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Identifying management actions to increase foraging opportunities for shorebirds at semi-intensive shrimp farms

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Summary

1. The expansion of aquaculture has resulted in widespread habitat conversion throughout the world. Identifying beneficial management measures may dramatically reduce negative impacts of aquaculture for migratory birds.

2. We studied how densities of foraging shorebirds varied at ponds within a semi-intensive shrimp aquaculture farm on the north-western coast of Mexico, as related to timing of harvest and tidal cycles. Further, we estimated the total daily available area for each shorebird species throughout two entire harvesting seasons at the shrimp farm.

3. High densities (average ca. 50 individuals per ha) of foraging shorebirds were found during the first days following pond harvest. The most abundant species were Willet *Tringa semipalmata* and Black-necked Stilt *Himantopus mexicanus*, followed by Marbled Godwit *Limosa fedoa* and American Avocet *Recurvirostra americana*. Other regular, but less abundant, species were whimbrel *Numenius phaeopus* and dowitchers *Limnodromus* spp.

4. Densities of shorebirds sharply declined daily following harvest. In addition, the time-window availability of harvested ponds was related to each species' foraging behaviour: <2 days for godwits and dowitchers, 4 days for stilts, 5 days for willets and more than a week for avocets and whimbrels. However, birds continued to use harvested ponds that received a low, but continuous water influx.

5. Our results demonstrate that a tropical shrimp farm represents a patchy environment that provides 4·3–12·7% (depending on species) of its total area as foraging opportunities for shorebirds.

6. *Synthesis and applications*. Sequential harvesting of shrimp aquaculture farm ponds and increasing moisture of the substrate by providing some water supply to harvested ponds, at least throughout the harvesting period, could integrate shorebird conservation into shrimp-farm production. These low-cost and easy management procedures would not increase costs or affect shrimp production – thus representing a win-win opportunity – and would have potential applications for shorebird conservation throughout the world.

Key-words: aquaculture, habitat use, harvest operations, man-made habitats, Mexico, non-breeding season, shorebirds, shrimp farms, tropics

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Introduction

Land-use change is a driver of biodiversity loss (Newbold *et al.* 2015). The development and implementation of measures to increase the suitability of existing modified habitats for wildlife appears essential to conserve biodiversity. The task is a special challenge in habitats dedicated to food production, which face increasing pressure to meet demands of global markets (FAO 2011). Advances have been made to provide benefits for wildlife in anthropogenic habitats such as rice fields (e.g. Navedo *et al.* 2015a) and coffee plantations (e.g. Caudill, de Clerck & Husband 2015). However, although aquaculture is the fastest expanding global animal food production sector (Jones *et al.* 2015), the potential of these habitats has been largely ignored (but see Green *et al.* 2015; Walton *et al.* 2015a). There is a need, therefore, to further explore aquaculture management practices that improve quality as habitats for wildlife.

Coastal wetlands are one of the most altered habitats world-wide (Duarte 2009). A large proportion of this change (38% of total mangrove area) has resulted from development of shrimp aquaculture production in tropical areas (Valiela, Bowen & York 2001). The industry has expanded greatly in recent years, with a production of less than 9000 tons in 1970 rising to 3·2 million tons in 2007 (FAO 2010). Typically, shrimp aquaculture results in major wetland changes (Paez-Osuna *et al.* 2003), including (i) loss of natural habitats (saltmarshes and mangroves), (ii) reducing the extent of natural systems within which aquaculture ponds are embedded, (iii) alteration of physical and biological processes associated with tidal cycles, and (iv) changing nutrient cycles and increasing environmental pollution through effluents. The magnitude of these changes depends primarily on type of aquaculture system. There are three types of shrimp aquaculture systems (*sensu* Edwards 1993): intensive, extensive and semi-intensive. Intensive shrimp aquaculture does not allow coexistence with wildlife at any stage of the growing cycle due to intensive management practices and mechanization. Extensive shrimp aquaculture entails an important reduction of tidal processes at coastal wetlands where they are built, while semi-intensive aquaculture represents a mid-point where some natural processes can still occur in a modified environment. The appropriate management of semi-intensive shrimp aquaculture systems can help to mitigate their impacts on natural systems and may result in trophic subsidies to wildlife (Walton *et al.* 2015a), mimicking other agroecosystems (e.g. Navedo *et al.* 2015a).

Millions of shorebirds migrate along flyways experiencing global change (Boere *et al.* 2007), with many species undergoing population declines (Butchart *et al.* 2010). These declines are particularly severe in the East Asian Australasian Flyway where conversion of intertidal mudflats into shrimp farms is ongoing (Murray *et al.* 2014; Green *et al.* 2015). Shorebirds are challenged by choices of if, how and for what duration they use 'new' (anthropogenic) habitats when they become available. Apart from shorebird use of restored wetlands (Weber & Haig 1997; Armitage *et al.* 2007), several studies have focused on the role of modified coastal areas as foraging habitats for migratory shorebirds, such as salt production ponds (Masero 2003; Athearn *et al.* 2012), rice fields (Toral & Figuerola 2010) and coastal pastures (Navedo *et al.* 2013). Coastal aquaculture ponds, including shrimp farms, can provide foraging habitats for declining shorebird populations in south-western Europe, Asia and America. Extensive aquaculture ponds in south-western Europe (Kloskowski *et al.* 2009; Marquez-Ferrando *et al.* 2015; Walton *et al.* 2015a) or Mexico (Navedo *et al.* 2015b) are used by large numbers of shorebirds and waterbirds. In contrast, despite currently supplying 89% of global aquaculture production (FAO 2012), aquaculture ponds in Asia do not appear to provide relevant foraging opportunities for shorebirds (Yasué & Dearden 2009; Sripanomyom *et al.* 2011; Li *et al.* 2013; Green *et al.* 2015). Therefore, understanding the factors that limit use of aquaculture ponds by shorebirds may identify management actions to increase their quality as foraging habitats.

