

Foraging behaviour and habitat partitioning in sympatric invasive birds in French Polynesia

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Abstract Interactions among invasive bird species have received relatively little attention despite the potential important consequences for community dynamics and invasion spread. Where species occupy similar environments the outcome may be particularly unpredictable. In this study we examined the foraging behaviours of 2 sympatric invasive birds in Mo'orea, the common myna (*Acridotheres tristis*) and the red-vented bulbul (*Pycnonotus cafer*), to determine if they exhibit behavioural or habitat partitioning. We investigated the ratio of foraging to vigilance behaviour of both species at novel food stations, as well as the effects of foraging group size and species composition on their behaviour. While the myna and bulbul exhibit similar behaviour, sites where they occur were partitioned within habitats. Novel food stations however, encouraged foraging at the cost of vigilance behaviours. Behaviours were not influenced by conspecific group size, and intraspecific interactions were more frequent, and of a greater intensity than interspecific interactions. These results suggest that the 2 species minimise competitive interactions by occupying different sites within the same habitat, and prioritise food acquisition in a new environment. Sympatric introduced species may avoid competitive exclusion if habitat usage limits the frequency of interactions.

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INTRODUCTION

Interactions between coexisting invasive species could either facilitate or inhibit the persistence of each species, leading to outcomes such as invasional meltdown (Simberloff & Von Holle 1999; O'Dowd *et al.* 2003) and changes in community composition and structure (Vitousek 1990; Russell 2011). Coexisting species are more likely to interact

with one other if they are functionally similar and occupy comparable niches. Overlapping resource requirements can further exacerbate interspecific competition (Dhondt 2011). Introduced species with similar habitat preferences and diets may competitively exclude one another if they do not partition habitat differently (Reed 2001; Poling & Hayslette 2006). Interactions among introduced birds have received relatively little attention compared to other species (Orchan *et al.*, *in press*) despite their potential to influence

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invasion success; bird introductions in particular may often be unsuccessful because of competitive exclusion (Lockwood *et al.* 1993; Blackburn & Duncan 2001; Cassey *et al.* 2005; Blackburn *et al.* 2008). Where multiple introductions have occurred, success can be higher if species differ from each other taxonomically and in habitat preferences, highlighting the importance of competition in avian invasion dynamics (Lockwood *et al.* 1993). To date, much of the research on invasive species has focused on the consequences for native ecosystems, with relatively little emphasis on interactions among multiple introduced species (Simberloff 2006). Taxonomic bias also exists, with more focus on direct impacts, such as introduced predatory mammals (Courchamp *et al.* 2003), and less work on introduced birds where negative impacts are less obvious or indirect (Blackburn *et al.* 2009).

Partitioning of habitats can occur either when species occupy different sites within the same habitat (Edington & Edington 1972) or when foraging behaviours or diets are different and lead to different patterns of resource use (Wiens *et al.* 1987). Interspecific competition is often asymmetric, with larger species generally competitively superior to smaller species in aggressive interactions (Shelley *et al.* 2004; Zeng & Lu 2009). The nature and extent of interactions are predicted to be context-dependent, with factors such as the presence and number of nearby conspecific and heterospecific individuals influencing behaviour (Harrington *et al.* 2009). Behavioural responses can be directional, and dominant species may be superior at controlling resources, while subordinate species may be better at discovering novel resources (Perfecto & Vandermeer 2011). Uncovering the nature of interactions between introduced species is especially important in novel and disturbed ecosystems, where interactions may either facilitate or inhibit the persistence of both species.

The common myna (*Acridotheres tristis*) and the red-vented bulbul (*Pycnonotus cafer*) originate from and coexist in southern Asia. Both species are widespread in French Polynesia, where only 17% of well documented bird introductions have succeeded in the 20th century (Lockwood *et al.* 1993). Partitioning of substrates and behaviours developed in the native range may have facilitated the coexistence of these 2 species in French Polynesia, where they are sympatric and have similar generalist diets (Sontag & Louett 2007; Bhatt & Kumar 2001). Both species exhibit aggressive behavior towards heterospecifics and conspecifics (Pernetta & Watling 1978; Watling 1978; Long *et al.* 1981; Martin 1996; Pell & Tidemann 1997; Feare & Craig 1998; Millett *et al.* 2004; Crisp & Lill 2006), and are widespread in human-modified (typically lowland) habitats of the Society Islands. The myna was introduced to the

