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FORAGING BEHAVIOR PARTITIONING AND INTERACTIONS OF TWO ISLAND INVASIVE BIRDS: THE COMMON MYNA (*ACRIDOTHERES TRISTIS*) AND THE RED-VENTED BULBUL (*PYCNONOTUS CAFER*)

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Abstract. The study of systems containing multiple invasive species has long been superseded by the study of invasive impacts on native species. However, systems containing more than one invasive are likely to see the presence of ecological effects as a result of the relationships between those species. These effects are likely to be magnified in situations where invasives occupy similar niches. In this study I examine the foraging behaviors of two sympatric invasive bird species to determine if there is partitioning in either how, or where they forage. I also investigate their behavioral responses to the introduction of novel food stations, and natural fluctuations in foraging group size and species composition. Lastly I examine both their interspecific and intraspecific interactions. Results show that partitioning is present for both foraging behaviors and certain substrates being foraged on. Additionally, behavior at feeding stations trended towards foraging as opposed to vigilance. In conspecific groups, there were no behavioral changes observed with increasing group size in either species. However, the presence of heterospecifics was so rare, that no conclusions could be drawn about changes in foraging behavior for either species. Furthermore, intraspecific interactions were far more frequent, and of a greater agonistic intensity than interspecific interactions. These results imply that the two species are actively avoiding competition with each other, which contributes to both species being successful invasives.

Key words: *tropical invasion; Passeriformes; sympatric species, feeding stations; vigilance; Mo'orea, French Polynesia*

INTRODUCTION

Invasive species are being introduced into novel ecosystems at a rapidly increasing rate (U.S. Congr. Off. Technol. Assess. 1993). To date, most research involving invasion biology has focused on the impact of one invasive species on a native species and its ecology. Such research is typically undertaken in order to draw conclusions about population biology and conservation (Pell and Tidemann 1996, Blanvillain et al. 2003, Sakai et al. 2001). However, there is currently a lack of literature touching on the interactions between, and coexistence of multiple invasive species. The relationships between multiple invasives are equally important to study because of potential facilitative or inhibitory effects they may have on each other, which can lead to consequences such as invasional meltdown (Simberloff and Von Holle 1999, O'Dowd et al. 2003) and changes in community composition and structure (Vitousek 1990). These effects are in turn relevant to answering questions about their impacts on native taxa. Two of the

most invasive species in the world, as listed by the International Union for Conservation of Nature (IUCN), are the Common Myna (*Acridotheres tristis*) and the Red Vented Bulbul (*Pycnonotus cafer*), making them ideal study organisms for investigation (Lowe et al. 2000), and they are both present in significant numbers in Mo'orea.

A. tristis was introduced to the Society Islands around 1910 as a caged bird, and for the purpose of biological control of invasive wasps (Blanvillain et al. 2003). They are generalist feeders that scavenge for nearly any type of food, which contributes to their effectiveness as an invasive (Sontag and Louette 2007). *P. cafer* was introduced more recently circa 1970, also as a popular caged bird (Blanvillain et al. 2003). While they are also generalists, fruits and berries make up a significant portion of their diet (Bhatt and Kumar 2001), so they are considered to be more of an agricultural pest (Islam and Williams 2000, Walker 2009). Both species originate from Southern Asia and have spread to many other parts of the Old World as well

as Australia, New Zealand, and many of the Pacific Islands (Kannan and James 2001, Islam and Williams 2000). Both have also been observed to exhibit aggressive behavior towards conspecifics and heterospecifics (Feare and Craig 1999, Short 1964, Ralph 1984, Pernetta and Watling 1978).

Today, both species are rampant in human impacted areas of Mo'orea. Individuals of both species are frequently seen foraging and perching within several meters of each other. Typically, species which are able to coexist in such a manner exhibit partitioning behaviors that push each species into a different niche to avoid excessive competition that could otherwise be detrimental to both populations, a critical concept brought up by MacArthur (1958) in his paper explaining the coexistence of sympatric warblers. Partitioning most often occurs when there is a resource in limited supply such as food or foraging space (Udvardy 1951). Because *A. tristis* and *P. cafer* are both generalist feeders, there is likely some overlap in their foraging sites and behaviors. Studying these species' foraging behavior and interactions can shed light on how they coexist and utilize similar ranges, which is what this study aims to do.

