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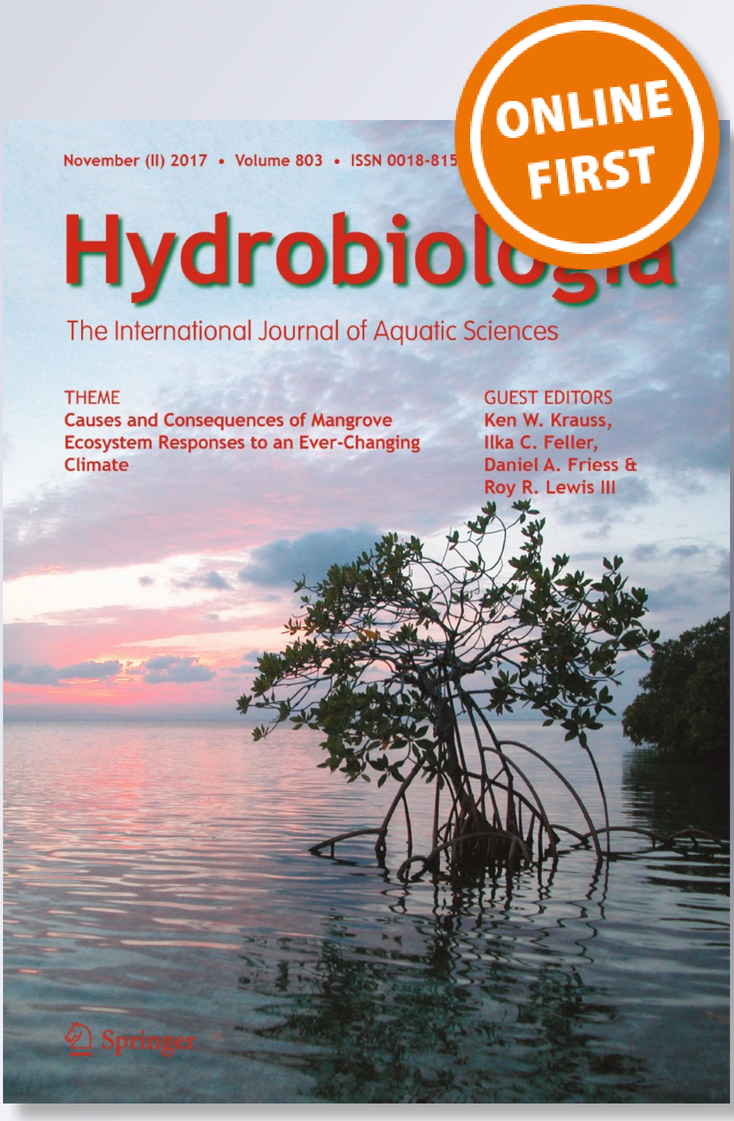

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PRIMARY RESEARCH PAPER

Effects of intertidal habitat availability on the use of anthropogenic habitats as foraging grounds by shorebirds: a case study on semi-intensive shrimp farms

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Abstract Loss of wetlands may restrict foraging opportunities for many species of migratory shorebirds that depend on such habitats during the non-breeding periods. In addition, tidal cycles, both daily (high and low tides) and lunar (spring and neap tides), periodically modulate the availability of foraging areas within coastal wetlands, which can limit area and foraging time for shorebirds. We tested whether densities of shorebirds (marbled godwit, willet, western sandpiper, black-necked stilt, American avocet, two dowitcher species, and whimbrel) observed at a shrimp farm varied with predictable tidal cycles on the coast of northwestern Mexico. We found that most species occurred in higher densities during high- and neap-tides, when nearby intertidal areas were flooded and thus unavailable for foraging shorebirds. The majority of shorebirds at the shrimp farm were actively feeding, indicating that the shrimp farm can provide an alternate foraging habitat. As an exception, western sandpipers were found in lower densities during neap tides, and we suggest that predation risk from peregrine falcons at the shrimp farm may displace this species to other nearby safe habitats. Understanding the spatio-temporal variability on the use of shrimp farms will increase the general knowledge about the function of alternative anthropogenic habitats for migratory shorebirds.

Keywords Aquaculture · Mexico · Predation danger · Anthropogenic wetlands · Nearctic shorebirds

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Introduction

Coastal wetlands are being degraded around the world (Boyer & Polasky, 2004; Siikamäki et al., 2012), largely due to expansion of cities (airports, ports, urban expansion) and development of the aquaculture industry (Ma et al., 2010; Sundar et al., 2015). It has been estimated that in the last 100 years between 54 and 57% of natural wetlands have been lost worldwide, mainly in the tropical and sub-tropical zones of the Western Hemisphere and Asia (Davidson, 2014). This alteration has resulted in severe consequences, such as reduction of ecosystem services and a relevant impact on their associated biodiversity (Green et al., 2017). These biodiversity concerns include migratory shorebirds that depend on coastal wetland areas to survive during non-breeding seasons (Galbraith et al., 2002; Piersma, 2007), and serve as essential components coupling transport and trophic cycles between distant areas (Bauer & Hoye, 2014). In spite of their pivotal function, many shorebird populations are declining worldwide (Simmons et al., 2015) with habitat loss thought to be a main cause (Bart et al., 2007; Nebel et al., 2008; Pearce-Higgins et al., 2017).