Semi-intensive shrimp ponds in north-western Mexico are harvested sequentially by draining water levels to concentrate shrimp at the exit gate. After shrimp harvesting, each pond is isolated from tidal influence using lock gates and eventually dries out (Navedo *et al.* 2015b). During this post-harvest period, shrimp ponds briefly mimic intertidal areas until they dry due to high evaporation rates. As ponds are harvested at different times, the shrimp farm as a whole provides shorebirds with a mosaic of foraging areas with differing profitability. North-western Mexico provides important non-breeding grounds for large numbers of several Nearctic shorebird species (Morrison & Ross 2009) and includes four coastal wetlands recognized within the Western Hemisphere Shorebird Reserve Network (www.whsrn.org). Most of these birds rely on natural intertidal areas for foraging (Fernández & Lank 2008; Navedo, Sauma-Castillo & Fernández 2012), but they can also opportunistically exploit harvested ponds in semi-intensive shrimp farms located adjacent or near these intertidal areas. Generally, shorebirds arrive at the harvested ponds and forage for several days, typically less than a week (Navedo *et al.* 2015b). Differences in diet and foraging behaviour (van de Kam *et al.* 2004; Colwell 2010) between species can result in differential shorebird use of harvested ponds. Addressing pond availability for each species is a key question to estimate daily available area for foraging shorebirds. These calculations can be used to develop adaptive shrimp-farm management plans that integrate shorebird conservation actions.

Here, we studied how densities of foraging shorebird species varied over time from the day of harvest in ponds in a shrimp farm within a tropical coastal lagoon in north-west Mexico. We conducted shorebird surveys in two types of harvested ponds: (i) ponds with the entry gate fully locked, and (ii) ponds where the entry gate was not fully locked after shrimp harvest, thus allowing low-but-continuous water flux into the pond for extended periods. The comparative approach allowed us to assess potential effects on shorebird density of managing water flux once ponds were harvested. Finally, as ponds are sequentially harvested, we estimated the total daily available area for each shorebird throughout the entire harvesting cycle at the shrimp farm. We predicted that shorebird densities would decline daily after pond harvesting, with differences among species and ponds related to foraging performance, microhabitat requirements and water flux, respectively. We provide recommendations on ecological applications to provide foraging grounds for shorebirds in semi-extensive aquaculture developments throughout the tropics.

Materials and methods

STUDY AREA

We conducted our study at Acuícola Don Jorge shrimp farm situated in Estero de Urías, a low-energy tropical coastal lagoon (Lankford 1977) located south of the city of Mazatlán (23°13′ N 106°25′ W), Sinaloa, Mexico (see Navedo *et al.* 2015b for details). The lagoon covers an area of 18 km^2 and contains a diverse mosaic of habitats, including intertidal mudflats, mangroves and emergent brackish marshes (Navedo, Sauma-Castillo & Fernández 2012). Shrimp farms have been developed in the upper part of the lagoon since the 1980s, occupying ca. 400 ha. Don Jorge shrimp farm is the biggest and oldest, with 50 ponds (size range: 1·1–11·1 ha) spanning over 300 ha. A typical shrimp-growing cycle entails the preparation of ponds during February to March with flooding and introduction of shrimp larvae in March to April. An early pre-harvest of some ponds occurred in May to June by lowering water levels, fishing a fraction of the shrimps and then the pond is flooded again. A complete harvest is done in October to November by emptying the water of each pond and fishing all the shrimp production. Ponds are sequentially harvested by emptying water, at a rate of 1–2 ponds per harvesting day. However, dependent on shrimp market prices, there can be several days without harvesting. Thus, the entire shrimp harvest cycle typically lasts 40 days at this farm. Once the last pond is harvested, a drying period of 3 months occurs (December to February).

Thousands of shorebirds feed on the intertidal mudflats of the coastal lagoon during the non-breeding season (Navedo, Sauma-Castillo & Fernández 2012; Navedo *et al.* 2015b). Although some aquaculture ponds have high densities of benthic invertebrates (Arias & Drake 1994; Walton *et al.* 2015a), this food source is unavailable to shorebirds because the ponds are too deep and steep-sided. However, drainage of the ponds to harvest the shrimp allows shorebirds to forage on these invertebrates (Navedo *et al.* 2015b). At the study area, available foraging area for shorebirds within each harvested pond is gradually reduced from day to day as the sediment becomes dry, ending with a small pool close to the outflow before becoming fully dried. Occasionally, when the entry gate is not fully locked after harvesting, pond drying is delayed. At the end of harvest period, once the last pond is harvested, available foraging grounds at the farm become reduced in area and suitability due to a total release of water from the reservoir and internal channels. Subsequently, the sediment surface of harvested ponds dries and the shrimp farm becomes unsuitable as a foraging area for shorebirds.