First, I examine the foraging behaviors and foraging locations of each species to determine if partitioning is present and to what extent. If present, partitioning would explain a great portion of how both species are able to be successful. Feeding stations were also introduced to compare each species' behaviors at these novel sites and at regular observation sites. As invasive human commensals, these birds constantly have to adjust to disturbance and novel presences. Therefore their behaviors at my observation sites and feeding stations may reflect such adaptability. Additionally, the effects of foraging group size and species composition on foraging behavior are examined for each species. Furthermore, this study investigates the interspecific and intraspecific interactions amongst these species to look for the presence of competition or dominance relationships.

The following hypotheses were considered: (1) *A. tristis* and *P. cafer* exhibit partitioning in both their foraging locations and foraging behaviors. (2) Behaviors observed at feeding stations are expected to trend towards vigilance because of the unnatural and novel presence of the stations. (3) Larger conspecific foraging groups would result in a decrease in vigilance behavior per

individual (Pulliam 1973), but a greater presence of heterospecifics increases competition and therefore would result in an increase in vigilance behavior. (4) Both interspecific and intraspecific interactions will be frequent, however intraspecific interactions will tend to be more agonistic. Exploring these questions and hypotheses via behavioral observations provides insight into the two species' foraging behaviors and interactions.

METHODS

Study sites

The two bird species were observed between October 2011 and November 2011 in Mo'orea, French Polynesia. The primary study site was located at the Richard Gump Research Station and its surrounding areas, which are approximately 3 ha in size (17°29'25"S, 149°49'36"W). The second major site was a public beach located near the northern tip of the island and approximately 2.5 km away from the Gump Station (17°29'30"S, 149°51'0"W). No feeding stations were set up at this location due to the significant amount of human traffic that passes through the area. There would have been potential for human traffic to alter either the legitimacy of the feeding station or the data collected. A third site was the island's Agricultural School situated in the 'Opunohu Valley (17°31'54"S, 149°50'9"W). However, due to both human traffic, and limited visits to this site, no feeding stations were set up.

Foraging behavior and substrates

Throughout the study, neither species were ever captured or handled. All data collected were based solely on visual observation. Data on foraging behavior were collected at various times between 0800 and 1600. Observations were done either with the naked eye, or with the aid of 8x42 binoculars. Foraging behavior was measured by selecting an individual to track for as long as possible before the individual was out of view. The maximum amount of time any one individual was observed for was 10 minutes. Every 30 seconds, three main observations were collected: 1) Behaviors were recorded as one of the following: preening, beak cleaning, flying, perched scanning, ground scanning, perched gleaning, or ground gleaning. Perched scanning and ground scanning are categorized as "vigilance", perched gleaning and ground

gleaning as “foraging”, and preening, beak cleaning and flying as “other” behaviors. 2) Approximate height of the individual from the ground was estimated and recorded as: 0m, 0-3m, 3-6m, 6-9m, 9-12m, or 12-15m. 3) Substrate the individual resided on was recorded as: air, dead brush, dirt, grass, man-made structure, or tree branches.

At feeding stations, an individual was selected randomly to observe for that period. Observation periods lasted only as long as the individual was in view. When that individual was no longer observable, a new individual would be selected randomly to observe for the next period. Individuals not observed at feeding stations were selected by standing at an observation point, then quickly scanning the surrounding ground and vegetation.

Feeding stations

Three novel feeding stations were set up around the Gump Station. Feeding station 1 (FS1) was placed approximately 1.5m above ground and spaced several meters on each side in between two buildings. The structure of the station was constructed out of wood and tape, and three layers of fixed cardboard made up the platform of the station (Fig. 1). Feeding station 2 (FS2) was located near the hill bungalows. A dish was set on a concrete block jutting out from the ground to provide a few inches of elevation off the ground and to deter ants. For all data analysis, feeding station 2 was considered to be located on the ground. Feeding station 3 (FS3) was placed approximately 1m off the ground and 5m away from a dirt road. Every day new food was added to each of these stations and would include small amounts of 1-2 of the following: avocados, bananas, papayas, and oranges.



FIG. 1. Photograph showing the platform of feeding station 1, with an individual of *P. cafer* present. (Photo by J. Bates)

Observations at feeding stations were conducted in the same manner as other foraging behavior observations, with the exception that the absolute time the focal individual was present at a station was recorded as well.

Interspecific and intraspecific interactions

Chase events and agonistic encounters between conspecifics and heterospecifics were sampled for on a presence-absence basis during the observation period of a focal individual. The observation period would end once the focal individual was no longer visible, or had been observed for 10 minutes, the maximum amount of time any individual was to be observed.

