

A Potential Role of Shrimp Farms for the Conservation of Nearctic Shorebird Populations

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Abstract Shrimp aquaculture farms have greatly expanded at tropical areas worldwide, especially during the past three decades. One of the main core areas of this expansion was the northwestern coast of Mexico, prompting conservation concern for the shorebird populations that spend the non-breeding period (October to March) in the region. We conducted a series of counts and behavioral observations to evaluate the importance of a shrimp farm as foraging habitat for shorebirds, relative to adjacent intertidal areas, during and after the shrimp harvest period at a tropical wetland in Sinaloa, Mexico, 2012 and 2013. Overall, low-tide counts within the entire wetland had an average of $3,168 \pm 605$ (SE) shorebirds during the shrimp harvest period (October–November) and subsequently dropped to $1,408 \pm 373$ birds following harvest (December to January), when shrimp ponds were emptied and foraging opportunities were reduced. The proportion of counts at the shrimp farm relative to total counts over the entire wetland ranged from 10 to 80 % for different shorebird species and dropped to 0 to 10 % in the postharvest period. During the harvesting period, black-necked stilt, American avocet, willet, and whimbrel selected shrimp ponds over intertidal areas to forage during low tide, while marbled godwit, western

sandpiper, and dowitchers did not. The proportion of shorebirds observed feeding at the shrimp farm ranged between 60 and 90 % for most species and did not differ between low- and high-tide counts. These results suggest that shrimp farms can provide ephemeral but important complementary foraging areas for shorebirds, and appropriate management of existing farms may aid in conservation efforts for these species.

Keywords Coastal management · Complementary habitats · Foraging behavior · Habitat selection · Tropical wetlands

Introduction

Coastal wetlands have been diminishing rapidly, especially in tropical areas (Duarte 2009). A global estimate indicates that approximately 3.6 million ha of mangrove forests in tropical and subtropical areas was lost between 1970 and 2000, especially in Asia and the Americas (Valiela et al. 2001). The largest percentage (38 %) of this loss resulted from the construction of shrimp aquaculture ponds (Valiela et al. 2001). Shrimp farming has continued to expand greatly in the Pacific tropical coasts, transforming mangroves and saltmarshes by dyking (Li et al. 2013). Apart from the overall biodiversity loss (Valiela et al. 2009) and other impacts (Páez-Osuna et al. 2003; Sohel and Ullah 2012), this wetland habitat replacement can reduce the availability of intertidal foraging habitats and roosting sites for overwintering shorebird populations at coastal wetlands (Schaeffer-Novelli et al. 2006), particularly within both the Australasian and Pacific flyways.

Habitat loss has been postulated as a main factor explaining the overall decline of shorebird populations throughout the world (Delany et al. 2009). Under loss of habitat, shorebirds could be forced to use risky areas where they are more vulnerable to predators (Yasué et al. 2003) or crowd into remaining foraging grounds and deplete prey (Durell et al.

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2000), which could reduce overall overwintering survival or breeding success. However, areas above high tide adjacent to the shore can provide complementary or supplementary foraging habitats for overwintering populations at temperate areas (Elphick and Oring 1998; Masero 2003; Navedo et al. 2013; Brand et al. 2014), potentially buffering the effects of habitat loss for some species. Nevertheless, very little research has been conducted in tropical and subtropical areas (but see Yasué and Dearden 2009; Choi et al. 2013).

The northwest coast of Mexico is one of the main shrimp-farming areas in the Americas. Shrimp farms covered more than 24,000 ha by 1999 (Páez-Osuna 2001), and this area doubled to reach ca. 51,000 ha by 2002 (Páez-Osuna et al. 2003). Within this region, the State of Sinaloa is the most important with ca. 37,000 ha dedicated to shrimp aquaculture (Páez-Osuna et al. 2003). The northwest coast of Mexico also supports important populations of several Nearctic shorebird species during the nonbreeding season (Morrison and Ross 2009) and includes four coastal wetlands recognized within the Western Hemisphere Shorebird Reserve Network (www.whsmn.org): a Site of Hemispheric Importance (Bahía Santa María), two Sites of International Importance (Ensenada de Pabellones and Marismas Nacionales), and a Site of Regional Importance (Laguna Huizache-Caimanero). Shrimp farms in this area are typically composed of large containment ponds of semi-intensive shrimp production that are filled with seawater (Páez-Osuna et al. 2003) and stocked with postlarvae to produce one crop a year. Harvest of fully grown shrimp typically occurs at the end of October. Shrimp ponds are not available foraging areas for shorebirds during the shrimp-growing stage due to high water depths (Yasué and Dearden 2009). However, they could provide foraging habitats for different shorebirds during the harvest period, as they do for some other wading species (Cheek 2009), when water levels drop as ponds are gradually drained (Choi et al. 2013).