Tidal cycles periodically modulate the availability of foraging areas within coastal wetlands, both daily (i.e., high and low tides) and lunar cycles (i.e., spring and neap tides), critically limiting the area and foraging time for shorebirds (Navedo et al., 2012; Calle et al., 2016). Wetland loss could further restrict the availability of optimal intertidal areas to forage, thus increasing the vulnerability of migratory shorebird populations (Sebastiani et al., 1994; Senner et al., 2016). This reduction would displace birds towards remnant areas with higher predation danger, higher rates of human disturbance, or increasing density-dependent interactions (Masero & Pérez-Hurtado, 2001; Yasué et al., 2003; Rocha et al., 2017). In the light of significant and irreversible wetland loss, it has been proposed that anthropogenic wetlands (e.g., saltworks, ricefields, and aquaculture ponds) could be used as alternative foraging habitats for shorebirds (Weber & Haig, 1996; Masero & Pérez-Hurtado, 2001; Czech & Parsons, 2002; Smart & Gill, 2002; Warnock et al., 2002; Masero, 2003; Yasué & Dearden, 2009; Ma et al., 2010; Choi et al., 2012; Gomez-Sapiens et al., 2013; Navedo et al., 2015; Rocha et al., 2017). Since foraging time is not limited by tidal cycles at these supratidal areas, anthropogenic wetlands may have important ecological functions when intertidal foraging grounds are reduced (Masero, 2003; Yasué & Dearden, 2009). Several studies have demonstrated that use of artificial coastal habitats by shorebirds depends on the daily tidal stage (high- and low-tide periods) (Masero et al., 2000; Dias, 2009; Navedo et al., 2013, 2015); however, the effect of intertidal habitat variation associated to longer and periodical monthly lunar tidal cycles (neap and spring tide periods) has not been specifically tested.

The Gulf of California in northwestern Mexico represents a useful area to test these effects. First, environmental characteristics favor semi-intensive aquaculture development linked to numerous coastal wetlands with high primary productivity (Páez-Osuna et al., 2003). This has led to establishment and expansion of the shrimp industry in the northwest of Mexico in the last three decades, with the State of Sinaloa currently leading this industry (to date more than 27,000 ha; CESASIN, 2017). This development has had a structural and functional impact in coastal wetlands, causing the loss of mangroves and salt-marshes (Páez-Osuna et al., 2003; Páez-Osuna, 2005). Second, the coastal wetlands of the Gulf of California are critical areas for the conservation of Nearctic shorebird populations (Morrison & Ross, 2009). Third, due to particular topographic conditions at the Gulf of California (Carbajal & Backhaus, 1998), the amplitude of tides during the peak of the biweekly neap tide periods is negligible at small coastal wetlands, greatly reducing availability of intertidal foraging grounds for shorebirds during these times (Navedo et al., 2012).

Recent studies conducted in northwestern Mexico have suggested that shrimp farms can provide alternative foraging habitats for several species of shorebirds during the harvesting season (Navedo et al., 2015), although pond use is limited to a few days after pond harvesting (Navedo et al., 2017). However, this role of shrimp farms as alternative foraging areas might be even more important during neap tide periods, when intertidal foraging grounds are significantly reduced. Here, we examined variations in the abundances of different Nearctic shorebird species within a shrimp farm throughout the harvesting season in relation to monthly lunar tidal cycles. We predict that the relative abundance of shorebirds in the shrimp farm will increase during periods of restricted intertidal foraging areas (i.e., neap tides). Further, we expect a differential use among the shorebird assemblage related to specific differences in bill morphology, microhabitat selection, and territorial behavior (Navedo et al., 2012, 2017). Additionally, predation danger could have a great influence in habitat use for shorebird species that are frequently attacked by raptors (Pomeroy, 2006; Dekker & Drever, 2016). Understanding the spatio-temporal variability on the use of shrimp farms will increase the general knowledge about their function as alternative anthropogenic habitats for migratory shorebirds.

