeds may offset these benefits. In plants which produce a high number of seeds per fruit, even a low gut passage survival rate may contribute to substantial rates of dispersal. For instance, seeds of *Rubus rosifolius*, a common invader with 246 seeds per fruit, on average, had a mean gut passage survival rate of 5.4% for Kalij Pheasants. Given that an average of 38% of *Rubus rosifolius* seeds germinated following Kalij Pheasant ingestion, we predict five dispersed seeds to germinate after a single fruit is consumed by a Kalij Pheasant. Native plants with many seeds/fruit may similarly be dispersed. For instance, if we apply the same formula to *Cyanea tritomantha*, a native and federally endangered species, we predict nine dispersed seeds to germinate for each fruit consumed by a Kalij Pheasant. Further, we found that the duration of galliforms gut passage was notably long (median day that last seed was detected per trial = 5, range = 0–53 days, Appendix Fig. 1). Thus, in conjunction with animal movement, galliforms may be capable of long-distance dispersal events, potentially aiding in the range expansion of native or non-native plant species.

The effect of gut passage on seed germination varies across plant-frugivore species interactions, with both positive and negative effects observed (Traveset et al. 2001, Dracxler and Kissling 2021). We found that ingestion by non-native galliforms significantly reduced germination rates, and the effect was greater for the native plants that we tested. This suggests that even if ingestion rates were equal for seeds of native and non-native plants, intact seeds from non-native species would still be more likely to germinate compared to native seeds. Similar results have been found in other systems with introduced galliforms. For instance, in Patagonia, following gut passage of the introduced Silver Pheasant (*Lophura nycthemera*), seeds of non-native species are more likely to germinate compared with seeds native to the study area (Martin-Albarracin et al. 2018). From the 20 plant species that we tested, only 4 had higher

germination rates following gut passage, 3 of which were non-native and belonged to the genus *Rubus* (Appendix Table 2); a genus that comprises numerous invasive species worldwide (Caplan and Yeakley 2013). The native and non-native species we examined did not significantly differ in seed width for species used in both survival and germination experiments, and broadly, fruit and seed traits are similar between native and non-native plants in Hawaiian forests (Sperry et al. 2021). It is currently unclear why native species may be more vulnerable to novel species interactions, and traits not examined here, such as seed-coat thickness (Traveset 1998), may be important for interaction outcomes. Further work is needed to identify the mechanisms that bias dispersal outcomes in relation to plant origin.

In novel ecosystems, one important consideration is how selection on functional traits may be altered following changes to communities (Strauss et al. 2006, McConkey et al. 2012). In modern forests of the Hawaiian Islands, non-native Passeriformes, with their small gape widths, dominate seed dispersal networks (Vizentin-Bugoni et al. 2019; 2021) and, as found here, smaller-seeded plants are more likely to survive and germinate following ingestion by galliforms. Thus, we may expect negative selection on seed width driven by the current frugivore assemblage, which may alter species interactions and affect the evolutionary trajectories of plants over time. For example, in Atlantic forests of the Amazon, the recent loss of large-gaped frugivores led to a rapid reduction in seed size in a common palm species (Galetti et al. 2013). If smaller seed widths are consistently selected for through interactions with frugivores, we may observe turnover in plant communities in relation to seed size or an evolutionary response in certain plants. A reduction in seed size may increase the probability of consumption, survival, and germination, but may reduce growth rate, reproduction, and survival in the later life history stages (Ambika et al. 2014). This will result in differing impacts on plant populations depending on which life stage is most important to population growth (Ambika et al. 2014).

Non-native birds now dominate seed dispersal networks in Hawaiian forests (Vizentin-Bugoni et al. 2019) and fill the most important roles in the seed dispersal network (Vizentin-Bugoni et al. 2021). The extent to which these birds disperse native versus non-native plant species may, not surprisingly, depend on the extent to which non-native plants are established where birds reside. For instance, on the island of Maui, non-native birds in native-dominated forests dispersed mostly native seeds in montane rain forests (Foster and Robinson 2007) and mostly non-native seeds in dry forest (Chimera and Drake 2010). On O'ahu, where forests are highly invaded, non-native birds dispersed mostly seeds from non-native plants (Vizentin-Bugoni 2019). However, frugivore preferences for certain plants may also affect observed rates of seed dispersal (Aslan and Rejmánek 2012). Between our sites on O'ahu and Hawai'i, we did not detect differences in the probability of whether a given seed species within feces was native or non-native in origin (Appendix Table 3). To further distinguish how dispersal patterns for native versus non-native plants may depend on plant community composition, future work should consider the relative abundance of different fruits and galliform preferences for native and non-native plants. Further, we examined just two of at least 10 non-native galliforms with populations established in the Hawaiian Islands (Carpenter et al. 2020), and more work is needed to determine the impacts of the other species.

