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# RESOURCE PARTITIONING BY WINTERING SHOREBIRDS: A BEHAVIORAL COMPARISON OF TWO SPECIES IN A TROPICAL ESTUARY

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**Abstract.** Shorebirds often feed in multispecies groups that display interesting niche dynamics. On Moorea, French Polynesia, the Wandering Tattler (*Tringa incana*) and Pacific Golden Plover (*Pluvialis fulva*) are the dominant shorebird species during the northern winter. These species' feeding behavior was observed at the Temae estuary on the northeast side of the island. Relative abundance of the two species was determined using transect counts at the estuary and an adjacent beach. *T. incana* displayed more striking and sprinting behavior, while *P. fulva* displayed more picking and walking behavior. *T. incana* also consumed more crabs than *P. fulva*. The two species existed in relatively equal abundance in the estuary; *T. incana* was more common on the beach. Though these data suggest some differences in feeding niche, a great deal of overlap was observed. The degree of niche partitioning appears to be greater in this study than in similar studies conducted on these species' breeding grounds.

**Key words:** feeding behavior; *Pluvialis fulva*; *Tringa incana*; Moorea, French Polynesia; resource partitioning; estuary

## INTRODUCTION

The niche concept, first suggested in the early 1900s, evolved greatly in the first half of the 20<sup>th</sup> century (Vandermeer 1972). Hutchinson (1957) defined the niche as the place where all environmental variables are within the survival limits of a given species. Gause's axiom states that no two species can inhabit the same niche (Vandermeer 1972). Schoener (1974) found that the most important niche parameters that segregate species are habitat, food type, and timing of habitat use.

Shorebirds often form dense, multispecies aggregations, making them a good model system for the study of niche dynamics. Resource partitioning, particularly regarding feeding behavior, has been studied extensively in shorebirds. For example, Thomas & Dartnall (1970) showed that when multiple species of sandpipers feed in one area, they segregate by species into different microhabitats. These microhabitats reflect the

spatial distribution of each bird species' preferred prey (Ribeiro et al. 2004).

The migratory nature of many shorebirds' life histories presents an extra factor in determining the extent of niche partitioning. Holmes and Pitelka (1968) found that the diets of four sympatric sandpipers overlapped considerably during breeding season on the Arctic tundra. During migration, shorebirds are often opportunistic feeders with a great deal of dietary flexibility (Davis & Smith 2001, Isacch et al. 2005). Many species come together during this period, forming multispecies aggregations in which competition for food intensifies (Recher 1966). Baker & Baker (1973) found that shorebirds are usually pushed into a narrower, more specialized feeding niche during winter due to food scarcity. Because of this, tropical wintering grounds are an ideal place to study niche partitioning in migratory shorebirds.

The island of Moorea, in French Polynesia, hosts wintering Wandering Tattlers (*Tringa incana*, (Gmelin 1789)) and Pacific Golden Plovers (*Pluvialis fulva*, Gmelin 1789), both of

which nest on Arctic tundra during the northern summer. The two species are not closely related, belonging to different families in the order Charadriiformes. *P. fulva* is a member of Charadriidae, the plover and lapwing group; *T. incana* is a member of Scolopacidae, the sandpiper group. The two species are also significantly different morphologically: *T. incana* has a long, narrow bill, while *P. fulva* has a shorter, thicker bill.

Despite these differences, the two species seem to inhabit superficially similar niches at the Temae beach and estuary on Moorea. Moreover, these species show little difference in resource utilization during the breeding season, both feeding almost exclusively on insects (Johnson and Connors 1996, Gill et al. 2002). The purpose of this study was to identify significant differences in resource utilization of these two species on their wintering grounds by studying their feeding behavior and distribution within a small study site.