Harvest season in the northwest coast of Mexico typically begins in October, varying from farm to farm. The duration of the harvest season at each farm depends on the overall aquaculture area, with larger farms having longer harvest seasons. Once harvested, water input is cut off from the ponds, which thus dry out in a short period. From 2007 onward, every shrimp farm in the region must be dried out in January and February due to food health policies aiming at minimizing aquaculture losses associated with viral diseases. This practice results in a harvest season that typically lasts 2 months. Therefore, existing shrimp farms can provide a mosaic of foraging patches throughout the harvest period with different suitability for wintering shorebird populations within the wetland complex where they are located. Some studies have indeed assessed the potential role for aquaculture ponds as alternative roosting areas for shorebirds (Ma et al. 2004). However, to the best of our knowledge, there is only a single study assessing their potential role as alternative supratidal foraging habitats

for shorebirds, although focused on one species (Choi et al. 2013) rather than on the whole shorebird assemblage.

The objective of this study was to assess the potential role of a shrimp farm as a complementary foraging area for the whole shorebird assemblage during the nonbreeding season at a tropical wetland complex in Mexico. We evaluate whether the availability of harvest ponds affects the total number of shorebirds that can be sustained at the wetland complex and compare total abundance of all shorebirds and of seven individual species over the entire wetland complex during and after the shrimp harvest period. Further, we examine habitat selection by shorebirds and compare how the proportion of total counts of shorebirds found at the shrimp farm varies with tidal cycle during and after the shrimp harvesting period. In addition, we conducted foraging observations to quantify the proportion of birds feeding at the shrimp farm, and how this proportion varied with tidal cycle, to evaluate the value of the shrimp farm as foraging habitat relative to adjacent intertidal mudflats. Moreover, if the shrimp farm represents a supplementary foraging area for a given shorebird species, we expect a higher number of foraging shorebirds at shrimp ponds at high tide relative to low tide as individual birds extend their foraging during high tide to counteract a shortfall in the overall energy intake that occurs at low tide (Urfi et al. 1996; Navedo et al. 2013). Given the large expanses of wetland areas dedicated to shrimp harvesting within the tropics throughout the world (Schaeffer-Novelli et al. 2006), our results are important for the conservation of different shorebird populations, especially both in the Pacific and Australasian flyways where most of the world's shrimp farms are located.

Methods

Study Site Acuicola Don Jorge shrimp farm is located at Estero de Urías, a low-energy tropical coastal lagoon (Lankford 1977), located south of the city of Mazatlán (23° 13' N 106° 25' W), in the Mexican state of Sinaloa (Fig. 1). The lagoon covers an area of 18 km² and contains a diverse mosaic of habitats, including intertidal mudflats, mangroves *Rhizophora mangle*, and emergent brackish marshes (Navedo et al. 2012). It has mixed but predominantly semidiurnal tides with an average range of 1.0 m, and the salinity range is 25.8–38.4 ‰ with limited freshwater input (Montaño-Ley et al. 2008). Available intertidal foraging areas are affected by tidal level; when the tide is at mean lower low water of −0.6 m, approximately 315 ha of intertidal mudflats is available as feeding site for shorebirds (<20 % of the total wetland area), whereas this area is reduced to 185–200 ha when the lowest tide reaches only −0.3 m during neap tides (Navedo et al. 2012). Shrimp farms were developed in the upper part of the lagoon since the 1980s, including the Don Jorge shrimp farm

that spans 300 ha (Fig. 1). Other shrimp farms in the area cover 110 ha.

Ponds at the Don Jorge shrimp farm are sequentially harvested by emptying water, resulting in one to three ponds becoming available for foraging shorebirds each day (J.G.Navedo, personal observation). After shrimp harvesting, each pond is cut off from tidal influence using a series of lockgates. The high temperatures and high evaporation rate at the study site, even during the wintering season, result in daily progressive drying and reduced suitability of each harvested pond as a foraging ground for shorebirds. A shrimp harvest cycle typically lasts 40 days in this farm, with each pond becoming available for foraging shorebirds for a short time window typically less than 1 week (J.G.Navedo, personal observation). Available foraging surface for shorebirds within ponds was gradually reduced from day to day, ending up with just a small pool close to the outflow at the lower part of the pond before becoming fully dried. Typically, shorebirds used harvested ponds during 2–3 days and were generally absent from harvested ponds from day 5 onward (J.G.Navedo, in preparation of). With a mean pond size of 4.7 ha, the maximum daily available foraging surface for shorebirds was 35.25 ha. Therefore, this artificial foraging area represents a maximum 10.1 % of the total available foraging area within the wetland complex during spring tide periods (i.e., intertidal

areas plus shrimp farm = 350 ha). Moreover, once the last pond is emptied for shrimp harvesting, available foraging patches at the farm showed a daily reduction in area and suitability. After 2 weeks, the overall shrimp-farm area was thus unavailable as a foraging area for shorebirds, at least for tactile foragers, until the next harvesting cycle resumed.