Materials and methods

Study area

This study was conducted at the shrimp farm 'Acuícola Don Jorge' located in Estero de Urías coastal lagoon, south of Mazatlán (23°13′ N, 106°25′ W), Sinaloa, Mexico (Fig. 1). The Estero de Urías has a surface area of 18 km^2 (Montaño-Ley, 1985) and comprises a mosaic of habitats, mainly mangrove forest (*Rhizophora mangle* L.), intertidal mudflats, and brackish marshes (Montaño-Ley et al., 2008). Available nearby intertidal areas for shorebirds cover 315 ha during spring tides, and are reduced to 185–200 ha during neap tides (Navedo et al., 2012). This shrimp farm covers 300 ha divided in 57 ponds (Fig. 1) that measure an average of 4.7 ha each (Navedo et al., 2015). The production system is semi-intensive, operating in an annual growing cycle that lasts between 120 and 140 days (Páez-Osuna et al., 2003). The harvesting cycle usually lasts 40 days in this shrimp farm, beginning in October–November. During this period, harvested ponds are lowered in water depth, and become available for shorebirds to forage. Pond harvesting is sequential (i.e., one to three ponds each day) and consists of pond draining and gathering the shrimps. Pond availability as foraging areas dramatically decreases day-by-day as ponds dry out. In general, ponds are functional during a few days for shorebirds to forage (see below). After that period, the substrate dries out and hardens, preventing access for shorebirds to invertebrate prey.

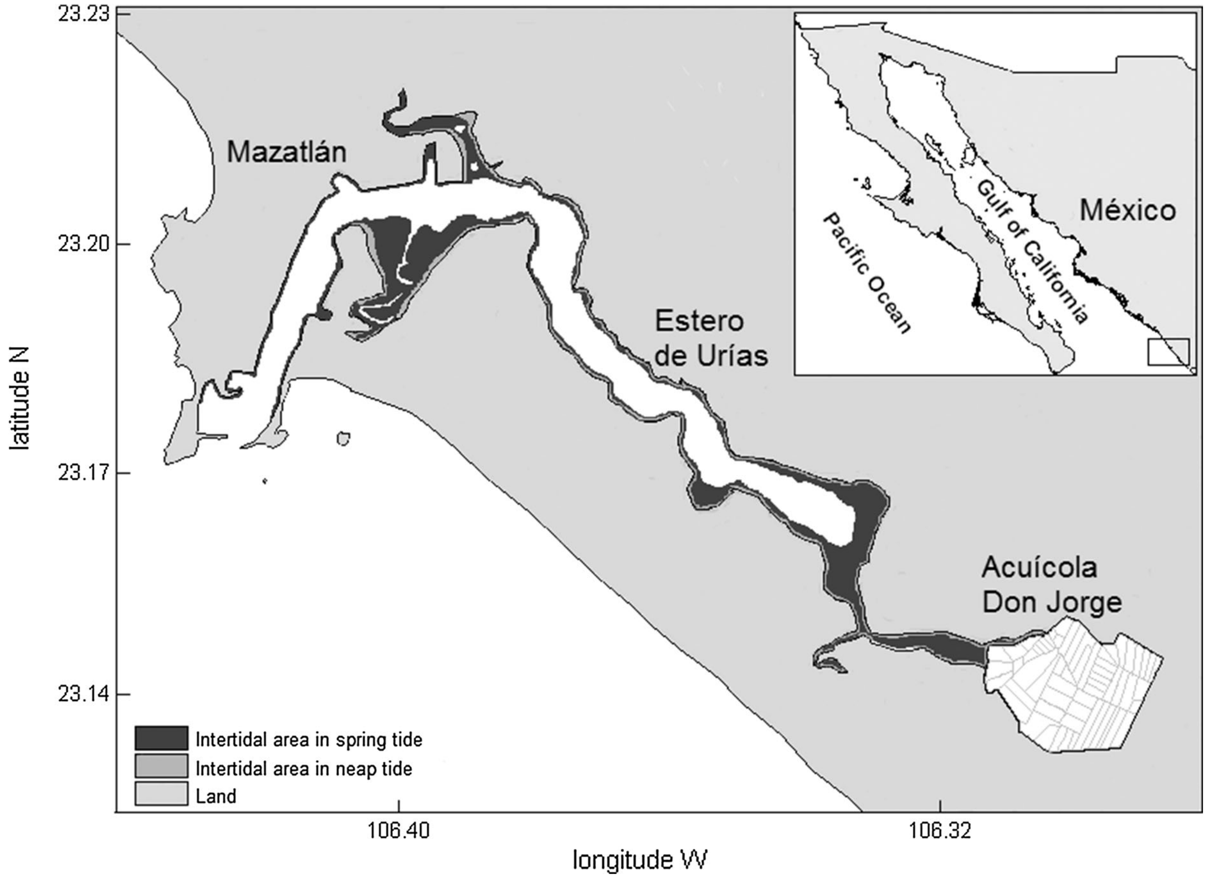

Fig. 1 Study area near Mazatlán City, Sinaloa, México, showing availability of intertidal areas at 'Estero de Urías' during spring and neap tides, as well as the location and extent of Acuícola Don Jorge Shrimp Farm, with pond delimitation (gray borders inside the shrimp farm). We used a tidal amplitude of −60 cm to represent the intertidal area availability during spring tides and 40 cm during neap tides, with reference to Mean Lower Low Water