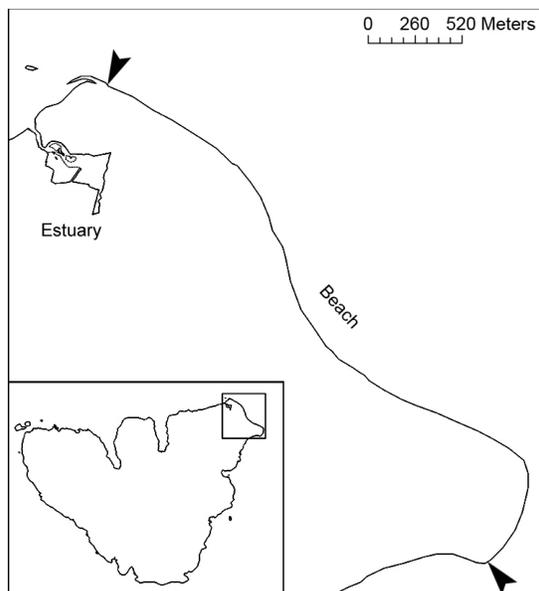


FIG. 1. Map of study site. Inset shows position of site relative to the entire island of Moorea. Arrows indicate boundaries of the beach transect.

## METHODS

### Study site

All behavioral observations were made at the Temae estuary, in the northeast corner of Moorea (Fig. 1). This site was selected because both species were present in sufficient numbers to conduct a behavioral study there. The estuary is 350 m long and 200 m wide. The water depth in the estuary averages 20-30 cm. The substrate is primarily calcium carbonate sand (L. LaRue, pers. comm.). The eastern half of the estuary is heavily impacted by runoff by a nearby golf course (LaRue 2006), so behavioral observations and transect counts were limited to the western half.

Transect counts were also carried out along a 4 km stretch of beach adjacent to the Temae estuary.

The substrate type along the shore is a mixture of coral sand, loose coral rubble, and aggregated coral rubble. The reef crest is approximately 40 m from the shore along the entire length of the study area.

### Study organisms

The Wandering Tattler (*Tringa incana*) and Pacific Golden Plover (*Pluvialis fulva*) are the dominant migratory shorebird species found on Moorea during the northern winter. They are also the only shorebirds commonly found at the Temae estuary. *P. fulva* breeds in northeastern Siberia and western Alaska, whereas *T. incana* breeds only in Alaska (Johnson and Connors 1996, Gill et al. 2002). Both have large winter ranges that extend from the California coast to the Pacific islands. Both also are found in a wide array of open habitats within this range (Johnson and Connors 1996, Gill et al. 2002). *T. incana*, however, more strongly favors rocky intertidal habitats for foraging (Gill et al. 2002).

### Behavioral sampling

Feeding behavior of individual birds was observed in 10-minute observation sessions.

Observations were made through 8-power binoculars. The estuary was arbitrarily divided into 3 zones: the south shore, the north shore, and the islands in between. In a typical morning or evening of observations, one bird of each species was observed in each zone. When a zone was sampled, an actively-foraging bird was randomly selected within it and observed for 10 minutes. The nearest individual of the other species was then observed as well. This procedure was designed to avoid biased sampling of any one section of the estuary.

A systematic procedure was followed for the behavioral observations. When an individual bird was selected for observation, the date and time were noted, as well as the bird's location. The following pieces of data were recorded each minute for 10 minutes thereafter:

- Distance of bird from shore: measured in meters. Positive numbers indicated the bird was on land, negative numbers indicated the bird was in the water.
- Distance moved: The distance the bird moved, in meters, from the previous minute's observation.
- Water depth: The bird's depth in the water, measured in centimeters and based on the proportion of the bird's legs that were submerged. A value of 0 indicated the bird was on land.
- Behavior type: Behavior type was assigned based on the dominant behavior during the last ten seconds of each minute. A behavior category was chosen from the following list of stereotyped behaviors:
  - Scanning: Bird is visually searching for prey, but bill use is negligible.
  - Picking: Bird is using bill to pick items off the substrate.
  - Striking: Bird is aggressively using bill to strike a prey item.
  - Eating: Bird is manipulating and/or consuming a recently-caught prey item.
  - Preening: Bird is using bill to groom feathers, or is bathing.
  - Resting: Bird has ceased activity, and bill is tucked between wings.

- Movement class: Bird was noted to be standing still, walking, running, or sprinting. As with the behavior types above, the movement class was assigned based on the dominant movement class during the last ten seconds of each minute.