Statistical analysis

All statistical analyses were performed in the software program JMP (Version 9). Foraging behavior was analyzed using analysis of variance (ANOVA) on behavior and substrate data with species as a fixed factor. Data on feeding station behaviors was also analyzed using ANOVA to compare and contrast the ratio of vigilance behavior to foraging behavior with observation sites as a fixed factor.

RESULTS

Partitioning of foraging behavior and substrates

There was no significant difference between *A. tristis* and *P. cafer* with regards to the amount of time spent being vigilant, foraging, or doing other activities (Fig. 2) Both species allocated the same percentage of their time to each three categories of behavior

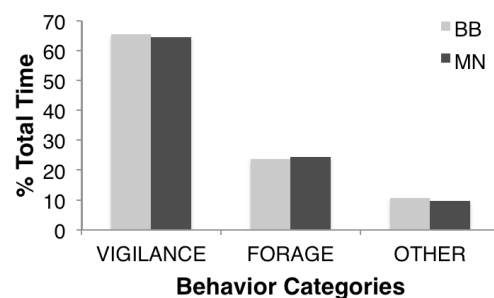


FIG. 2. The percentage of total observation time spent being vigilant, foraging, or doing other activities for *A. tristis* (MN) and *P. cafer* (BB).

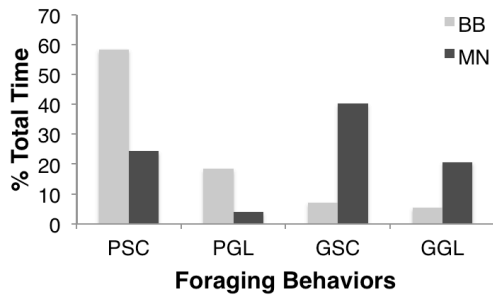


FIG. 3. The percentage of total observation time that was spent perch scanning, perch gleaning, ground scanning, or ground gleaning for *A. tristis* (MN) and *P. cafer* (BB).

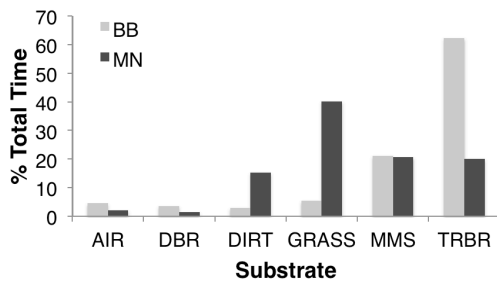


FIG. 4. The percentage of total observation time that was spent on each substrate for *A. tristis* (MN) and *P. cafer* (BB).

(one-way ANOVA, $F_{1,202} = 0.0431$, $P = 0.8357$; $F_{1,202} = 0.0236$, $P = 0.8780$; $F_{1,202} = 0.2120$, $P = 0.6457$). However, partitioning was found between the species for both foraging behaviors and foraging locations.

Out of eight behaviors, four did not differ (preening, vocalization, beak cleaning, and flying) between the two species, and four were significantly different (perched scanning, perched gleaning, ground scanning, and ground gleaning). The four significantly different behaviors all fall under the behavior category of foraging (Fig. 3). MN was spending significantly more time ground scanning and ground gleaning (one-way ANOVA, $F_{1,202} = 82.2179$, $P < 0.0001$; $F_{1,202} = 23.8313$, $P < 0.0001$). BB on the other hand was spending significantly more time perch scanning and perch gleaning (one-way ANOVA, $F_{1,202} = 55.7798$, $P < 0.0001$; $F_{1,202} = 14.6750$, $P = 0.0002$).

Preferred substrate for *P. cafer* was tree branches, whereas preferred substrates for *A. tristis* were dirt and grass (Fig. 4). The three substrates that showed the greatest difference

between the two species were dirt, grass, and tree branches (one-way ANOVA, $F_{1,202} = 13.8421$, $P = 0.0003$; $F_{1,202} = 63.3059$, $P < 0.0001$; $F_{1,202} = 64.5443$, $P < 0.0001$). *P. cafer* and *A. tristis* spent equal amounts of time on man-made structures, and dead brush (one-way ANOVA, $F_{1,202} = 3.0630$, $P = 0.0816$; $F_{1,202} = 2.9599$, $P = 0.0869$). *P. cafer* was shown to just barely prefer air over *A. tristis* (one-way ANOVA, $F_{1,202} = 8.0011$, $P = 0.0051$). The average height found for *A. tristis* was 2.1853 meters, and the average height for *P. cafer* was 6.0701 meters, which was much higher (one-way ANOVA, $F_{1,202} = 56.1022$, $P < 0.0001$).