Shorebird Surveys We carried out a series of repeated low-tide counts to estimate shorebird populations at intertidal areas of the lagoon and at the shrimp farm simultaneously. A motorboat was used to census intertidal mudflats, and one or two 4 × 4 vehicles were used to census the shrimp farm. Counts started 1 h before low tide and typically lasted between 2 and 2.5 h, thus covering the main period of the low tide. Censuses were conducted during spring tides to minimize the potential influence of tidal amplitude at Estero de Urias (see above). The shrimp-harvesting period lasted from 5 October to 10 November 2012 and from 25 October to 30 November 2013. During each season, counts were coordinated with the harvesting period at the shrimp farm to evaluate seasonal changes in shorebird abundance comparatively between the intertidal areas on the lagoon and the shrimp farm: The first census was conducted just before harvesting started and the last one 2 months after the last shrimp pond was emptied. We conducted five comprehensive surveys during each year from

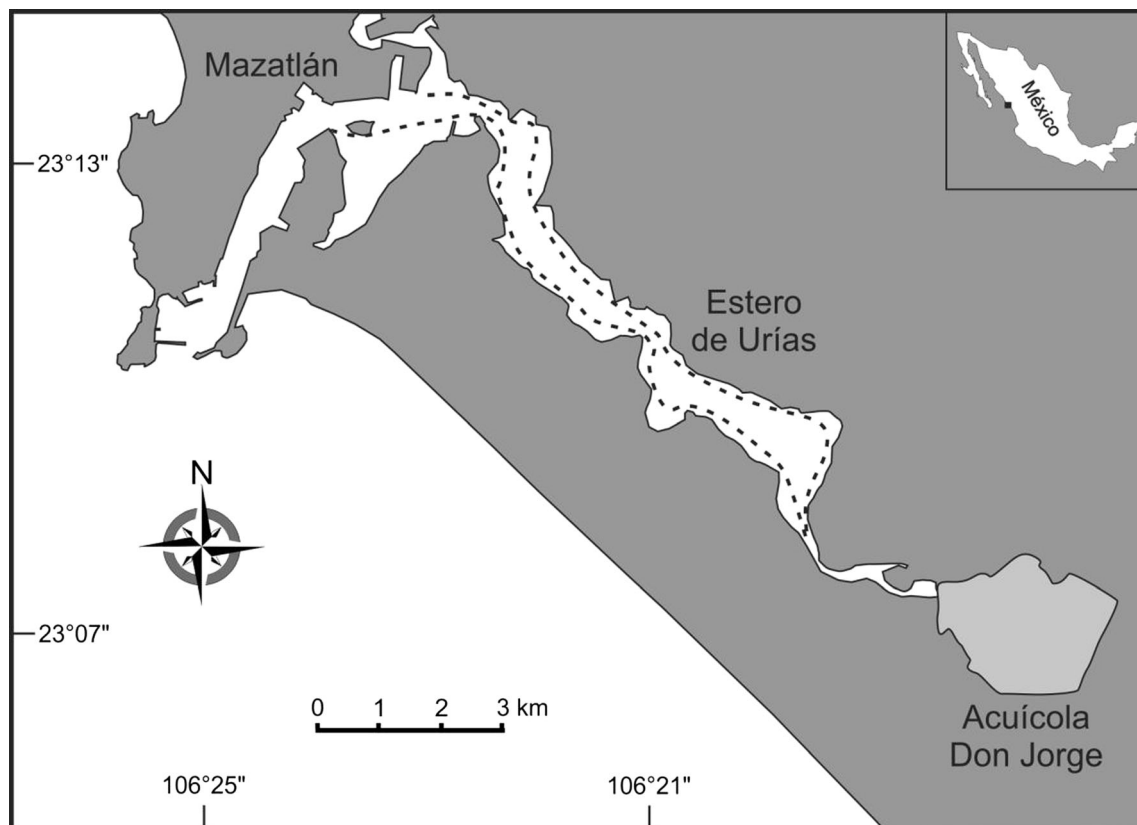


Fig. 1 Study area near Mazatlán city, Sinaloa, México, showing intertidal areas (outside the port) at Estero de Urias (areas between land and broken line) and the location and extent of Acuicola Don Jorge shrimp farm (filled polygon)

October to January. All shorebirds were identified to species, except for the two dowitcher species, short-billed dowitcher *Limnodromus griseus* and long-billed dowitcher *Limnodromus scolopaceus*, which could not be reliably distinguished in the field; all counts were combined into one dowitcher group.

We complemented these comprehensive surveys with supplementary counts at the shrimp farm during high-tide periods on the same dates as low-tide counts. Also, during low- and high-tide counts, we conducted focal observations on individual birds and quantified the proportion of all birds counted that were actively feeding. If the activity of an individual could not be determined instantaneously (e.g., a bird with its back to the telescope), the individual was observed for 1–5 s to determine its foraging activity (Navedo and Masero 2007).

Analyses We found no significant differences in abundance between years (t tests all $p > 0.29$ for any of the most abundant and frequent species), so we combined data from both years. We conducted the following analyses to evaluate the relative importance of the shrimp farm for shorebirds in the entire wetland complex. First, to examine how harvesting activities at the shrimp farm might affect shorebird abundance, we compared overall counts for all shorebirds and for individual species over the entire area (both shrimp farm and intertidal areas) between two periods (“during” and “after” the harvest period when all ponds had been emptied). Second, we evaluated the relative distribution of shorebirds and their potential selection of the shrimp farm. We calculated the proportions of each shorebird species found at the shrimp farm by dividing the count of each species relative to their total abundance over the entire wetland complex during that survey. Under no selection, birds should be distributed over the wetland complex in proportion to the surface area for each type of habitat. We compared how this proportion varied with harvesting activities at the shrimp farm during and following the harvest period. Third, we evaluated how shorebird use of the shrimp farm varied with the tide cycle and compared total counts of individual species and the proportions of birds observed feeding at the shrimp farm, between the high- and low-tide periods.