In addition to these specific behavioral data, incidental observations were also recorded. These included any interactions with other birds, the distance of any flights made, and, when possible, type of prey caught. After the 10 minutes had elapsed, a GPS waypoint was recorded at the bird's location.

A total of 46 10-minute observation sessions were carried out for *P. fulva* and 49 for *T. incana*. Equal numbers of observations were made in the morning (5:00-9:00 am) and evening (4:00-6:00 pm), when the birds were most active. Five observations of each species were also made during the middle of the day, but midday observations were terminated because the birds were less active during this time.

In order to statistically compare different observation sessions, the mean distance moved per minute, mean distance to shore, and mean water depth were all calculated for each session. The frequencies of each behavior and movement type were also determined for each session. A series of Student's t-tests were used to determine the significance of any differences in these means and frequencies between the two species. These tests were performed using JMP software (SAS Inc. 2004).

#### Transect counts

In order to determine the relative abundance of the two species studied, transect counts were performed both in the estuary and along the shoreline. In the estuary, two parallel 225 meter transects were performed, one on the north shore, the other on the south shore. Each visible individual of the two species was marked on a map of the estuary as it was seen. The two transects were sufficient to cover the east side of the estuary, therefore

every individual within that area was counted. This procedure was carried out twice, once in the morning, once in the evening.

A 4 km linear transect count was performed along the beach north of the estuary (see Fig. 1). Every bird seen was noted in a notebook and a GPS unit was used to mark its location. GIS software was used to project these points onto a map of the shoreline. This procedure was also performed twice.

The large difference in the length of the transects (225 m vs. 4 km) made direct comparison of the results impossible. To make comparison possible, two random 225 m pieces were selected from each of the beach transects, and these were compared directly to the two 225 m transects from each of the estuary counts.

## RESULTS

### Behavioral Sampling

T-tests determined the significance of the differences between the two species' positions and movement rates while foraging. *T. incana* had a significantly higher mean water depth while foraging ( $p=0.0004$ ) (Fig. 2). *P. fulva* on average was farther inland, though not significantly. *T. incana* had a slightly higher movement rate, but this difference was also not significant.

There were significant differences in the frequencies of the various behavior types between the two species. The frequency of scanning behavior was significantly higher in *T. incana* ( $p=0.0041$ ) (Fig. 3). Picking behavior was significantly more frequent in *P. fulva* ( $p=0.0003$ ). The rarely-seen striking behavior was observed only in *T. incana*, and this was consequently significant ( $p=0.0007$ ). There were no significant differences in the frequency of eating, preening, or resting behaviors between the two species.

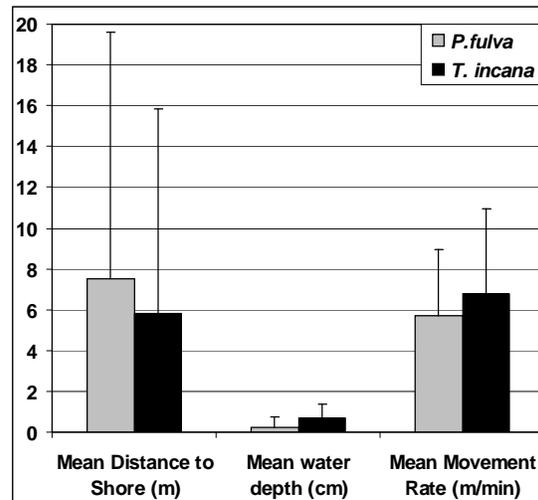


FIG. 2. Mean distance to shore, water depth, and movement rate during feeding observations, by species.

Among movement classes (Fig. 4), there were no significant differences in the amount of time spent still or running between the two species. Walking was slightly, yet significantly, more common in *P. fulva* ( $p=0.0493$ ). Sprinting was much more frequent in *T. incana* ( $p=0.0002$ ).

### Transect Counts

Table 1 shows the number of individuals of each species counted during the estuary transects and in an equivalent length of beach transects. Density for both species was much higher in the estuary. The proportional abundance of *P. fulva* was slightly higher in the estuary, while *T. incana* was more abundant along the shore. Figures 5 and 6 show the results of one estuary transect and one beach transect, respectively.