Feeding stations

Only two of the three feeding stations (FS1 and FS2) were visited frequently by birds. I was only able to collect observational data twice for FS3, and therefore excluded data from that station entirely. Vigilance behavior was the same across all observation sites that were not feeding stations (Fig. 5). However at FS1 and FS2, both species exhibited a decreased level of vigilance as compared to the other sites (one-way ANOVA, $F_{9,190} = 23.8054$, $P < 0.0001$) (Fig. 5a). In addition, FS1 and FS2 showed increased levels of foraging behavior for both species as compared to the other sites (one-way ANOVA, $F_{9,190} = 25.8735$, $P < 0.0001$) (Fig. 5b).

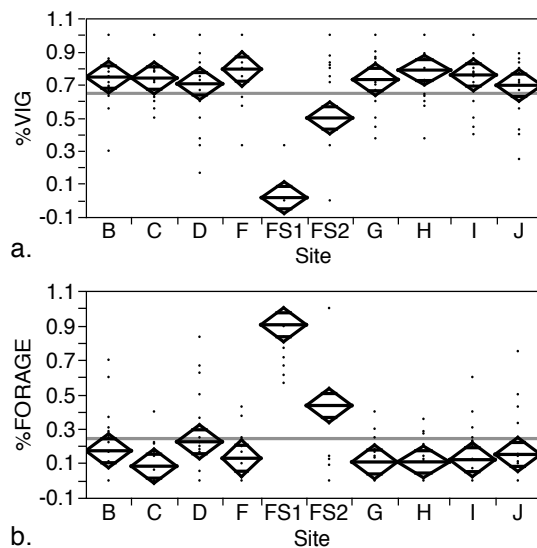


FIG. 5. (a) Percent time being vigilant at each observation site. (b) Percent time foraging at each observation site. Rhombuses show means and standard error for each site. Vertical axis denotes percent time as a fraction of 1.

Average total time spent in view at feeding stations was less than 50% of the average total time spent in view at other sites.

P. cafer was first observed at the feeding stations the same day that the station was placed. The first appearance of *A. tristis* at the feeding stations occurred 10 and 16 days after the first appearance of *P. cafer* (at FS1 and FS2, respectively).

Group size and species composition

A. tristis and *P. cafer* were observed with conspecifics more frequently than with heterospecifics. Both species were rarely observed with heterospecifics. Time with heterospecifics present made up only 4.8% of total observation time. On the other hand, conspecifics were present in 54% of the total observation time. However, the presence of conspecifics had no effect on foraging behavior for either species (Fig. 6). The number of conspecifics present ranged from 0 to 9 for *A. tristis* and 0 to 4 for *P. cafer*. As the number of conspecifics increased for either species, the percent time spent being vigilant, foraging, or exhibiting other behaviors had no change.

Interspecific and intraspecific interactions

Interspecific interactions did occur, but were rare. There were only 3 observed interspecific interactions, and all 3 involved an individual of *A. tristis* displacing one or more individuals of *P. cafer* (Table 1). However, intraspecific interactions were frequent, and nearly all of them were agonistic. Interactions within *A. tristis* consisted of threat calls, chases and occasionally fights. Two fights were observed, and both occurred between two or more mating pairs of *A. tristis*. One fight

TABLE 1. Count of interspecific and intraspecific interactions. Vertical axis is the instigator of the interaction, and the horizontal axis is the supplanted/chased individual.

	<i>P. cafer</i> (BB)	<i>A. tristis</i> (MN)
<i>P. cafer</i> (BB)	17	0
<i>A. tristis</i> (MN)	3	3 (2)

Note: Under *A. tristis* x *A. tristis*, the number in parentheses indicates number of fights, whereas all other counts indicate chases or displacements.

occurred at the base of a tree containing a large nest cavity. The other occurred on an open sandy beach near a picnic table. Interactions within *P. cafer* consisted of threat calls, air borne chases, and at times courtship rituals. All of the events occurred at different sites, and none of them were at or near a feeding station.

DISCUSSION

In this study I examined four different, but related questions about the foraging behavior and interactions of *A. tristis* and *P. cafer* to determine how both of these species are able to be successful.