DATA COLLECTION

Twenty-one shorebird species occur in the study area, but relative usage of natural wetlands and the shrimp farm varies among species (Navedo *et al.* 2015b). During October and November of 2011 and 2012, we recorded the abundances of the six shorebird species that are locally common (mean abundance >10 individuals in the shrimp farm at low tide) and regularly forage in the shrimp ponds (Navedo *et al.* 2015b). These species were Marbled Godwit *Limosa fedoa,* Willet *Tringa semipalmata,* Black-necked Stilt *Himantopus mexicanus,* American Avocet *Recurvirostra americana,* whimbrel *Numenius phaeopus* and dowitchers *Limnodromus* spp. Long-billed Dowitcher *L. scolopaceus* and short-billed Dowitcher *L. griseus* could not be reliably distinguished in the field, so count data from the two species were pooled. We expected daily use of the ponds to vary with specific foraging and microhabitat requirements of each shorebird species. Gregarious and obligate tactile foragers preying on infaunal polychaetes, such as godwits (Gratto-Trevor 2000) and dowitchers (Weber & Haig 1997), would use recently harvested ponds and then abandon them after a few days. Use of harvested ponds was expected to be more protracted for territorial shorebirds with high foraging plasticity, that is willets (Lowther, Douglas & Gratto-Trevor 2001), and even longer for territorial and obligate visual foragers preying upon mobile crabs, that is whimbrels (Skeel & Mallory 1996). Further, we predicted a different use of harvested ponds by stilts and avocets that forage in shallow water areas rather than on the bottom of the ponds (Hamilton 1975).

We surveyed two recently harvested ponds each week (a total of 8 and 7 ponds in 2011 and 2012, respectively; average pond area 5·1 ± 0·5 ha) throughout the whole harvesting cycle to assess potential differences in pond use associated with overall surface availability at the shrimp farm. Surveys were made in the morning, between 6 and 11 h, adjusted to account for low or high tide period (see below). Once harvested (harvest day = day 0), ponds were surveyed daily or, when not possible, every second day, until the presence of shorebirds was negligible. Following the same procedure, we surveyed recently harvested ponds that were noticed to have the entry gate not securely locked ($n = 4$ in 2011 and $n = 1$ in 2012; average pond area 4·7 ± 1·1 ha). In addition, we calculated the area of each pond by marking their corners and using a GPS and GIS software (Esri ARCGIS 10, Redlands, CA, USA) to calculate the area of the resulting polygon. The area in any harvested pond that would be available to different shorebird species at any one time depends on their specific microhabitat preferences (Isola *et al.* 2000) and small-scale variation in bathymetry. However, we assumed that the whole area of each harvested pond was available as foraging area, since the area covered with water over 5 cm (i.e. unsuitable for foraging shorebirds) was restricted to a shallow channel typically present only on day 1 after harvest and was therefore considered negligible.

STATISTICAL ANALYSES

Densities (ind. ha^{-1}) of each bird species were analysed separately as dependent variables. We used generalized additive

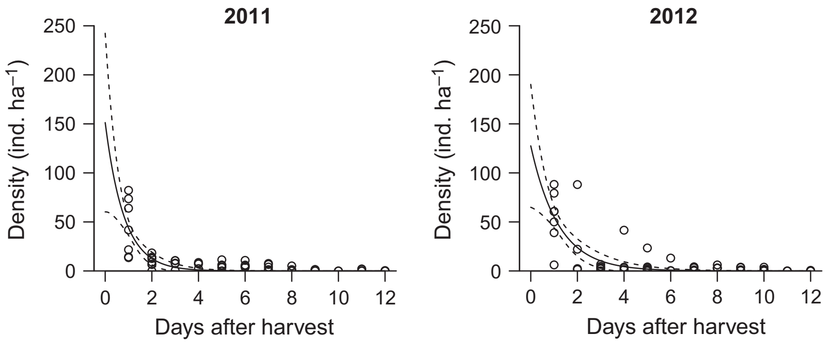

Fig. 1. Total shorebird density during 2011 and 2012 seasons throughout the 12 days following day of harvest (day 0) at ponds in Acuícola Don Jorge shrimp farm on north-west coast of Mexico.

models (GAMs) to evaluate how shorebird densities varied with the number of days after harvest, starting with Day 1 after harvest. The models also included tidal amplitude class (two levels: neap or spring tides), tidal state (two levels: high or low tide), as surrogates of foraging grounds' availability in the adjacent intertidal habitat (Granadeiro *et al.* 2006), year (2011 or 2012), and pond identity as independent variables. Tidal amplitude was considered as neap when daily low tide height did not reach mean lower low tide and considered spring when it exceeded mean lower low tide. We considered that counts at the shrimp farm were made during low tide if they occurred within 2 h before or after the low tide nadir. Following the same criteria, counts were considered made during high tide if they occurred within 2 h before or after high tide peak.

We estimated all models using the gam function in the mgcv package of R statistical environment (R Core Team 2014). The smoothing terms for the days after harvest variable were fitted with thin plate penalized regression splines, and the smoothing parameters were selected by generalized approximate cross-validation (GACV). The best models were selected according to Bayesian (Schwartz) information criterion (BIC). The model with the lowest BIC value had the best support, but if the difference of BIC (ΔBIC) between two models was <2, they were considered to be equivalent (Burnham & Anderson 2004).