Society Islands around 1910 as a caged bird, and for the biological control of invasive wasps (Blanvillain *et al.* 2003). The bulbul was introduced *c.*1970, also as a caged bird (Blanvillain *et al.* 2003). Each species has been introduced to a number of other locations, and they are considered invasive in Australia, New Zealand, and many Pacific Islands (Dhondt 1977; Pernetta & Watling 1978; Watling 1978; Long *et al.* 1981; Watling 1983; Williams & Giddings 1984; Martin 1996; Pell & Tidemann 1997; Gill 1999; Islam & Williams 2000; Blanvillain *et al.* 2003; Millett *et al.* 2004; Higgins *et al.* 2005; McAllan & Hobcroft 2005). Fruits and berries make up a significant portion of their diets, and both are considered agricultural pests (Long *et al.* 1981). Both species are also thought to compete with native birds in French Polynesia (Blanvillain *et al.* 2003). For example, mynas are suspected of killing other birds and have been observed to expel eggs from nest boxes of native birds in the Seychelles (Martin 1996; Blanvillain *et al.* 2003; Millett *et al.* 2004). The myna is larger, with a body size of 240 mm and a mass of 82 - 138 g compared to 200 - 220 mm and 26 - 45 g in the bulbul (Long *et al.* 1981). While individuals of both species are frequently seen foraging and perching within several meters of each other, evidence for substrate partitioning exists in the native range, and mynas are more terrestrial than bulbuls (Long *et al.* 1981).

We examined the behaviour and substrate preferences for each species on the island of Mo'orea to determine the presence and extent of both behavioral and site partitioning. We also investigated the interactions between these 2 species and the effects of group size and species composition on foraging behaviour. We expected mynas to be competitively superior in any direct interaction involving aggression due to its size, and we predicted that partitioning behaviours that might minimise the extent of interactions between the 2 species would be maintained in the introduced range. Additionally, we expected that interactions between individuals would depend on context, and that novel food sources, group size, and the presence of heterospecific individuals should all influence whether an individual's behaviour is biased towards active foraging or being vigilant. Specifically, we predicted that: (1) vigilance at novel food stations should be higher, (2) larger conspecific foraging groups would result in increased foraging time, (3) the presence of heterospecifics should increase vigilance behaviour, (4) intraspecific interactions should be more frequent than interspecific interactions, with greater agonistic behaviour during intraspecific interactions. Studying differences in the foraging behaviour between the 2 species and the levels of aggressive interactions can shed light on how they

successfully establish and coexist while occupying apparently similar ranges. The results may further assist in developing behaviourally tailored control and management techniques for these 2 invasive species.

METHODS

A total of 111 focal observations (686 counts) of bulbuls and 101 focal observations (784 counts) of mynas were made during the study. Of the bulbul observations, 76 (72%) were from non-feeding stations and of the myna observations, 85 (87%) were from non-feeding stations. Bulbuls were observed for an average of 132 seconds (± 133 SD) at feeding stations and 217 seconds (± 102 SD) at non-feeding stations. Mynas were observed for an average of 85 seconds (± 70 SD) at feeding stations and 265 seconds (± 120 SD) at non-feeding stations.

Study sites

The mynas and bulbuls were observed over a period of 17 days between October 2011 and November 2011 in Mo'orea, French Polynesia. The breeding period is not well known for either species in French Polynesia, but is thought to begin during the onset of the rainy season in October and November for the bulbul (Holyoak & Thibault 1984) and to occur between February and September for the myna (Long *et al.* 1981). Both species are frugivorous, and in a recent study, fruit was found in 95% of bulbul droppings on Moorea and Tahiti (Spotswood *et al.* 2012). While no detailed study of the myna diet has been conducted on Moorea, unpublished data (E.N. Spotswood) indicate that this species consumes a variety of arthropods, and may be less frugivorous than the bulbul. Neither species uses communal roosts. However, mynas do exhibit communal roosting behavior in other areas (Pell & Tidemann 1997), including on other islands within French Polynesia (E.N. Spotswood, *pers. obs.*). Both species are considered sedentary or resident (Long 1981) and are territorial during the breeding season. In other locations, mynas are often found in pairs whereas bulbuls form larger groups ranging from 2-10 individuals (Long 1981).