I asked if there is partitioning in their foraging behaviors and foraging locations, and hypothesized that partitioning would be present for both. I found that both species allocate their time between foraging and being vigilant similarly, suggesting that neither of the species is making a more significant effort than the other in searching for food. However, my results support my hypothesis and indicate that there is partitioning for both behaviors and foraging locations. The four behaviors that were found to be significantly different (perched scanning, perched gleaning, ground scanning, and ground gleaning) all make up my behavior category of "foraging behavior". *A. tristis* predominantly exhibited ground scanning and ground gleaning behaviors, which is similar to what previous studies on the species have found (Crisp and Lill 2006, Asokan and Mohamed Samoor Ali 2010), whereas *P. cafer* predominantly exhibited perched scanning and perched gleaning behaviors. Because of the way I defined behaviors in my ethogram, there is some inherent substrate preference built in to the way I collected data on foraging behavior. By defining a behavior as ground scanning, I included information about the individual being on the ground. This is an important bias to consider when evaluating the data on behavior.

My results suggest behavioral partitioning is present, because of both the observed differences between the two species for foraging behavior, and the lack of differences in behaviors categorized as "other". This means that when it comes to flying, vocalizing, or cleaning their beak, *A. tristis* and *P. cafer* are exhibiting these behaviors equally as often as each other, but for behaviors involved in either searching for food or scanning their surroundings, they differ.

Substrate preference also showed significant partitioning. *A. tristis* preferred dirt and grass, while *P. cafer* preferred tree branches above all else. It's possible that this substrate partitioning is a result of dietary differences (MacArthur 1958). As mentioned before, *P. cafer* has a diet that is composed primarily of fruits and berries (Islam and Williams 2000), both of which grow in trees and shrubs off the ground.

Morphology and evolutionary history could also play an important role in how and why these species are partitioned in this manner (Gokula and Vijayan 2000). Through personal observation, I noted that *A. tristis* moves across the ground in a bipedal fashion. This is consistent with most other members of its family, Sturnidae, which have long, strong legs and prefer walking as opposed to hopping (Feare and Craig 1999). Conversely, *P. cafer*, as with the rest of its family Pycnonotidae, is built more as a perching bird with short slender legs (Harrison and Worfolk 1999). When *P. cafer* moves around on the ground or along tree branches, it hops, and typically does not do so for as extended a period of time, as *A. tristis* is able to walk. This implies that *A. tristis* may have preferred ground behaviors and substrates, because of the ease with which they move on the ground. On the other hand, *P. cafer* must hop from place to place, which could explain why they weren't typically found on the ground.

Another hypothesis I tested is that in the presence of a feeding station, individuals would exhibit more vigilance behavior to account for the novel factor of the station. My results indicated that percent time spent being vigilant at both FS1 and FS2 was significantly less than the amount of time spent being vigilant at any other observation site. Consequently the percent time spent foraging at feeding stations was much higher than at other observation sites. These results do not support my original hypothesis.

I also made note of the amount of time individuals were observed at a feeding station before they flew out of sight, and found that this time was significantly less than the time spent observed at any other site. It appears that they are still wary of the station. However, instead of increasing vigilance behavior to account for novelty, they decrease both vigilance and time spent at the station, and instead focus on maximizing food intake in a short period of time. The decrease in vigilance behavior, while counter-intuitive, may be due to an invasive characteristic of the

bird. Invasive species are typically more adaptable to disturbance and human-impacted areas (Lowe et al. 2011). The birds may also be executing a "stuff and run" method of acquiring food at these stations. They may be doing this because of potential predator threats, or because they want to avoid competing with other birds for food at the station.

A previous study comparing birds in urban and natural habitats suggests that the urban environment may actually be less dangerous for certain species (Shochat et al. 2004). The use of feeding stations in that study yielded results that indicate birds spend more time at feeding stations in urban environments rather than identical feeding stations in a natural environment. Shochat et al. conclude that those results were observed because their primary study species, *Carpodacus mexicanus*, House Finch, *Columbina inca*, Inca Dove, *Zenaida macroura*, mourning dove, and *Passer domesticus*, House Sparrow are highly adapted to urban environments. Their conclusions imply that *A. tristis* and *P. cafer*, both highly adapted to urban environments as well, should exhibit the same patterns of behavior, however, my results show the exact opposite. This may be because I did not specifically test feeding stations in both natural and urban environments. Instead, I considered the presence of a feeding station enough of a novel presence to elicit certain behavioral responses that would differ from natural observations.