Finally, we fitted negative exponential (decay) functions to these daily count data in order to estimate the day after harvest at which bird densities reached negligible values (<1 bird ha^{-1}, hereafter referred to as ElapseDay). Compared to other arbitrary criteria such as a 90% or 95% reduction in initial bird density, we considered that 1 bird ha^{-1} represented a biologically meaningful threshold taking into account that the average pond size was 4·7 ha in our study area (Navedo *et al.* 2015b). Further, for less abundant species showing initial average densities below 2 ind. ha^{-1}, a threshold of, for example, 10% of initial density, would artificially enlarge our estimates of total daily pond availability.

We followed the same procedure using counts from ponds receiving a low-but-continuous water influx once harvested (see above). Using the nonlinear fit, we computed the estimate and confidence intervals for the day after harvest that corresponded to ElapseDay. With these ElapseDay values, we estimated the total daily available area for each species throughout the entire harvesting cycle at the shrimp farm. We obtained harvest date information from the shrimp-farm official statistics. We considered each pond as unavailable if (i) it was currently unharvested and thus water levels were too high for shorebirds, or (ii) it surpassed the ElapseDay estimated for each species. Conversely, we considered a pond as available from the day of harvesting to the ElapseDay estimated for each species. We further calculated total daily available surface for each shorebird species during 2011 and 2012 harvesting seasons, by adding up the area of available ponds each day. All results are presented as means ± SE.

Results

Mean initial density of all shorebirds across all ponds on the day after harvesting was 49·7 ± 7·4 ind. ha^{-1} (range: 13–80 ind. ha^{-1}), showing a steep reduction the following days (Fig. 1), with a similar pattern for both 2011 and 2012. The most abundant species were willets (mean initial bird density 32·7 ± 6·5 ind. ha^{-1}) and stilts (12·3 ± 2·2 ind. ha^{-1}), with abundance of godwits and avocets about one order of magnitude lower (1·6 ind. ha^{-1}). Dowitchers and whimbrels had lower abundances (below 0·5 ind. ha^{-1}), although they were regularly present on the shrimp farm.

Days elapsed after harvest was the main explanatory variable of bird density within ponds for almost all species. The variable was the only one included in the best model for willets, stilts, godwits and dowitchers (Table 1). Also, tidal period was retained in an equivalent model for avocets (Table 1), with a significantly higher density during counts made at high tide (0·79 ± 0·13 ind. ha^{-1}) with respect to low tide (0·52 ± 0·11 ind. ha^{-1}). The exception was whimbrel, for which the best model included only year (Table 1), with significantly higher densities observed during 2012 (0·13 ± 0·02 ind. ha^{-1}) than 2011 (0·04 ± 0·03 ind. ha^{-1}). Comparable models (ΔBIC < 2·0) for whimbrel included the effects of pond identity, indicating density of this species varied significantly among individual ponds, as well as day after harvest, showing a weaker effect of this variable in explaining density of whimbrels (Table 1).

As predicted, density of shorebirds declined daily following harvest, and the time-window availability of harvested ponds differed among species (Fig. 2). Ponds were used for <2 days after harvest by godwits (mean: 1·6 days; confidence interval [CI]: 1·3–2·2 days), nearly 3 days by stilts (mean: 2·9; CI: 2·2–3·6 days) and more than 4 days by willets (mean: 4·4; CI: 2·9–5·5) (Fig. 2). We could not statistically estimate time availability of harvested shrimp ponds for the other three species because of their low abundances. Initial bird density for dowitchers was below 0·5 ± 0·2 bird ha^{-1} (Fig. 2), thus lower than the

Table 1. Results of model selection for density (ind. ha^{-1}) of six shorebird species at ponds in Acuícola Don Jorge shrimp farm within the Estero de Urías, Sinaloa, north-western Mexico, during the wintering season

Species	Model	Dev. expl.	BIC	ΔBIC
Limosa fedoa (Marbled godwit)	s(days after harvest)	0·269	309·73	0·00
	s(days after harvest) + tide class	0·281	312·79	3·05
Tringa semipalmata (Willet)	s(days after harvest)	0·443	945·73	0·00
	s(days after harvest) + tide class	0·447	949·10	3·37
Himantopus mexicanus (Black-necked stilt)	s(days after harvest)	0·522	677·44	0·00
	s(days after harvest) + year	0·530	679·64	2·20
Recurvirostra americana (American avocet)	s(days after harvest) + tide period	0·166	339·13	0·00
	s(days after harvest)	0·131	339·58	0·45
	s(days after harvest) + year	0·139	343·18	4·06
Limnodromus spp. (dowitchers)	s(days after harvest)	0·252	63·95	0·00
	s(days after harvest) + year	0·269	66·05	2·10
Numenius phaeopus (Whimbrel)	year	0·036	8·73	0·00
	Pond + year	0·035	8·77	0·04
	Pond	0·035	8·77	0·04
	s(days after harvest)	0·005	8·83	0·10
	s(days after harvest) + year	0·042	9·44	0·71

Predictor variables for each general additive model (GAM) included the smooth of days after harvest (1–12 days), year (2011 or 2012), pond identifier, tide class (neap or spring tide) and tide period (high or low tide). Model selection criteria include proportion of deviance explained (Dev. expl.), Bayesian information criterion (BIC), and the difference in BIC from the best model ($\Delta BIC = BIC_i - BIC_{min}$). For each species, the model with lowest ΔBIC_i was model best supported by the data.

considered threshold for estimation of pond availability (see Methods). Therefore, the number of days that ponds appear to be used by dowitchers seems to be even lower than for godwits. However, for avocets and whimbrels, densities did not sharply decline over the first 12 days after harvesting (Fig. 2).