The first study location with 8 observation sites was located at the Richard B. Gump South Pacific Research Station and its surrounding areas, which totaled ~3 ha in size (17°29'25"S, 149°49'36"W). The second location, with 2 observation sites, was a public beach located near the northern tip of the island and ~2.5 km away from the Research Station (17°29'30"S, 149°51'0"W). The third location, also with 2 observation sites, was the island's Agricultural School situated in the 'Opunohu Valley (17°31'54"S, 149°50'9"W). Observation sites were



Fig 1. Feeding platform with a red-vented bulbul present.

chosen at random along walkable paths, and no 2 sites were within 25 m of each other. All observation sites were chosen to include resident populations of both species.

Foraging behaviour and substrates

Data on foraging behaviour were collected between 0800 and 1600. Observations were conducted either with the naked eye, or with the aid of 8 x 42 binoculars. The observer remained in a fixed location throughout an entire observation period and in view of birds; a method that was feasible because both species are habituated to human presence. Behaviours were measured using focal observations in which individuals were tracked for as long as possible until the bird flew out of view. The maximum time any one individual was observed was 10 minutes. Every 30 seconds, we recorded the behaviour of the focal bird according to whether it was preening, beak cleaning, flying, perched scanning, ground scanning, perched foraging, or ground foraging. Perched scanning and ground scanning are categorised as "vigilance", perched foraging and ground foraging as "foraging", and preening, beak cleaning and flying as "other" behaviours. During behavioural observations, the approximate height of the individual in meters from the ground was estimated (recorded in 3 m intervals up to 15 m), and habitat substrate was recorded as either: air, dead brush, ground, grass, man-made structure, or tree branches.

Feeding stations

Two novel feeding stations were established on the property of the Gump Station. Feeding station 1 (F1) was placed ~1.5 m above ground and spaced

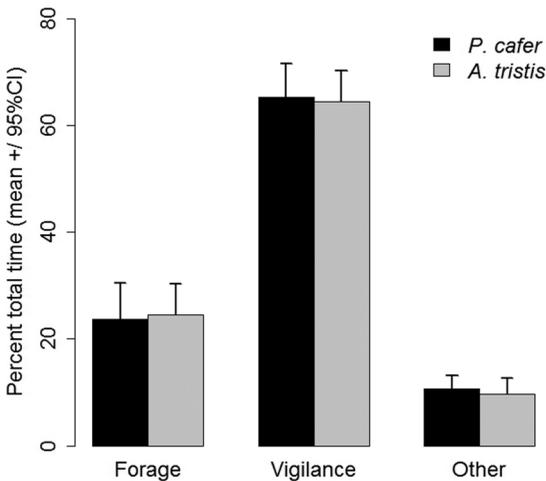


Fig 2. The percentage of total observation time spent being vigilant, foraging, or doing other activities for common myna and red-vented bulbul. Percentages are average time spent per individual (+ 95% confidence intervals).

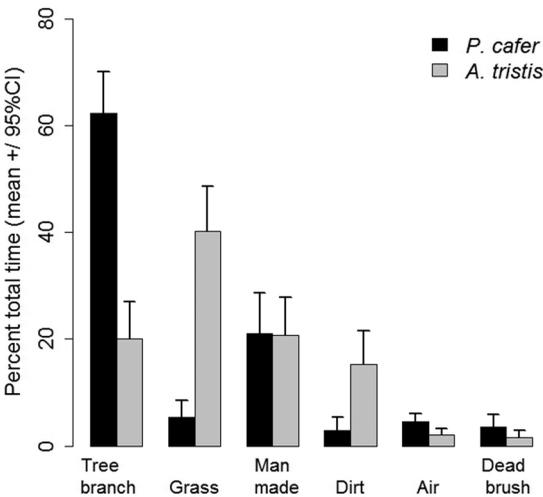


Fig 3. The percentage of total observation time spent on different substrate types for common myna and red-vented bulbul. Percentages are average time per individual (+ 95% confidence intervals).

several meters on each side in between 2 buildings. The station was constructed of wood and tape, and 3 layers of fixed cardboard made up the platform (Fig. 1). Feeding station 2 (F2) was a dish set on an ~1 m² concrete block jutting out from the ground to deter ants. F1 experienced greater human traffic nearby, whereas F2 presented a station that had fewer disturbances. Food was replaced each day, and included avocados, bananas, papayas, and oranges. Observations at feeding stations were recorded the

same way as other foraging observations, except that the total time the focal individual was present at a station was recorded. Observation periods lasted as long as the individual was in view. When a focal individual was no longer observable, a new individual was selected.