Statistical Analyses Specific abundances were transformed ($\log_{10} x + 1$) to satisfy assumptions of normality and homoscedasticity of variances. We used t tests to test for differences in numbers of the most frequent and abundant species at the wetland complex between surveys during ($n = 6$) and after ($n = 4$) the harvesting cycle, as well as for differences between years. For the case of *Limnodromus* spp., a Mann-Whitney U test was used. To investigate differences among shorebird species in use of the shrimp farm during high and low tides, we used a Wilcoxon matched-pair test. To evaluate whether the proportion found at the shrimp farm relative to total counts

for each species varied with harvest period, we fit a general linear model (GLM) with harvest period (during and after) as the explanatory variable. We evaluated habitat selection by shorebirds using a t test to examine whether the predicted values from the GLM were significantly different from 10.1 % (i.e., the proportion of maximum available foraging surface at the shrimp farm with respect to the entire wetland complex; see above). Due to logistic impediments, one high-tide census was missed in 2012, so we compared five censuses rather than six. All results are presented as average (\pm SE).

Results

The shorebird assemblage at the Estero de Urias wetland complex during low tide was composed of a mean of $2,817 \pm 459$ individuals belonging to 21 species throughout the study period (Table 1). The most common species were western sandpiper *Calidris mauri*, willet *Tringa semipalmata*, dowitchers *Limnodromus* spp., marbled godwit *Limosa fedoa*, black-necked stilt *Himantopus mexicanus*, American avocet *Recurvirostra americana*, and whimbrel *Numenius phaeopus*. Each of these taxa had maximum numbers above 150 individuals and was present during at least eight out of ten counts at the wetland. To help the interpretation of the role of the shrimp farm, we excluded from further analysis those species (i) that were not frequent or (ii) whose mean abundances during low tide at the shrimp farm throughout the harvesting cycle did not exceed ten individuals. These criteria restricted the analyses to the seven most frequent and abundant species.

When ponds at the shrimp farm were available for shorebirds during the harvesting cycle (October and November), the overall abundance within the wetland during low tide was $3,168 \pm 605$ shorebirds ($n = 6$). This abundance decreased to $1,408 \pm 373$ shorebirds ($n = 4$) once harvesting season was finished (December to January). This general pattern was consistent for most of the common species, such that only a fraction remained at the wetland in December and January (Fig. 2). Western sandpiper and whimbrel decreased nonsignificantly from the harvest period to the postharvest period (Fig. 2).

The proportion of each species counted at the shrimp farm relative to total counts over the whole wetland varied with harvest activity. All seven focal species had higher mean proportions observed during the harvest period than after the harvest period (Fig. 3), although the mean difference of 15 % was not significant for the western sandpiper and the dowitchers, which were absent from the entire wetland complex after the harvest period. During the harvest period, the shrimp farm supported >75 % of all black-necked stilt and American avocet observed at the wetland during low tide, including nearly all birds of these species in some counts (Fig. 3). The

Table 1 Frequency of occurrence during surveys ($N=10$) and maximum numbers of shorebird species observed at simultaneous low-tide counts at intertidal areas of Estero de Urias and at the shrimp farm during two consecutive harvesting periods, 2012 and 2013

English name	Species	frequency	maximum number
American avocet	<i>Recurvirostra americana</i>	0.9	184
American oystercatcher	<i>Haematopus palliatus</i>	1	64
Black-bellied plover	<i>Pluvialis squatarola</i>	0.7	53
Black-necked stilt	<i>Himantopus mexicanus</i>	1	452
Dowitchers	<i>Limnodromus</i> spp.	0.9	663
Dunlin	<i>Calidris alpina</i>	0.1	1
Greater yellowlegs	<i>Tringa melanoleuca</i>	1	15
Killdeer	<i>Charadrius vociferus</i>	0.1	1
Least sandpiper	<i>Calidris minutilla</i>	0.8	30
Lesser yellowlegs	<i>Tringa flavipes</i>	0.6	10
Long-billed curlew	<i>Numenius americanus</i>	1	89
Marbled godwit	<i>Limosa fedoa</i>	1	592
Red knot	<i>Calidris canutus</i>	0.1	1
Semipalmated plover	<i>Charadrius semipalmatus</i>	0.7	400
Spotted sandpiper	<i>Actitis macularia</i>	1	39
Stilt sandpiper	<i>Calidris himantopus</i>	0.1	16
Western sandpiper	<i>Calidris mauri</i>	0.8	3,329
Whimbrel	<i>Numenius phaeopus</i>	1	69
Willet	<i>Tringa semipalmata</i>	1	1,605
Wilson's phalarope	<i>Phalaropus tricolor</i>	0.2	5
Wilson's plover	<i>Charadrius wilsonia</i>	0.2	6