The pattern of shorebird usage differed at ponds that received a low-but-continuous water influx once harvested, where a gradual, rather than steep, decline of shorebird density over time was observed (Fig. 3). Time availability of harvested ponds for all species increased under these conditions, even surpassing the day 12 for willets. We could only statistically estimate a ElapseDay value for stilts, and this value lasted until nearly 5 days (mean: 4·7; range: 3·3–6·7 days), thus a ca. 60% increase with respect to 'regular' ponds.

Harvest was conducted at slightly different periods over the two study years (from 19 October to 26 November in 2011 and from 6 October to 12 November in 2012), although they had similar durations from day of first pond harvest until the day the last pond was harvested (39 days; Fig. 4). Estimated daily available area (using time availability obtained at 'regular' ponds) at the shrimp farm differed between species: on average 12·8 ± 1·1 ha for dowitchers, 19·2 ± 1·4 ha for godwits, 25·6 ± 1·7 ha for stilts and 38·5 ± 2·1 ha for willets, having a small but higher area during 2012 season (Fig. 4).

Discussion

We recorded high densities of shorebirds foraging at semi-intensive shrimp-farm ponds during the first days following harvest. Densities within each harvested pond declined sharply with each day after harvest, with differences among species presumably related to functional morphology such as exposed leg length and/or foraging specializations (*sensu* Ntiamoa-Baidu *et al.* 1998). According to the estimated daily available area for foraging, the shrimp farm presented a mosaic of foraging opportunities during the harvesting season, with different values for each shorebird species. The provision of such foraging opportunities presents an important trophic subsidy for shorebirds. The beneficial role of such semi-intensive shrimp farms during the harvesting season for shorebirds could be further enhanced if ponds were sequentially harvested without interruption during the season, resulting in a steady supply of prey for overwintering Nearctic shorebird populations.

More than 40 willets per hectare were observed in recently harvested ponds at the shrimp farm at this coastal lagoon (1600 birds; Navedo *et al.* 2015b). The average densities of willets on 1 day after harvesting were higher than mean densities observed at a nearby intertidal mudflat (Navedo, Sauma-Castillo & Fernández 2012). Further, densities of willets in the harvested ponds were similar to those in restored wetlands in southern California (Armitage *et al.* 2007). The shrimp farm may have even higher value for stilts, which are more abundant at aquaculture ponds than at intertidal areas (Ma *et al.* 2004; Ackerman *et al.* 2007; Navedo *et al.* 2015b). In contrast, maximum densities of godwits at the shrimp farm were lower than those observed at the nearby mudflat (Navedo, Sauma-Castillo & Fernández 2012) and other intertidal areas (Armitage *et al.* 2007), although higher than densities observed at other artificial wetlands, such as salt production ponds located in the Pacific region (Athearn *et al.* 2012).

Shorebird density at the shrimp farm was strongly and negatively related to the number of days since harvest. Other important ecological drivers that affect shorebird density at nearby intertidal areas, such as daily or monthly tidal cycles (Navedo, Sauma-Castillo & Fernández 2012), had a secondary role. Although food supply should be another essential driver explaining daily reductions in shorebirds densities within ponds (Masero *et al.* 1999), neither year nor pond was retained by the models. These findings suggest that different ponds were similar in terms of prey density across years, or alternatively, that