Interspecific/intraspecific interactions and group size

Chases and agonistic encounters between conspecifics and heterospecifics were recorded on a presence-absence basis during the observation of a focal individual. The number of incidences was not recorded. Additionally, the outcome of encounters was recorded (*i.e.*, which individual was displaced). The observation period was terminated once the focal individual was no longer visible, or had been observed for 10 minutes. Group size was recorded by counting the number of individuals of each species within a 5 m radius of the focal individual. Number of other individuals was classified as 0, 1 (assumed to belong to mating pairs), and 2+ (assumed to be a group).

Statistical analysis

We investigated interactions among variables using log-linear mixed effects models with individual as a random effect to account for repeated observations of the same individual in one focal period. Individual birds could not be uniquely identified and subsequent focal observations on previously monitored individuals were likely to occur, but we treat these as independent observations. We fitted multiple pair-wise models between explanatory variables of interest in which the counts within each focal session (recorded every 30 seconds) were compared to determine their dependence upon time of day (within the period 11 am and 2 pm, outside this period), behaviour, substrate, height (ground or aerial), species, the number of conspecifics, the number of heterospecifics, or the presence of a feeding station. The significance of each factor was assessed using Wald statistics. Models were fit using maximum likelihood with Laplace approximation. All analyses were conducted using R 2.13.1 and package lme4 (R Core Development Team 2012).

RESULTS

Factors affecting behaviour

Depending on context, the types of behaviour observed were dependent on the time of day, location, and the number of adjacent conspecifics. Foraging and vigilance accounted for the majority of observations of both species, and both species spent more time being vigilant (1072 counts) compared to foraging (230 counts, $P < 0.001$) and other behaviours

(168 counts, $P < 0.001$). Both species foraged more in the middle of the day (between 11 am and 2 pm, $P = 0.033$), and both species were less vigilant and spent more time foraging ($P < 0.001$) at feeding stations compared to other locations.

Vigilance decreased while foraging increased when conspecifics were present, and vigilance was most strongly affected when 2 or more conspecifics (*i.e.*, a group) were present ($P < 0.001$) compared to a lone individual or a pair. Both species were observed significantly more frequently alone than with conspecifics ($P = 0.005$), and both were rarely observed with heterospecifics (85 counts total, $P < 0.001$ compared to without heterospecifics). Conspecifics were present in 40% of scans with bulbuls and 62% of scans with mynas whereas heterospecifics were present in only 2% of scans with bulbuls and 5% of scans with mynas. The presence of one conspecific significantly increased foraging ($P = 0.007$) for both species compared to when individuals were alone, when they spent most of their time being vigilant ($P < 0.001$ compared to foraging and other behaviours). The number of conspecifics present ranged from 0 to 9 for the myna (mean 1.4 ± 1.0 SD) and 0 to 4 for the bulbul (mean 1.3 ± 0.7 SD). No differences were found in behaviour when heterospecifics were present, mainly because heterospecifics were rarely present within 5 m of a focal individual, limiting the ability to detect significant differences in the presence of heterospecifics.

Both species varied in the amount of time they spent on different substrate types. Compared to observations on grass, both species spent significantly less time on bare ground (dirt) substrate ($P = 0.010$), more time on man-made structures ($P = 0.028$), and more time on tree branches ($P < 0.001$).