Data collection

During two consecutive shrimp harvesting cycles (2015 and 2016), following Navedo et al. (2015), we recorded the abundance and foraging activity of the most frequent and abundant shorebird species in recently harvested ponds at the shrimp farm. These species were marbled godwit *Limosa fedoa* Linnaeus, 1758, willet *Tringa semipalmata* Gmelin, 1789, western sandpiper *Calidris mauri* Cabanis, 1857, black-necked stilt *Himantopus mexicanus* Statius Muller, 1776, American avocet *Recurvirostra americana* Gmelin, 1789, two dowitcher species (long-billed dowitcher *Limnodromus scolopaceus* Say, 1822, and short-billed dowitcher *Limnodromus griseus* Gmelin, 1789) and whimbrel *Numenius phaeopus* Linnaeus, 1758. Since it is difficult to differentiate long-billed dowitcher from short-billed dowitcher from a distance, these two species were recorded at genus level. Using tidal calendars for Mazatlán City (http://wwww.predmar.cicese.mx/calendarios/), we planned daily surveys in relation to the diurnal tide height (i.e., low and high tide). Counts were made twice a day: from 1 h before to 1 h after low-tide; and from 1 h before to 1 h after high-tide. Each count lasted on average 2 h. Since we surveyed the shrimp farm on a daily basis throughout the whole harvesting cycle (i.e., 4–5 weeks), therefore, it allowed us to evaluate the natural variability associated to tidal amplitude derived from monthly lunar cycles (i.e., neap and spring tide periods).

After harvesting (day 0), each pond was sampled during three consecutive days (days 1–3), because this is the window during which they are available as foraging grounds for shorebirds (Navedo et al., 2017). We sampled six ponds on average each day once the harvesting started at the shrimp farm, with a total of 40 and 52 ponds (out of 57) surveyed during the season 2015 and 2016, respectively. Surveys consisted of counting shorebirds within each pond and recording their activity (i.e., foraging or resting) using instantaneous scan sampling method (Altmann, 1974). Foraging activity was determined according to each species' feeding strategy to search for prey invertebrates (i.e., tactile or visual) (Barbosa & Moreno, 1999). For tactile foragers, we considered the active probing of the mud as foraging (marbled godwit and dowitchers), while for the visual foragers we considered walking and pecking of the substratum as foraging (willet, western sandpiper, and whimbrel). On the other hand, black-necked stilt (tactile forager) wade and peck while American avocet (visual forager) wade and probe the water surface within shallow pools. An individual was recorded as resting when it displayed comfort behavior (preening) or cessation of activity (Hamilton, 1975). When it was not possible to determine a specific behavior, we waited 3 s before determining the type of activity (Navedo & Masero, 2007). Observations were all made by the same person (EB) using a spotting-scope.

Statistical analyses

We used generalized linear mixed models (GLMMs) to evaluate whether availability of intertidal foraging areas associated to tidal cycles was a driving factor in the use of the shrimp farm by shorebirds. To explain the variability of shorebird density (ind ha^{-1}), we generated the models with count as a response variable and the area of the ponds as an offset (Zuur et al., 2009). We included tide height (two levels: high and low tide), days after (pond) harvest (order factor: first, second, and third day), year (two levels: 2015 and 2016), tidal amplitude (cm), and foraging activity (proportion of birds actively feeding) as fixed predictors. Pond identity (52 levels) was included as random intercept to partially account for potential differences in pond quality in our models (Zuur et al., 2009). Tidal amplitude ranged from -46 to $+ 64$ cm in relation to Mean Lower Low Water (0 cm). Negative values (i.e., spring tides) are indicators of a higher availability of nearby intertidal areas, and positive values (i.e., neap tides) indicate a lower availability of intertidal foraging areas for shorebirds. The number of days after pond harvesting was included to control for the quick day-by-day desiccation of harvested ponds (Navedo et al., 2017). Finally, foraging activity was included as a variable to control for the potential effect on shorebird density associated with an increase in birds using shrimp ponds as resting areas.