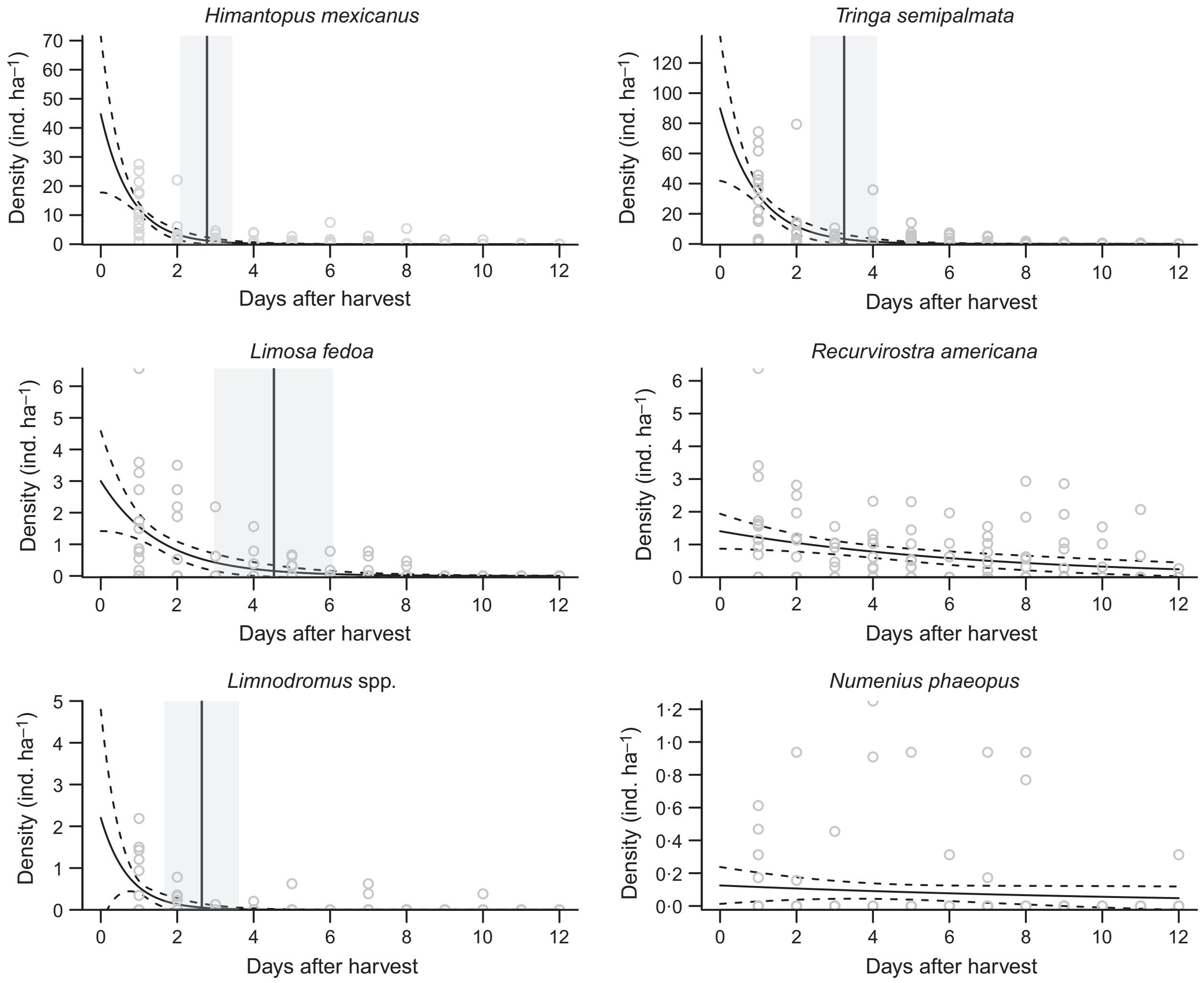

Fig. 2. Negative exponential fits to bird density data (ind. ha^{-1}) during the first 12 days after harvesting (day 0) for six shorebird species observed at shrimp harvest ponds in north-western Mexico. Solid and dashed black lines denote mean response ± 95% CI of fits, respectively. Green lines and rectangles represent the estimated time ± 95% CI, respectively, at which bird density was considered non-significant (< 1 ind. ha^{-1}). Note the different scales of the *Y*-axis.

differences in food supply among ponds and/or seasons were diluted by the high evaporation rate that drastically changes day-by-day habitat availability within harvested ponds. The overall increase in time availability for harvested ponds that received a low-but-continuous flux of water supports this argument. The differences in temporal windows of pond availability that varied among species with different foraging requirements again suggest effects of shrimp farms were more related to food availability than to food depletion by shorebirds.

The temporal variation in use of harvested ponds by individual species was related to each species' foraging behaviour. Shrimp ponds became unavailable in <2 days after harvesting for gregarious shorebirds, such as marbled godwits and dowitchers, that forage by probing for polychaetes in soft mud (Weber & Haig 1997; Kober & Bairlein 2006; Castillo-Guerrero *et al.* 2009). In comparison, willets (mostly territorial individuals; McNeil & Rompre 1995), which forage by probing or pecking (Castillo-Guerrero *et al.* 2009), on a variety of prey (Stenzel, Huber & Page 1976; J.G. Navedo pers obs.), used harvested ponds for up to 5 days. Territorial shorebirds that feed on crabs, such as whimbrels (McNeil & Rompre 1995), continued to use ponds for 2 weeks following harvest. Also, harvested ponds present a different temporal availability for shorebirds that forage in channels and shallow pools of water that remain within ponds. Black-necked stilts used ponds for 4 days, whereas American avocets continued to use ponds for 2 weeks. Although both species often forage on similar foods and show a marked territorial behaviour (Robinson *et al.* 1997, 1999), their use of microhabitats and possibly aquatic prey items can differ (Hamilton 1975; Rintoul *et al.* 2003; Ackerman *et al.* 2007). Stilts visually detect prey in the water, whereas avocets are tactile foragers (Hamilton 1975). Thus, available foraging areas (i.e. shallow channels) within harvested ponds for visually foraging stilts that need