### Incidental Observations

During the course of the behavioral observations, additional items were noted outside of the prescribed data collection scheme. The identity of prey items was the most important of these. Small crabs were taken by both species. *T. incana* took

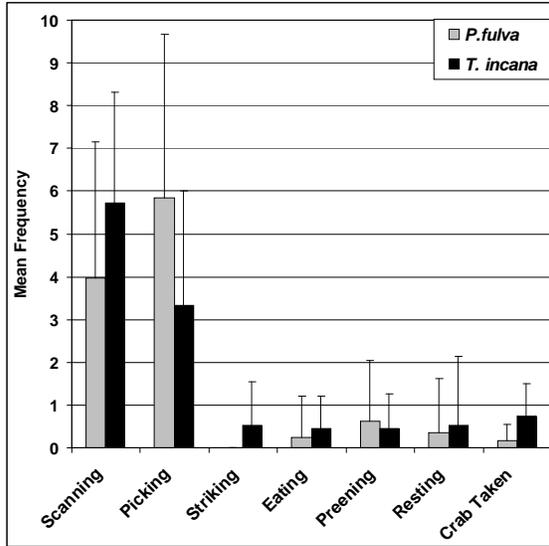


FIG. 3. Mean frequencies of behavior types, by species.

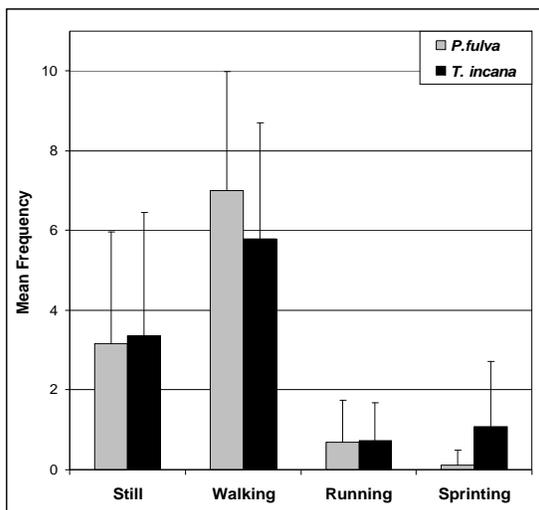


FIG. 4. Mean frequencies of movement types, by species.

#### Estuary Transects

	Transect 1	Transect 2
<i>P. fulva</i>	11	15
<i>T. incana</i>	10	11

#### Beach Transects

	Transect 1	Transect 2
<i>P. fulva</i>	0	1
<i>T. incana</i>	3	2

TABLE 1. Results of beach and estuary transects. Each value represents the number of birds seen along a 450 m transect length.

significantly more crabs than *P. fulva* ( $p < 0.0001$ ), averaging nearly one per 10-minute observation session (see Fig. 3). *P. fulva* typically took smaller, unidentifiable prey, though this could not be quantified. *P. fulva* was also seen pulling a worm out of a burrow in the substrate on two occasions. On four occasions, *P. fulva* was seen chasing *T. incana* after the latter had caught a crab.

#### DISCUSSION

These data clearly show a difference in feeding behavior between *P. fulva* and *T. incana*. The underlying food preferences of these species can be inferred from these behavioral differences. The dominant behavior regime displayed by *P. fulva*, deliberate walking and picking, suggests a preference for non-mobile prey. Byrkjedal & Thompson (1998) report that, when foraging on estuarine wintering grounds, *P. fulva* primarily take snails, bivalves, insects, and amphipods. Since the food items taken by *P. fulva* were generally too small to see, they were likely amphipods, insects, and perhaps very small snails. Although Kato et al. (2000) characterized polychaete worms as the most important food item for *P. fulva*, consumption of such worms was observed only twice in the course of the present study. *T. incana* showed a higher frequency of scanning, striking and sprinting. These behaviors all suggest a preference for larger, more mobile prey. The small burrowing crabs that are common in the estuary are one such prey item. Indeed, the behaviors observed are reflected in this species' preference for crabs.