Models were generated using glmer.nb function from the lme4 package (Bates et al., 2015) in R 3.3.1 (R Core Team, 2016); the glmer.nb function adjusts a GLMM with a negative binomial distribution (Bates et al., 2015). We selected this distribution (compared to Poisson) to control for overdispersion (Zuur et al., 2009) and avoid data transformation (O'Hara & Kotze, 2010). Since models were restricted to a single random effect, we used Gauss–Hermite quadrature to increase parameter calculation precision (Bolker et al., 2009). For model selection, we used Akaike information criterion (AIC; Burnham & Anderson, 2002; Bolker et al., 2009). For each species, we compared a suite of models that included all variables as single explanatory variables, as additive effects, and all possible two-way interactions. We then used the AIC difference from the best supported model ($\Delta AIC = AIC_i - AIC_{min}$), AIC model weight (i.e., the relative likelihood of a model; w_iAIC), and evidence ratio (i.e., the relative likelihood of the best model with regard to an alternative model; $ER = w_{best}/w_j$) to gauge empirical support for best models (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). The most parsimonious models for each species were selected based in the lowest AIC. We retained any equivalent model with less than 2 AIC units (Burnham & Anderson, 2002). Values (except were indicated) are presented as mean ± SE.

Results

Of the seven species considered in this study, western sandpiper and willet occurred with the highest densities within the shrimp farm, followed by black-necked stilt and marbled godwit (Table 1). The other three species, whimbrel, dowitchers, and American avocet, occurred at much lower densities (Table 1). The number of birds differed strongly between years, with fewer birds observed in 2016. For example, maximum density of any species was 2,917 ind ha^{-1} in 2015 and 167 ind ha^{-1} in 2016 (western sandpiper in both cases, Table 1). Focal observations revealed that shorebirds at the shrimp farm were primarily foraging (i.e., 60–80% for all species), irrespective of the tidal stage.

As expected, shorebird densities significantly differed between ponds. There were significant differences between years, with higher densities in 2015 for all species but whimbrel (Table 1). Shorebird densities within the shrimp farm were also significantly higher during high tides (Fig. 2). The effect of tidal amplitude varied by species (Fig. 2), and there was no significant interaction between tidal height and tidal amplitude for any species (Fig. 2). Noticeably, there was also no interaction between year and both tidal variables for any species, indicating effects of tides were consistent over the 2 years.

Model selection indicated tidal amplitude, tide height, and year were the main predictors of the observed variation in shorebird density within the shrimp farm for the majority of shorebird species (Table 2). The most parsimonious and equivalent models (i.e., $\Delta AIC < 2$) included these three variables for marbled godwit, willet, black-necked stilt and whimbrel, similar to results for dowitchers and American avocet but excluding year (Table 2). Specifically, foraging activity was also retained within an equivalent model for willet (Table 2), showing a positive correlation with density of this species. The year was the only variable retained in the most parsimonious model for western sandpiper (Table 2). In addition, for all species but whimbrel, the marginal ΔAIC (i.e., $2 < \Delta AIC < 3$) retained the model with tidal amplitude and tide height as additive effects (Table 2).

Discussion

During periods when feeding opportunities at intertidal foraging areas were restricted by tides, we consistently recorded higher densities of shorebirds

Table 1 Mean (± SE) density (ind ha^{-1}) and range of shorebirds observed at shrimp farm ponds during the harvest seasons 2015–2016, at the shrimp farm 'Acuícola Don Jorge' near Mazatlán, México

Season	2015		2016	
Species	Mean ± SE	Range	Mean ± SE	Range
Marbled godwit	3.7 ± 0.6	0–108	1.5 ± 0.3	0–55
Willet	14.6 ± 1.3	0–114	8.7 ± 1.1	0–116
Black-necked stilt	5.4 ± 0.4	0–42	3.6 ± 0.4	0–53
Dowitchers	1.4 ± 0.1	0–42	0.3 ± 0.03	0–5
Western sandpiper	143.6 ± 19.0	0–2,917	8.7 ± 1.4	0–167
American avocet	1.3 ± 0.1	0–32	0.03 ± 0.01	0–2
Whimbrel	0.3 ± 0.05	0–7	0.5 ± 0.1	0–25