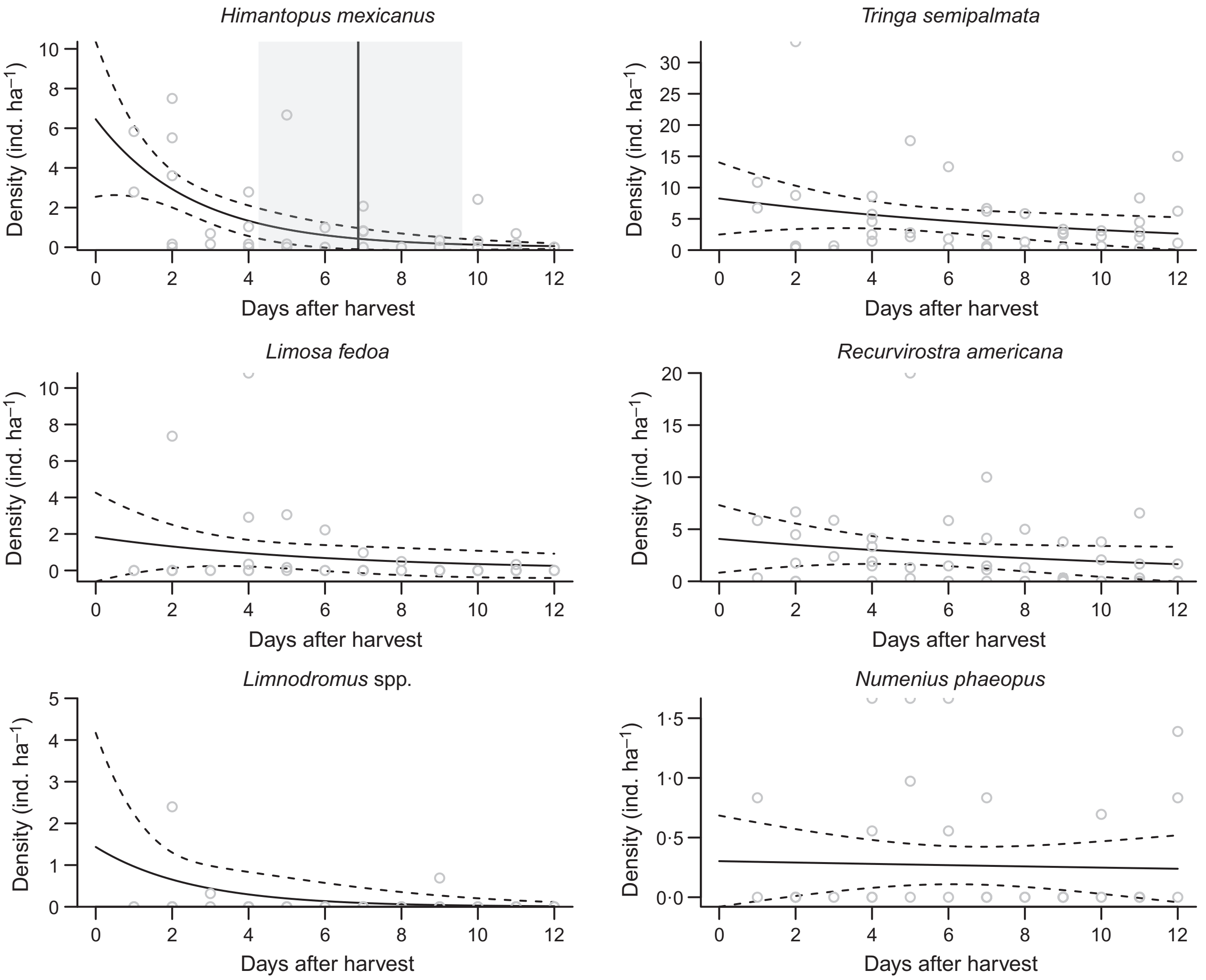

Fig. 3. Negative exponential fits to bird density data (ind. ha^{-1}) during the first 12 days after harvesting (day 0) for six shorebird species observed at shrimp harvest ponds experiencing a low-but-continuous water flux during the first 12 days after harvesting (day 0) (See details in legend of Fig. 2). Note the different scales of the *Y*-axis.

quiet water were likely negligible after a few days, whereas they remained used by tactile foraging avocets for longer periods.

In summary, the high evaporation rate at tropical latitudes seems to be an essential driver of use of harvested shrimp ponds by shorebirds. Therefore, maintaining moisture of the substrate within harvested ponds throughout a harvesting cycle would appear an important, easy and cheap management technique that could increase the trophic subsidy of semi-intensive shrimp farms for shorebird populations.

APPLICATIONS

We found that a tropical, semi-intensive, shrimp farm occupying approximately 300 ha is a patchy environment that provides 13–38 ha (i.e. 4·3–12·7% of the total area depending on species) of daily foraging opportunities for shorebirds. Breaks between harvests longer than 5 days resulted in a large reduction in available foraging area, with this effect being most pronounced for species that use the ponds for 1 or 2 days following harvest. The effect was not counterbalanced by a temporal extension of pond availability at the shrimp farm since both harvesting seasons had the same overall duration (39 days). As the intertidal areas within the wetland where the farm is embedded extend 200–315 ha in area (Navedo, Sauma-Castillo & Fernández 2012; Navedo *et al*. 2015b), the shrimp farm could have a major role in supporting the current carrying capacity of overwintering shorebirds and other waterbirds by supplementing their foraging opportunities. The potential benefits would be present without the foraging restrictions associated with tidal cycles (Masero & Pérez-Hurtado 2001). Our results suggest that the trophic subsidy provided by shrimp farms during harvesting period will be especially relevant for willets, stilts, avocets and whimbrels. While it is important to remark that we do not advocate the development of new aquaculture ponds for the conservation of shorebirds, we advocate more appropriately managing existing aquaculture