Global rates of species extinction are currently an estimated 1000 times greater than what would be expected without human influence (Pimm et al. 2014). Concurrent with species loss, humans have facilitated species invasions across all of the world's biomes (Ricciardi 2007), with effects being particularly severe on oceanic islands (Fernández-Palacios et al. 2021). In the Hawaiian Islands, we found that novel species interactions between non-native galliforms and fruiting plants are often negative for plants. Further, we identified a functional mechanism driving interaction outcomes, with seed size influencing both survival during gut passage and germination thereafter. Collectively, these results indicate that the non-native frugivores studied here are not filling the role of extinct native large-gaped frugivores, potentially contributing to the decline of large-seeded native plants. Further, results suggest that seed size may be useful for predicting interaction outcomes and could be used in aiding management strategies. In the Hawaiian Islands, land managers will need to weigh costs and benefits of seed dispersal versus predation for native and non-native plant communities where galliforms are established. High rates of seed predation may warrant the exclusion or removal of galliforms from areas with native fruiting plants of conservation concern.

Statements & Declarations

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DATA AVAILABILITY STATEMENT

In accordance with journal requirements, all data will be archived in a publicly available repository before article publication.

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Tables

Table 1. Results for models of (A) seed survival, (B) seed germination, and (C, D) seed dispersal on O'ahu and Hawai'i. An e.d.f value is provided for the smoothed term within our GAMM, whereas β values are provided for all other non-smoothed (linear continuous or categorical) terms from our GLMMs. Predictors in bold are significant (p-value <0.05).

Model	Predictor	e.d.f.	β	SE	p-value	
(A) Seed survival ($R^2 = 0.640$)						
	Bird species		Erckel's Francolin (intercept)	-3.850	0.540	<0.001
			Kalij Pheasant	-2.610	0.855	
	Plant origin		Non-native (intercept)	-3.850	0.540	0.162
			Native	-3.243	0.975	
	Seed width			-0.402	0.115	<0.001
(B) Seed germination ($R^2 = 0.372$)						
	Treatment		Control (intercept)	-0.817	-0.620	<0.001
			Gut passage	-1.676	-0.439	
	Plant origin		Non-native (intercept)	-0.817	-0.620	0.824
			Native	-0.651	0.127	
	Treatment*Plant origin		Gut passage*Native	-1.811	-0.378	<0.001
	Seed width		(smoothed term)	1.38		0.010
(C) Seed dispersal on O'ahu ($R^2 = 0.533$)						
	Bird species		Erckel's Francolin (intercept)	-2.087	0.587	0.994
			Kalij Pheasant	-2.084	0.939	
	Plant origin		Non-native (intercept)	-2.087	0.587	0.366
			Native	-3.439	2.083	
	Bird species*Plant origin		Kalij Pheasant*Native origin	-1.261	2.251	0.620
	Site		KAH (intercept)	-2.087	0.587	0.005
			PAH	-1.176	0.910	
(D) Seed dispersal on Hawai'i ($R^2 = 0.049$)						
	Plant origin		Non-native (intercept)	-2.503	0.339	0.198

	Native	-2.066	0.679	
Site	OLA (intercept)	-2.503	0.339	0.293
	PUA	-2.066	0.670	

Figures



Figure 1

Image of seeds of *Rubus rosifolius* (viewed through a microscope) that were ingested by an Erckel's Francolin, with three depredated seeds on the left and three intact seeds on the right.

Figure 2

Predicted relationship between seed width (mm) and seed survival from gut passage by the (A) Kalij Pheasant and (B) Erckel's Francolin. The yellow area surrounding the curves represents the 95% confidence intervals.

Figure 3

Predicted germination rates of seeds for (A) non-native (red) and native (gray) plant species between control (left) treatments and the gut-passed treatments (right, passed through the gut of Kalij pheasant) and (B) based on seed width for ingested seeds. For (A), diamonds depict predicted values with lines extending to the upper and lower 95% confidence intervals. For (B), shaded area around curves represents 95% confidence intervals.

Figure 4

Modelled probability of detecting a given plant species within feces for non-native (red) and native (grey) plant species at study areas for Kalij Pheasants at (A) KAH and PAH on O'ahu and (B) OLA and PUA on Hawai'i and for Erckel's Francolins at (C) KAH and PAH on O'ahu. Diamonds are predicted values and brackets represent 95% confidence intervals.

Supplementary Files

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