Species-specific differences

We found differences between the myna and the bulbul in behaviour, habitat usage, and responses to novel food stations. Bulbuls and mynas spent similar amounts of time being vigilant and engaged in other activities. Mynas spent significantly more time foraging ($P = 0.006$) compared to bulbuls, and was found foraging in 18% of counts compared to 12.7% for bulbuls (Fig. 2). Preferred substrate also differed, and bulbuls spent significantly more time on tree branches ($P < 0.001$) compared to all other substrates, whereas mynas spent more time on grass ($P < 0.001$, Fig. 3) and bare ground compared to all other substrates. Bulbuls preferred substrates at a slightly greater height (mean 4.8 m, SD = 4.6) than mynas (mean = 3.9 m, SD = 4.3) and mynas spent significantly more time on the ground than bulbuls ($P < 0.001$).

Bulbuls visited feeding stations significantly more often ($P < 0.001$) than mynas and 75% of observations conducted at feeding stations (20 at

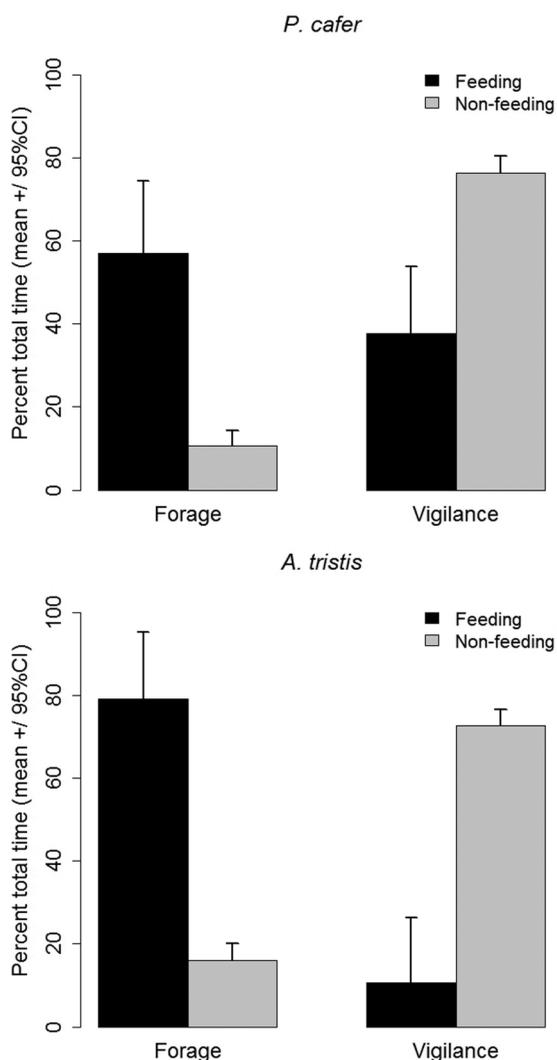


Fig. 4. Percent time spent foraging and being vigilant at feeding and non-feeding stations for the red-vented bulbul (top graph) and the common myna (bottom graph). Percent time is calculated as the percent of total time for each individual (+ 95% confidence intervals).

each of 2 feeding stations) were of the bulbul. The average total time spent in view at feeding stations (115 seconds) was less than 50% of the average total time spent in view at non-feeding station sites (242 seconds). Bulbuls were first observed at the feeding stations the same day that the station was erected. The first appearance of mynas at the 2 feeding stations occurred 10 and 16 days after the first appearance of bulbuls. On 2 occasions a myna was observed displacing a bulbul at a feeding station once it arrived. The displaced bulbul never returned to the station before the departure of the myna.

Interspecific and intraspecific interactions

There were only 3 observed interspecific interactions, and all involved an individual myna displacing one or more bulbuls. However, intraspecific interactions were frequent, and nearly all were agonistic. Interactions between mynas consisted of threat calls, chases and occasionally fights. Two fights were observed, and both occurred between 2 or more assumed pairs of mynas. Interactions amongst bulbuls consisted of threat calls, chases, and at times courtship rituals consisting of a male spreading its flight and tail feathers while subsequently bowing and opening its bill. None of the observed agonistic encounters occurred at feeding stations.