Highlighted in bold are the seven species with mean abundance during low tide at the shrimp farm over ten individuals and observed during at least eight out of ten counts

shrimp farm also held approximately 30 % of willet and whimbrel populations at the wetland during the harvesting period. These proportions were significantly higher than 0.101, as would be expected based on surface area alone ($t > 2.90$, $P < 0.01$ for all four species), indicating that these four species were selecting the shrimp farm during this period. In contrast, approximately 10–15 % of marbled godwit, dowitchers, and western sandpiper were observed at the shrimp farm during the harvest period, and these proportions were not significantly different from 0.101, the proportion expected based on relative areas of the habitats ($t < 0.75$, $P > 0.45$; Fig. 3). Once shrimp harvesting was finished, all shorebird species virtually disappeared from the shrimp farm, with the exception of whimbrel for which the shrimp farm still supported ca. 10 % of its population at the wetland (Fig. 3).

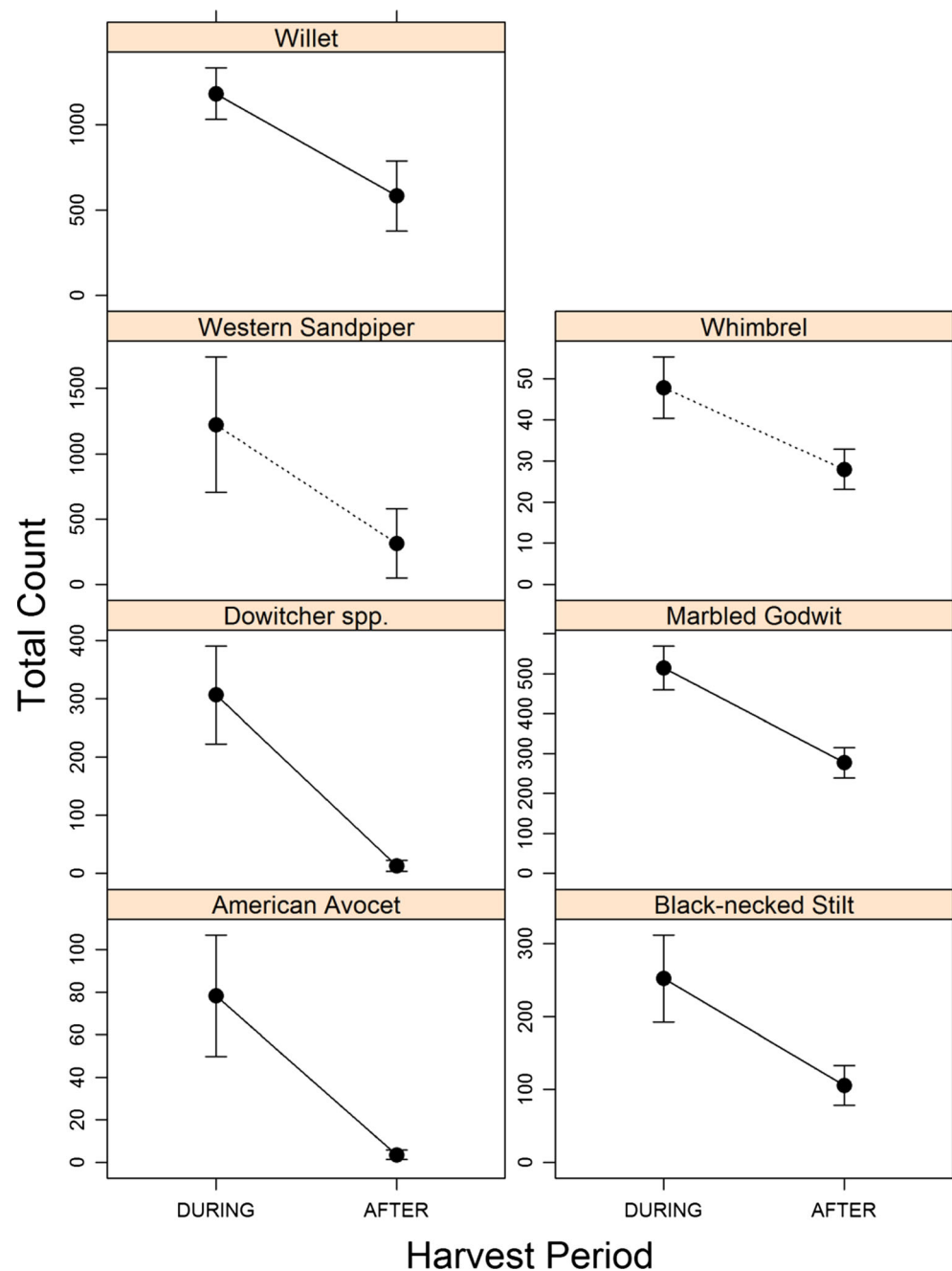
Finally, paired counts made the same day at low and high tide at the shrimp farm during the harvest period ($n=5$) indicated that shorebirds had similar abundance over the tide cycle, with nonsignificant differences for all species (Table 2). Most species were observed actively feeding during counts at the shrimp farm, typically ranging from 60 to 90 %. Proportion feeding was unaffected by the tide cycle for four of the seven most common species and did not differ between low- and high-tide counts (Table 2). The exceptions were marbled

godwit and western sandpiper that showed lower proportions of individuals feeding (i.e., more birds resting) during high-tide than low-tide periods. This effect was most pronounced for dowitchers, for which an average of 50 % was observed feeding during low tide, dropping to 10 % during high tide (Table 2).