The distributional data show a higher density of *T. incana* along the shoreline, which is consistent with its preference for intertidal habitat (Gill et al. 2002). Though feeding behavior was not observed on the beach, it is reasonable to infer that prey availability has some affect on the two species' distributions. Crabs were observed on the beach, although

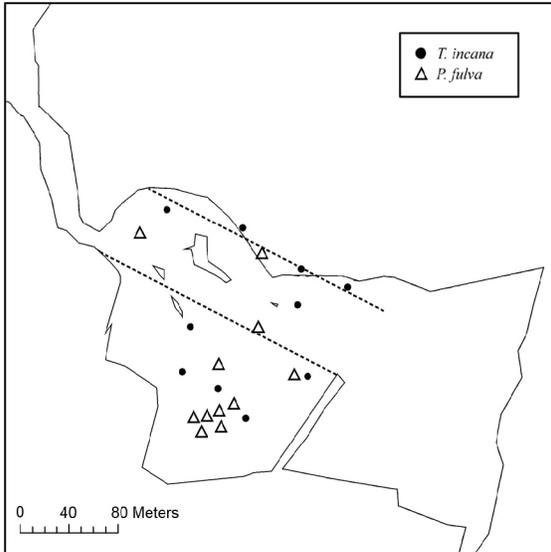


FIG. 5. Map showing birds counted during one estuary transect (n = 21). Dashed lines represent the location of the transects. Map from LaRue 2006.

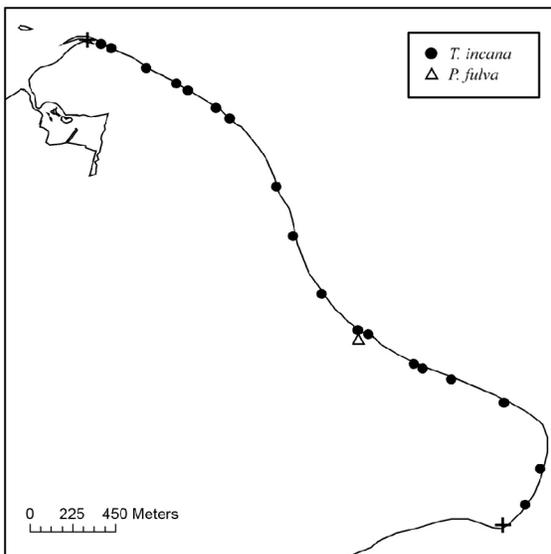


FIG 6. Map showing results of one beach transect. Cross symbols represent the beginning and end of transect.

not in the same density as in the estuary. The beach's rockier substrate likely did not support the same suite of small prey organisms favored by *P. fulva* in the estuary.

Many studies (Thomas & Dartnall 1970, Davis & Smith 2001, Skagen and Oman 1996, Isacch et al. 2005) have emphasized that shorebirds, as a group, display a great deal of

opportunism and flexibility in their feeding habits. The apparent attempted kleptoparasitism observed by *P. fulva* on *T. incana* is one example of such opportunism. These species also showed a degree of dietary flexibility: crabs were occasionally taken by *P. fulva*, and *T. incana* spent an appreciable amount of its foraging time picking small items off the substrate. Therefore, the two species do not occupy entirely separate feeding niches.

Recher (1966) suggested that competitive exclusion does not occur readily in migrant shorebirds due to both relative abundance of food in their habitats and the temporary nature of their sympatry. In this case, *T. incana* and *P. fulva* may not occupy exclusive feeding niches because they share a relatively rich feeding habitat and do so only seasonally.

In conclusion, the degree of overlap in resource utilization by these species clearly varies throughout the year. The degree of niche partitioning between these two species, while not absolute, is higher on wintering grounds than on breeding grounds, which is consistent with the pattern established by Baker & Baker (1973). Further study is needed to determine whether this pattern can be applied to other shorebirds, and perhaps to other migratory bird groups as well.

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APPENDIX A



*Tringa incana*



*Pluvialis fulva*