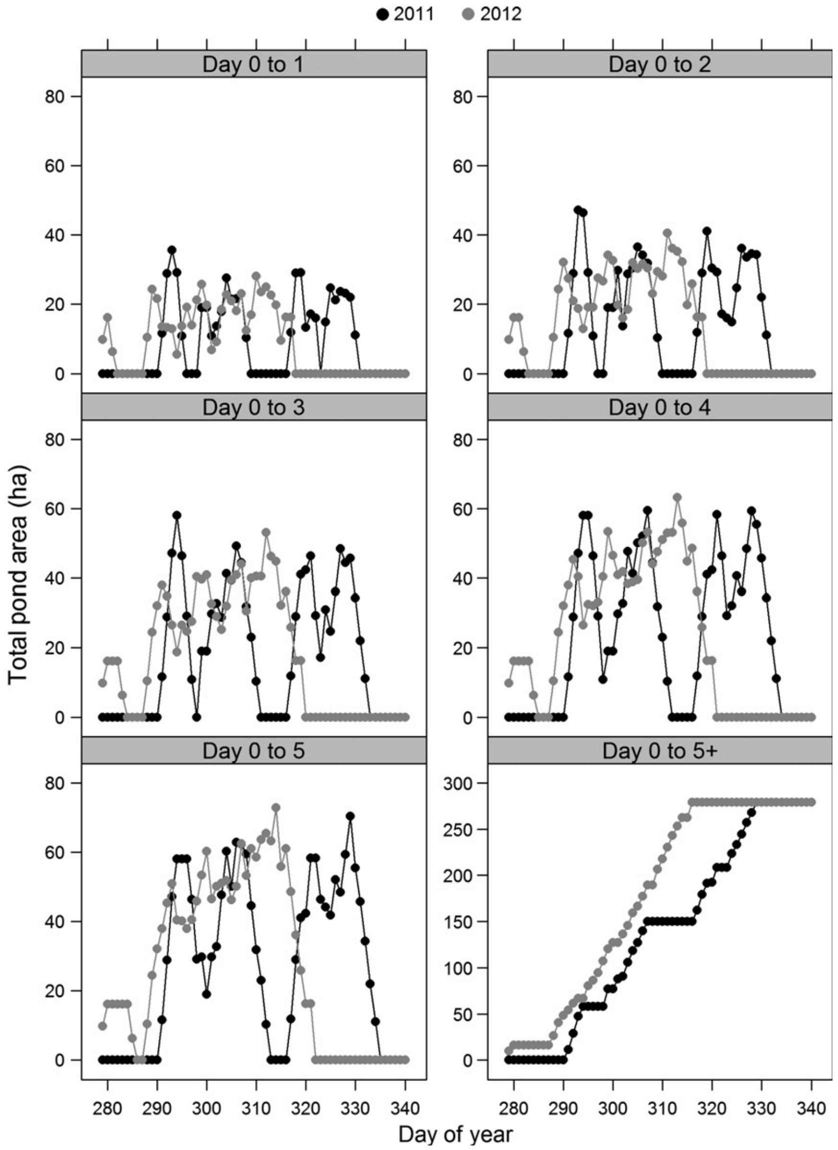

Fig. 4. Estimated daily available foraging surface at the shrimp-farm adding up area of each harvested pond from harvesting day (Day 0) up to 5 days (Day 5), during 2011 and 2012 seasons. Note the different scales of the *Y*-axis in the last panel, which shows the cumulative surface area of ponds harvested <5 days previously throughout the shrimp farm.

facilities, since avian diversity in artificial wetlands is generally reduced relative to both restored and natural wetlands (Sebastián-González & Green 2016).

We propose that (i) sequentially harvesting shrimp ponds without interruption, and (ii) increasing moisture of the substrate by providing some water supply to harvested ponds throughout the harvesting period could better integrate shorebird conservation into shrimp-farm practices. These low-cost and easy procedures would not increase production costs or affect shrimp production, representing a 'win-win' opportunity that could also improve the ecological credentials of the product and ecosystem services (Walton *et al.* 2015b). After taking into account local priorities (Rogers *et al.* 2015), these actions should be experimentally tested in other aquaculture ponds, especially those embedded in important wetland areas for the conservation of waterbird populations (e.g. Walton *et al.* 2015a). For example, in Bahía Santa María – a Mexican coastal wetland of 1350 km^2 holding more than 380 000 shorebirds (Engilis *et al.* 1998) – appropriate management of ca. 6500 ha of associated shrimp ponds (CESASIN 2013) has the potential to majorly increase the overall foraging areas for shorebirds. An additional management measure would be to extend the flooding of ponds after the harvesting period, mimicking an agroenvironmental recommendation implemented at rice fields for the conservation of waterbirds (Pernollet *et al.* 2015a) and thus potentially enlarging the temporal availability of the shrimp farms for foraging shorebirds. However, local implementation of flooding would need to be evaluated (Rogers *et al.* 2015) in terms of cost for the farmer (e.g. Pernollet *et al.* 2015b) and current sanitary laws.

Finally, our results may be particularly relevant in the East Asian Australasian Flyway, where the conversion of tidal flats to aquaculture ponds is widespread (Murray *et al.* 2014). The flyway has more threatened shorebird species than all other flyways combined (van de Kam *et al.* 2010), with survival declines of several species signalling an entire flyway at risk (Piersma *et al.* 2016). Here, ponds are harvested by drawing water to a channel where reared shrimp and fish are then netted (Yasué & Dearden 2009, Green *et al.* 2015). Water is drained and ponds are refilled immediately to start the production cycle again. Such a management system does not allow shorebirds to use aquaculture ponds as foraging grounds (e.g. Ma *et al.* 2004), but our results show the potential exists for them to do so if a change in shrimp-harvesting practices occurs.

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Data accessibility

Data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.q1sq0 (Navedo *et al.* 2016).

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