Discussion

Our study suggests that a single shrimp farm can provide an important foraging area and could play a substantial role for maintaining shorebird populations within the wetland where it is embedded. The shrimp-harvesting period (October to November) in northwestern Mexico coincides with the arrival of Nearctic shorebirds following migration from breeding grounds (Castillo-Guerrero et al. 2009). Harvested ponds are regularly used as foraging areas during this period by significant fractions of populations of several shorebirds. The most abundant species observed at the shrimp farm was the willet, with counts frequently exceeding 400 birds, which represents ca. one third of their total population within the wetland (max 1,605 birds) during this period. The willets at the study site belong to *inornatus* subspecies (Lowther et al. 2001). Counts

Fig. 2 Average total counts of shorebird species (mean \pm SE) at low tide during ($N=6$) and after ($N=4$) the shrimp harvest period at Estero de Urías, México, including shrimp ponds and adjacent intertidal areas, October to January, 2012 and 2013. *Solid diagonal lines* indicate a significant difference ($P<0.05$) between harvest period (*during* and *after*) from a t test for differences between periods. Note different scales in the y-axis for each species

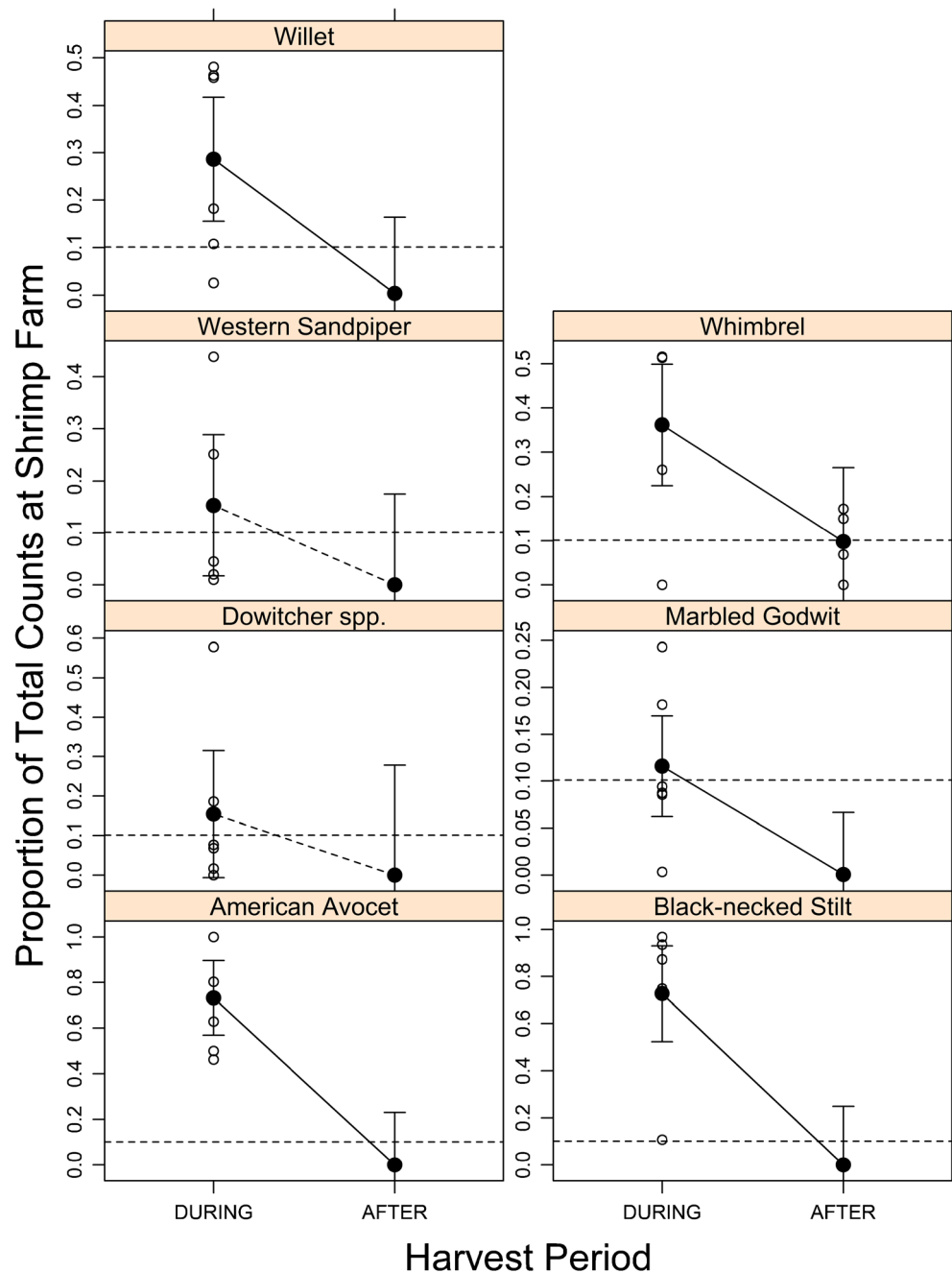


of willet at the Estero de Urías wetland complex exceeded 1 % of this population (1,600 birds; Andres et al. 2012), a threshold that qualifies this site to be of Regional Importance under the WHSRN program. However, following the shrimp-harvest period when ponds were dried from early December onward, shorebird abundance in the entire wetland complex decreased sharply, particularly for American avocet and dowitchers, which virtually disappeared from the Estero de Urías.

Declines in numbers of godwits, willets, sandpipers, and dowitchers were mirrored by rapid decreases in numbers at individual ponds at the shrimp farm following harvest

(J.G.Navedo, unpublished data). These species, particularly godwits, forage mainly on polychaetes (Gratto-Trevor 2000; Navedo et al. 2012), as has been observed at the shrimp farm (J.G.Navedo, personal observation). Therefore, the abundance of these shorebird species at shrimp farms may be directly related to polychaete availability. A reduction in prey availability, which could occur by a decrease in both substrate penetrability, due to declining water content of the substrate (Granadeiro et al. 2006; Kuwae et al. 2010), or decreased polychaete activity (Rosa et al. 2007), could explain the virtual absence of these shorebirds at the shrimp farm in the postharvest period. This pattern was inferred for dunlin