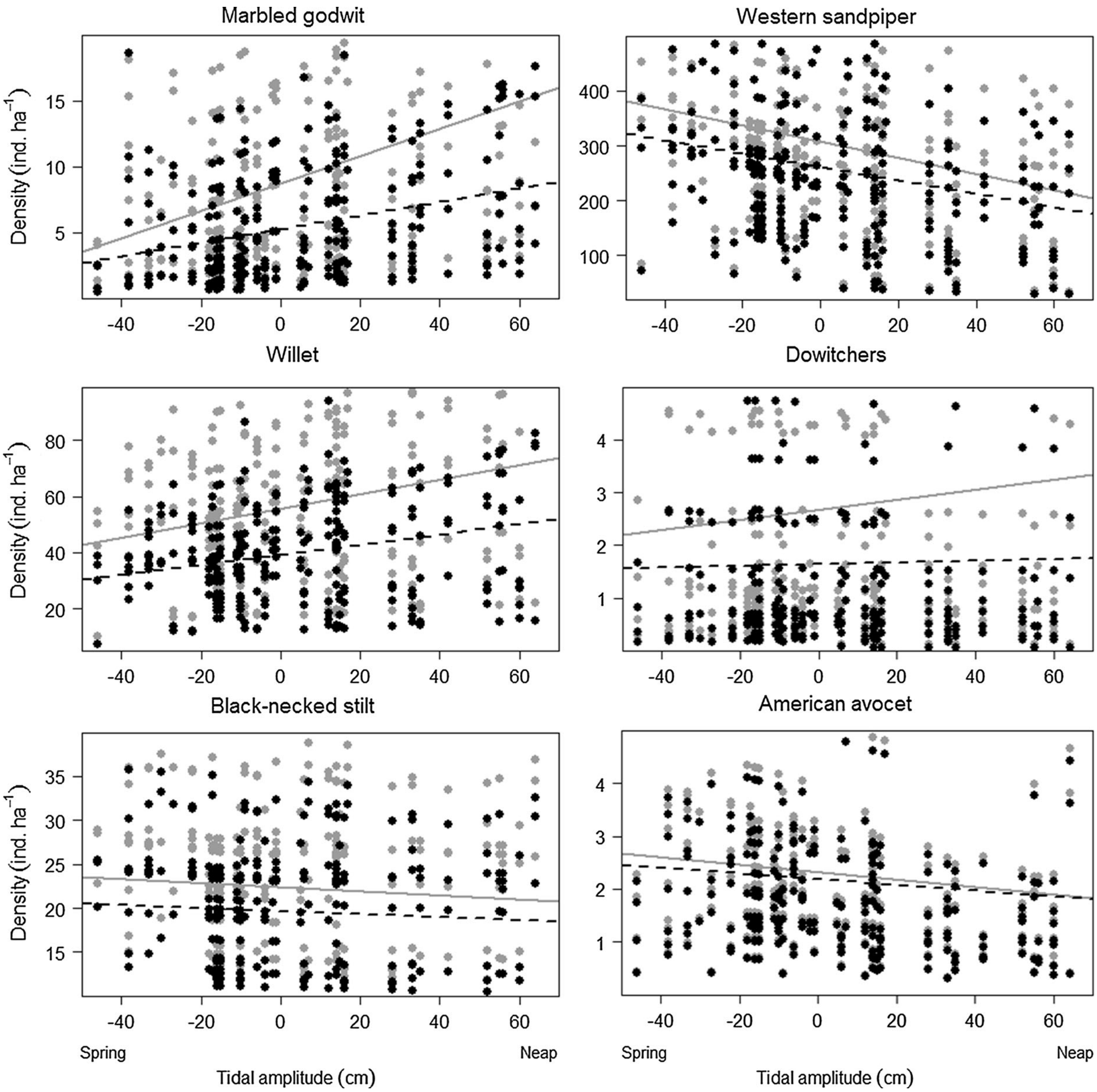

Fig. 2 Densities (ind ha^{-1}) of shorebirds observed at shrimp farm ponds during the two harvest seasons, 2015–2016, at the shrimp farm 'Acuícola Don Jorge' near Mazatlán, México, in relation to tidal conditions. Tide height was treated as a categorical variable with two levels (high/low). Gray circles and gray continuous line indicate high tide, and black circles with dotted black line indicate low tide. Lines correspond to additive models with tidal amplitude (continuous variable) and tide height as independent variables for each species. Tidal amplitude is shown on the *x*-axis, indicates monthly lunar period (spring/neap), and was considered as a variable ranging from −46 to + 64 cm in relation to Mean Lower Low Water (0 cm). Negative values (spring tides) indicate higher availability of nearby intertidal areas, and positive values (neap tides) indicate a lower availability of intertidal foraging areas for shorebirds. Note different scales on the *y*-axes for each species

foraging at recently harvested ponds within this semi-intensive shrimp farm. These results supported the potential role of semi-intensive aquaculture as trophic subsidy for migratory shorebird populations (Green et al., 2015; Navedo et al., 2015; Walton et al., 2015). Since foraging opportunities are restricted fortnightly by lunar tidal cycles, by providing trophic resources during these periods of limited foraging opportunity in intertidal areas, artificial habitats may help to maintain the current carrying capacity of coastal wetlands for

Table 2 Model selection results explaining variation in densities (ind ha^{-1}) of shorebirds observed at shrimp farm ponds during the harvest seasons 2015–2016 ($n = 571$), at the shrimp farm 'Acuícola Don Jorge' near Mazatlán, México