DISCUSSION

We found that while mynas and bulbuls allocate their time similarly between foraging, being vigilant, and other behaviours, the 2 species partitioned sites within the same habitat, and were found on different substrates. Mynas spent most of their time on the ground, whereas bulbuls were observed primarily in trees. This result is consistent with other studies for both species, and indicates that behavioural partitioning observed in the native range is conserved in the introduced range where these species co-occur (Crisp & Lill 2006, Asokan & Ali 2010). On the adjacent island of Tahiti, a large number of well-documented avian introductions have occurred but failed. In one study, the low success rates of introductions on this island were found to be related to similarity in ecology and taxonomy of introduced species, which may compete strongly with each other upon arrival (Lockwood *et al.* 1993). In contrast, introduced species with a shared evolutionary history of minimising interactions may be more likely to succeed, and the absence of interspecific interactions coupled with site partitioning suggest that avoidance mechanisms developed in the native range could have facilitated the success of the bulbul which was introduced after the myna was already naturalised.

Substrate preferences indicated in our results are likely the outcome of pre-existing differences in diet and feeding behaviour, as well as avoidance behaviour, both of which minimise the likelihood of aggressive encounters (Dhondt 2011). Intraspecific interactions were more common than interspecific interactions, implying greater realised competition between conspecifics. In all observed interspecific interactions, the myna displaced the bulbul. This result is consistent with evidence from birds (Robinson & Terborgh 1995) and other taxonomic groups (Harrington *et al.* 2009) indicating that larger body size leads to superiority in interactions involving aggression. In addition, mynas did

not arrive at feeding stations until after bulbuls, suggesting a possible discovery-dominance relationship between them (Perfecto & Vandermeer 2011). Most observations at feeding stations were of bulbuls, possibly indicating that they are less wary ('neophobic') of exploring novel food sources, and may be able to find and exploit food sources more easily. The few examples in which mynas displaced bulbuls after its discovery of the feeding stations suggest that while the bulbul may be the first to arrive, it is likely to be competitively subordinate to the myna in the acquisition of resources.

We found that individuals of both species were less vigilant, spent more time foraging and spent less total time at feeding stations compared to other observation sites. Reduced vigilance behaviour may result from a "stuff and run" method of acquiring food, in order to minimise threat from predators (Wilcox & Spotswood 2011), or to avoid competition with other conspecifics. Both species spent nearly half their time in the presence of conspecifics and group sizes were variable. However, group size had no effect on vigilance suggesting that Pulliam's "many eyes" hypothesis may be context-dependent (Pulliam 1973), although we did not directly test this. For example, individuals may determine their own level of vigilance by monitoring the vigilance levels of other group members. In a study on mixed flocks of dark-eyed junco (*Junco hyemalis*), and American tree sparrow (*Spizella arborea*), group size did not directly determine amount of vigilance behaviour exhibited (Lima 1995). Other work comparing birds in urban and natural habitats suggests that the urban environment may be less dangerous for certain species (Shochat *et al.* 2004). The potential threat of predation is unknown in the habitats we studied, and if predator threat is minimal, which it could be due to both species' success as invasives, it is possible that either individual vigilance behaviour is sufficient for birds to avoid predation or that reduced threat allows the birds to be less wary. It is also possible that vigilance behavioural cues depend on the location of individuals at distances greater than 5 m, in which case our method for determining group size could have included too small an area to correctly evaluate the effect on vigilance. The presence of heterospecifics could also have decreased vigilance behaviour, and other bird species can benefit from vigilance of other species within multi-species flocks (Mönkkönen *et al.* 1996). Unfortunately, heterospecifics were present in such low numbers that we were unable to test these hypotheses.

We did not evaluate the potential for negative impacts on other aspects of species biology that could inhibit the success of one or both of the species in this study. For example, we do not know whether sympatry affects reproductive success. Additionally, behaviours of each species may already be modified

in the presence of one another, which was something we could not test without single species control sites or islands. Evidence from mustelids suggests that context-dependent behaviours are modified by the presence of other competing species (Harrington *et al.* 2009). Future studies should focus on determining reproductive success and on comparing locations with only one species to locations in which the 2 species co-occur in order to determine the extent to which behaviours are altered when both species are present.

The myna and bulbul preferred different sites within the same habitat, and interactions between heterospecific individuals were rare, indicating that behaviours that allow coexistence of these species are conserved in the novel range of these species. We found evidence that one species may benefit from the other via a discovery/dominance relationship that allows the myna to capitalise on novel foods discovered by the bulbul. In locations where the 2 species co-occur, strategies for control should assume that the 2 species are unlikely to interact with one another.

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