Fig. 3 Proportion (mean \pm SE) of shorebirds, relative to total abundance counted at low tide, at the shrimp farm during ($N=6$) and after ($N=4$) the shrimp harvest period, within the wetland complex at Estero de Urías, México, including shrimp ponds and adjacent intertidal areas, October to January, 2012 and 2013. *Open dots* indicate observed proportions, and *solid dots* indicate mean values (\pm SE) from a general linear model (see “Methods”). *Solid diagonal lines* indicate a significant difference ($P<0.05$) between harvest period (during and after). *Dashed horizontal line* indicates proportion expected under no habitat selection during the harvesting period (see text for more details). Note different scales of the y-axis for the different species



Calidris alpina in aquaculture ponds in SE China (Choi et al. 2013). In contrast, whimbrels seem to use the shrimp farm for a longer period than other shorebirds, even when ponds are dry. *Numenius* spp. forage mainly on crabs, and thus, they are not strictly dependent on soil water content as are other shorebird species (Navedo et al. 2012). For this reason, the availability of the shrimp farm as a foraging area for whimbrels probably has a longer time window than for other species.

Stilts and avocets were more abundant at low tides in the shrimp farm than at intertidal areas during the harvesting

cycle. The shrimp farm held 80–90 % of these taxa counted during the harvest period, even when these ponds represented only ca. 10 % of available foraging surface within the Estero de Urías wetland complex. A similar result was obtained in SE China, where black-winged stilt *Himantopus himantopus* was exclusively observed in aquaculture ponds rather than in intertidal habitats (Ma et al. 2004). This selection is probably due to different microhabitat or prey requirements than other shorebirds, since both species mainly forage on small crustaceans and insects in the water column (Hamilton 1975). Willets and whimbrels also selected shrimp ponds during

Table 2 Abundance (mean \pm SE) and proportion of bird feeding of common shorebirds counted at the shrimp farm in northern Sinaloa, México, at low- and high-tide periods, October to January, 2012 and 2013

Species	Abundance		Fraction feeding	
	Low tide	High tide	Low tide	High tide
American avocet	29.6 \pm 9.7	44.6 \pm 13.7	0.8 \pm 0.1	0.7 \pm 0.1
Black-necked stilt	216.2 \pm 62.5	217.6 \pm 71.0	0.6 \pm 0.1	0.6 \pm 0.0
Dowitchers ^a	17.4 \pm 5.9	29.8 \pm 8.3	0.5 \pm 0.2	0.1 \pm 0.0
Marbled godwit	59.4 \pm 21.5	54.2 \pm 15.0	0.9 \pm 0.0	0.6 \pm 0.1
Western sandpiper	317.6 \pm 285.8	351.0 \pm 278.6	0.8 \pm 0.1	0.6 \pm 0.1
Whimbrel	20.0 \pm 4.1	16.6 \pm 1.8	0.6 \pm 0.2	0.7 \pm 0.1
Willet	421.4 \pm 83.8	433.0 \pm 138.7	0.6 \pm 0.1	0.6 \pm 0.1

No means were significantly different

^a *Limnodromus scolopaceus* and *Limnodromus griseus*

low tide. Since both species tend to defend foraging territories (J.G.Navedo, personal observation), further studies will be needed to disentangle whether there is differential selection based on age, sex, or social dominance (Vahl et al. 2005).