Species	Models	*k*	AIC	ΔAIC	w_iAIC	ER
Marbled godwit	Tidal amplitude + (1|Pond)	4	53.12	0.00	0.24	1.00
	Year + (1|Pond)	4	53.60	0.48	0.19	1.26
	Tide height + (1|Pond)	4	53.66	0.53	0.18	1.33
	Tidal amplitude + Tide height + (1|Pond)	5	55.38	2.25	0.07	3.42
Willet	Tidal amplitude + (1|Pond)	4	52.63	0.00	0.22	1.00
	Tide height + (1|Pond)	4	52.87	0.24	0.19	1.15
	Year + (1|Pond)	4	53.75	1.11	0.13	1.69
	Foraging activity + (1|Pond)	4	54.16	1.52	0.10	2.20
	Tidal amplitude + Tide height + (1|Pond)	5	54.87	2.20	0.07	3.14
Black-necked stilt	Tide height + (1|Pond)	4	59.48	0.00	0.25	1.00
	Tidal amplitude + (1|Pond)	4	59.90	0.42	0.20	1.25
	Year + (1|Pond)	4	60.11	0.63	0.18	1.38
	Tidal amplitude + Tide height + (1|Pond)	5	61.96	2.47	0.07	3.57
Western sandpiper	Year + (1|Pond)	4	43.83	0.00	0.36	1.00
	Tidal amplitude + Tide height + (1|Pond)	5	45.98	2.15	0.12	3.00
Dowitchers	Tidal amplitude + (1|Pond)	4	44.81	0.00	0.40	1.00
	Tide height + (1|Pond)	4	45.36	0.55	0.30	1.33
	Tidal amplitude + Tide height + (1|Pond)	5	47.19	2.38	0.12	3.33
American avocet	Tide height + (1|Pond)	4	60.67	0.00	0.46	1.00
	Tidal amplitude + (1|Pond)	4	60.88	0.26	0.37	1.24
	Tidal amplitude + Tide height + (1|Pond)	5	62.74	2.08	0.14	3.28
Whimbrel	Tidal amplitude + (1|Pond)	4	136.10	0.00	0.29	1.00
	Year + (1|Pond)	4	136.26	0.16	0.27	1.08
	Tidal amplitude + Year + (1|Pond)	5	137.92	1.82	0.18	1.63
	Tide height + (1|Pond)	4	138.45	2.35	0.09	3.26

Models were generalized linear mixed models that accounting for year (2015 and 2016), tidal amplitude, tide height (high and low), and foraging activity as fixed effects, and pond identity as a random intercept. The model selection criterion included the Akaike (AIC), the ΔAIC from the best model ($\Delta\text{AIC} = \text{AIC}_i - \text{AIC}_{\min}$), model weight ($w_i$AIC), and evidence ratio ($\text{ER} = w_{\text{best}}/w_j$); k = parameters calculated for each model

shorebirds. In addition, although shrimp farm use is restricted to the harvesting season (i.e., October–November in northwestern Mexico; Navedo et al., 2017), this short-time window coincides with the arrival of Nearctic migratory shorebirds from breeding grounds (Castillo-Guerrero et al., 2009). Most of these species complete their pre-alternate molt upon arriving at non-breeding grounds (Nebel et al., 2002; Atkinson et al., 2005; Tavera et al., 2016), which is one of the most energy-demanding and time-consuming events in the annual cycle of long-distance migratory birds (Newton, 2008). Hence, shorebirds can also take advantage of additional foraging opportunities during the highly demanding molting period.

Model selection results indicated that lunar and daily tidal cycles were the most important drivers in the use of recently harvested ponds (i.e., < 3 days) as foraging grounds by shorebirds within the shrimp farm. Indeed, the effect of intertidal area availability surpassed the relative weight of day-by-day drying of ponds, which is the main driver explaining variation in shorebird densities when considering longer periods (e.g., a week) during the harvest period (Navedo et al., 2017). Dias (2009) reported similar results at different anthropogenic habitats, with higher shorebird densities using salt ponds to forage due to low availability of intertidal areas. In addition, shorebird densities for all species were significantly different between ponds, thus indicating that pond characteristics also influenced shorebird use within the shrimp farm. Further studies on differences in pond shape, location within the shrimp farm, or food availability within each pond will significantly contribute to understand spatial variation in shorebird densities at shrimp farms.

Our results indicate that shrimp farms are used either as supplementary (Adair et al., 1996) or complementary (Masero et al., 2000) foraging areas, depending on shorebird species. Marbled godwit and willet seem to use the shrimp farm as a supplementary foraging area, based on the significant increase in densities recorded during periods of neap tides when foraging opportunities at adjacent intertidal areas are severely restricted (Navedo et al., 2012), with higher similar increases during high tide. An important fraction of non-breeding populations of these species would thus gain additional trophic resources at the shrimp farm to reach their daily energetic requirements during the first part of the non-breeding season. In the case of willets, higher densities are associated with higher foraging activity, an opposite pattern with the one reported at intertidal foraging areas in this wetland complex (Navedo et al., 2012). Compared to intertidal areas, where density-dependent processes in territorial species can reduce overall foraging activity (Vahl et al., 2005; Stillman & Goss-Custard, 2010), food availability during first days after pond harvesting should be very high, evenly distributed throughout the pond, and not restricted by tidal cycles. A reduction in territorial behavior can thus be expected, because of a high food availability with an even distribution will mean benefits of defending a foraging patch (McNeil & Rompre, 1995; van de Kam et al., 2004) will not counterbalance time spent in agonistic interactions.