The introduction of feeding stations also shined light on a possible discovery-dominance relationship between *A. tristis* and *P. cafer* (Perfecto and Vandermeer 2011). Individuals of *P. cafer* arrived at my feeding stations within a day of me setting them up. However, I did not observe *A. tristis* at those stations until several days after the first appearance of *P. cafer*. Additionally, on two occasions I observed *A. tristis* displacing *P. cafer* at a feeding station once it arrived. The displaced *P. cafer* would only return to the station once *A. tristis* had left. Three quarters of the observations conducted at feeding stations were on *P. cafer*. This could indicate that they're less wary of exploring novel food sources than *A. tristis*. It could also mean they are able to find and exploit food sources more easily (Perfecto and Vandermeer 2011). In any case, *P. cafer* is the first to arrive, but upon arrival of an individual of *A. tristis*, *P. cafer* leaves and *A. tristis* is able to dominate the feeding station.

I also investigated whether a larger group size or variable species composition of that group would influence foraging behavior in any way, and hypothesized that larger conspecific group sizes would result in decreased vigilance per individual due to Pulliam's "many eyes" hypothesis (1973). However, a greater presence of heterospecifics would result in increased interspecific competition and consequently increased vigilance behavior. Heterospecifics were present in such low numbers that I was unable to find any significance in the little data that I had. The fact that there was not a lot of data on heterospecifics, suggests that the two species do not spend much time together at all. Both species however, do spend a significant amount of time in the presence of conspecifics. For *A. tristis* the number of conspecifics ranged from 0 – 9, and for *P. cafer* 0 – 4. Even with these numbers of conspecifics, there was no effect on foraging behavior observed for either species, which does not support either my hypothesis or Pulliam's. Lima (1995) suggests that Pulliam's hypothesis is not as straightforward as suggested, and that it assumes several conditions. One of those conditions is that individuals determine their own level of vigilance by monitoring the vigilance levels of other group members. Lima's study on mixed flocks of *Junco hyemalis*, Dark-eyed Junco, and *Spizella arborea*, American Tree Sparrow, demonstrate that group size itself does not directly determine amount of vigilance behavior exhibited. It's possible that *A. tristis* and *P. cafer* do not follow Pulliam's hypothesis because they do not adhere to the assumed condition of behavioral monitoring. Individuals of each species may not feel the need to monitor the vigilance behaviors of others because the vigilance behavior they exhibit themselves is sufficient enough to keep an eye out for potential dangers.

Lastly, I observed the interspecific and intraspecific interactions amongst these two species to investigate the degree of interference competition present, and to test whether interspecific interactions were more frequent than intraspecific ones. Contrary to my hypothesis, I found intraspecific interactions to occur at a much greater frequency than interspecific ones.

The relative frequency of agonistic intraspecific interactions to interspecific ones implies that instead of there being competition between *A. tristis* and *P. cafer*, much of the competition is occurring within each species.

However, even though these agonistic interactions occur, none of them were observed at or near a feeding station, nor were they in the context of food at all. One of the two fights observed that occurred between three mating pairs of *A. tristis* happened at the base of a tree containing a large, deep nest cavity. This suggests that the fight may have actually been territorial in nature. It's possible that the limiting resource in this system is habitat rather than food availability.

The lack of interspecific interactions suggests the species may have developed avoidance behaviors to reduce interspecific conflict. In addition, the three observed interspecific interactions involved *A. tristis* displacing *P. cafer*, suggesting that the mechanism for avoidance behaviors may be the establishment of a dominance hierarchy between the two species where *A. tristis* is dominant to *P. cafer*. This lack of interspecific interaction, in conjunction with partitioning as a form of avoidance behavior suggests that the two species actively try to avoid each other, which could explain how they are both able to be successful.

Conclusion

A. tristis and *P. cafer* have been coexisting in Mo'orea for nearly 40 years. Their impacts on each other, and on the native flora and fauna undoubtedly exist, and the relationships between invasives such as these are often crucial in understanding invasive effects on natives. A potential future research direction would be to incorporate one or more of the island's native species into a study on *A. tristis* and *P. cafer*, and to examine all possible relationships amongst them. Another would be to study the actual foods these two species are consuming. I've concluded that they are foraging in different places and with different behaviors, but are they also eating different foods? Additionally, a comparative study of these two species on Mo'orea, an introduced range, and in South and Southeast Asia, where they both originate, could provide answers to invasive control problems. Partitioning and interspecific dynamics go a long way in explaining how these two species are able to coexist, but the relationship between them is a lot more complicated than how and why they avoid each other, and hopefully future studies on these species will be able to address those complications.

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