Our results imply that overall numbers of shorebird species within the entire wetland complex currently depend on the availability of alternative foraging areas out of tidal influence, such as recently harvested ponds at the shrimp farm. During a short time window, this artificial habitat seems to increase the carrying capacity of the wetland for shorebirds. Previous studies at different wetlands reported a general peak in abundance during December within this region (Fernández et al. 1998; Buenrostro et al. 1999; Carmona et al. 2011). The sharp decrease observed in the abundance of several shorebird species from their peak during November can thus indicate an ecological connectivity (Amat et al. 2005) between Estero de Urias and other important nearby wetlands, such as Laguna Huizache-Caimanero (<15 km south) with an estimated population of approximately 100,000 shorebirds in the early 1990s (Morrison and Ross 2009). Therefore, this shrimp farm might also be involved in maintaining wintering shorebird populations on a broader scale.

Most shorebirds at the shrimp farm were observed actively feeding, during both low and high tide, without differences in shorebird numbers or in proportion feeding for most species. This pattern suggests that, in general, the shrimp farm is a complementary foraging area and not just a supplementary one for shorebirds. However, we do not eliminate the potential role of shrimp farms as supplementary foraging areas for some species during periods of neap tides, when the availability of intertidal areas as foraging grounds was most limited in time and space (Navedo et al. 2012). Only dowitchers showed a notable decrease in proportion feeding during high tide (from 0.5 to 0.1), along with an overall increase in numbers during high tide, indicating that some individuals used the area as a roosting site during high tide. The other species were

primarily engaged in foraging while at the shrimp farm, indicating that none of these species used the shrimp farm as its main roosting area. Among other factors, a higher disturbance rate due to shrimp-harvesting activities, and the presence of several raptors (resident and wintering species) around the shrimp farm (J.G.Navedo, personal observation), can also play a role in this general avoidance of the shrimp farm as a roosting site for shorebirds (Ydenberg et al. 2002; Rosa et al. 2006). The exception might be the stilts and avocets, for which >75 % of the entire wetland's populations were counted at the shrimp farm. These two species have different micro-habitat requirements (see above), and the consistency of relatively high numbers indicates that they may have been spending most of their time at the shrimp farm.

In summary, we present the first evidence that shrimp farms during the harvest period could play a substantial role as foraging sites for the whole shorebird assemblage within a wetland complex, going beyond results of a recent study that proposed this role of aquaculture ponds for dunlin (Choi et al. 2013). Other similar aquaculture systems, such as shrimp ponds in Thailand, do not provide an available time window for foraging shorebirds due to particular procedures of harvesting (Yasué and Dearden 2009). In contrast, the sequential emptying of ponds during the harvest period at shrimp farms in Sinaloa can maintain the carrying capacity of associated wetlands for shorebirds. A similar role was proposed for aquaculture fishponds embedded in Doñana marshes (Kloskowski et al. 2009), the main wintering area for waterbird populations in southwestern Europe (Rendón et al. 2008).

Therefore, wetland loss and other impacts resulting from the construction of shrimp farms (Páez-Osuna et al. 2003; Valiela et al. 2009) during recent decades have probably contributed to the reduction in shorebird numbers in the area (e.g., current estimate at Huizache-Caimanero gives more than 50,000 shorebirds; G.Fernández, unpublished data). Nonetheless, similar to shorebird use of other man-made habitats such as salt ponds (e.g., Brand et al. 2014), during harvest periods, these artificial habitats can also provide complementary foraging sites for different shorebird species (some of which actively selected the shrimp farm for foraging), as well as for other wading species like egrets and herons (Cheek 2009). Therefore, appropriate management (e.g., Atheam et al. 2012) of the large area (ca. 37,000 ha) dedicated to shrimp farming in Sinaloa (Páez-Osuna et al. 2003), one of the main non-breeding areas for many Nearctic shorebird populations (Morrison and Ross 2009), could play a role in the conservation of these shorebird species, many of which are in decline (Bart et al. 2007).

Finally, we do not advocate transforming natural habitats within wetlands into new shrimp farms, as their role in providing forage opportunities for shorebirds is limited to a particular period, and it remains unknown whether these increased foraging opportunities offset any habitat loss that may

have taken place. In NW Mexico, the shrimp farm facilities were established mainly on saltmarshes (Berlanga-Robles et al. 2011) located within mangrove wetlands. Although such saltmarshes are not generally used as foraging sites for shorebirds, they are commonly used as roosting sites (Zharikov and Milton 2009). Therefore, similar to other artificial habitats that can be important for shorebirds (Masero and Pérez-Hurtado 2001; Navedo et al. 2013; Brand et al. 2014), our management recommendations are intended to apply to existing shrimp farms. Identifying abandoned shrimp farms and developing ways (e.g., Athearn et al. 2012) to restore them into natural habitats, or to include them into a management plan for the entire wetland complex, should be a priority for the recovery of ecosystem processes and ecological resilience (sensu Cumming et al. 2005). Nonetheless, further studies dealing with individual fitness and overwintering survival are needed to definitely establish whether shrimp farms can effectively buffer the impact of wetland habitat loss for the conservation of migratory shorebird populations.

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