Black-necked stilt and American avocet seem to use the shrimp farm as a complementary foraging area, based on the relative constant densities recorded there irrespective of availability of intertidal areas. Despite ecological limitations associated to restricted temporal and spatial scale of this study, the evidence suggests that shrimp farm may offer equivalent or better microhabitat requirements than intertidal areas within the wetland for both species. In contrast to the other shorebird species evaluated, both stilts and avocets mainly forage in shallow channels and pools, such as those that remain in recently harvested ponds (Navedo et al., 2017). Moreover, the near absences of both species throughout Estero de Urías wetland once the shrimp harvesting period has finished (Navedo et al., 2015) also support this argument. Therefore, stilts and avocets may prefer to forage at the shrimp farm because of higher resource profitability (McNeil et al., 1992). Dowitcher densities at the shrimp farm increased at high tide during neap tide periods, which suggest a supplementary foraging. However, since we were not able to reliably distinguish between the two dowitchers species in this study, further studies are needed to establish the actual function of the shrimp farm for dowitchers. In the case of whimbrel, despite tidal amplitude and tide height explained part of variability of density, year seemed to be the most important factor, a result already found by Navedo et al. (2017).

Finally, we recorded much higher densities of western sandpiper at the shrimp farm during spring tides. Contrary to our general prediction, these results indicate that western sandpipers may avoid using the shrimp farm as an alternative foraging area during periods of restricted availability of intertidal foraging areas. A trade-off between foraging opportunities and predation risk (Pomeroy, 2006) may explain this different pattern. Attacks from peregrine falcon *Falco peregrinus* Tunstall, 1771, on western sandpiper flocks are frequently observed at the shrimp farm, with very few attempts on other shorebird species being recorded (Basso and Navedo, *unpublished data*). Predation pressure from peregrines to *Calidris* spp. at other wetland areas is also high, and has been suggested as an important factor explaining the use of inland agricultural fields as anti-predator behavior (Ydenberg et al., 2004; van den Hout et al., 2008; Dekker & Drever, 2016). Therefore, during neap tide periods, western sandpipers at Estero de Urías could make use of other nearby areas (e.g., Huizache-Caimanero Lagoon, 15 km away) that have lower predation danger associated with more open habitats (Yasué et al., 2003; Pomeroy, 2006).

In conclusion, our results support a close relationship between the use of an anthropogenic area by shorebirds and the availability of nearby intertidal foraging areas within a tropical wetland. Moreover, despite the large differences in overall densities between years, probably derived from natural inter-annual variation in local shorebird abundance during the non-breeding season (e.g., Morrison & Ross, 2009), we observed a pattern of relative abundances among the shorebird assemblage that was similar to the pattern previously reported for the shrimp-farm (Navedo et al., 2015). In addition, densities of marbled godwit, willet, and whimbrel at shrimp farm ponds during the first days after harvesting were similar to those reported at intertidal foraging areas within the same wetland (Navedo et al., 2012). Therefore, it is likely that, similar to other anthropogenic habitats (Masero et al., 2000), the semi-intensive shrimp farm currently contributes to the maintenance of Nearctic non-breeding shorebird populations within this coastal lagoon. However, since shrimp farms are currently available as foraging areas only during the harvesting cycle (Navedo et al., 2015), their contribution to maintain overall wetland carrying capacity for shorebirds needs to be placed in the appropriate context. Future research should consider a larger spatio-temporal scale, e.g., longer interannual time scales, during years of high and low shorebird abundances. In addition, other important factors such as food quality (e.g., amount of heavy metals and other pollutants) that could affect individual fitness of birds foraging at shrimp farms should also be evaluated. Importantly, following previous recommendations (Masero, 2003; Yasué & Dearden, 2009; Navedo et al., 2015), we do not promote the creation of new shrimp farms since their proficiency to mitigate to additional wetland loss is limited, but rather evaluate the use of shrimp farms relative to adjacent wetlands as a way to offer management solutions that complement landscape level initiatives.

In crucial geographic areas for migratory shorebird populations such as northwestern Mexico (Morrison & Ross, 2009), where active shrimp farms are already present at the majority of coastal wetlands (Glenn et al., 2006), or at other sites such as the Yellow Sea (Murray et al., 2014; Piersma et al., 2016) where semi-intensive aquaculture is one of the main sources of wetland loss (Valiela et al., 2001), appropriate management of current semi-intensive aquaculture (e.g., Green et al., 2015; Walton et al., 2015; Navedo et al., 2017) can help to mitigate the effect of wetland loss and serve to gain positive conservation outcomes for migratory shorebird populations.

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