

Shorebirds can adopt foraging strategies that take advantage of human fishing practices

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Abstract. Human presence and activities are considered to be a potential threat to many species, mainly because they interfere with the abilities of many animals to exploit essential resources. In this study we investigate the influence of human presence and activities on the behaviour of nine shorebird species in an intertidal area at Baía de Todos os Santos, north-eastern Brazil. The area is used both by shorebirds and traditional human community to extract invertebrates for food, and also used by people for recreation. We analyse and compare the foraging behaviour of shorebirds under three different conditions: absence of humans, presence of humans manually gathering shellfish (shellfishing), and presence of humans engaged in recreational activity. Recreational activity was associated with greater behavioural change to the shorebirds than shellfishing. Shorebirds were less plentiful, showed lower foraging rates and moved around more when exposed to recreational activity. Larger shorebirds were less abundant when shellfishing or recreational activities were taking place. Intertidal areas of sediment manually overturned by shellfishers had higher rates of shorebird foraging and agonistic encounters, suggesting that shorebirds' foraging strategies take advantage of human shellfishing. These results can be interpreted within a conservation framework to provide guidelines for the management decisions in areas used by shorebirds.

Additional keywords: artisanal fishing, benthic, Charadriidae, coastal conservation, dependence, human–wildlife interactions, Scolopacidae, shellfish.

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Introduction

The presence of humans and human activities are considered a potential threat to many species, mainly because it interferes with the ability of many animals to exploit essential resources. This may occur through changes in environmental quality leading to reduced food availability as well as by limiting direct access to resources (e.g. flight or avoidance of the feeding area in the presence of humans) (Gill 2007; Blumstein and Fernández-Juricic 2010). From an evolutionary viewpoint, most animals detect humans *a priori* as predators, and their behavioural responses to human presence (disturbance) can be interpreted as anti-predatory strategies (Frid and Dill 2002). Even if disturbances caused by human presence are not immediately lethal, they may reduce the fitness of individuals by reducing the availability of food and promoting physiological stress, and may thus decrease the quality of reproduction or parental care or both (e.g. Gill *et al.* 2001; Gill 2007; Cresswell 2008; Weston *et al.* 2012).

The behavioural response of animals to human presence may be influenced by several factors such as: (1) the quality of the area that is currently being occupied; (2) availability, distance and

quality of other sites; (3) predation risk related to a specific human activity and (4) the physiological state of the animals (review in Weston *et al.* 2012). Thus, the behavioural response to human presence may vary temporally and among sites, depending on the predominant local conditions, and this must be taken into consideration when management and conservation guidelines are determined (Gill 2007; Glover *et al.* 2011; Weston *et al.* 2012).

Many charadrid and scolopacid shorebirds undertake long-distance migrations between breeding areas in the Arctic and non-breeding grounds in temperate and tropical zones (Morrison 1984; Morrison and Ross 1989). During the breeding period, individuals are typically homogeneously distributed whereas during migration and in the non-breeding period they congregate at restricted and specific sites. This poses a great challenge to the conservation of many of these species, because entire populations may become vulnerable when the quality of one of these restricted sites used during migration or the non-breeding period is threatened (Myers *et al.* 1987; Bildstein *et al.* 1991). Coastal regions with large intertidal areas are vitally important sites for many populations of shorebirds worldwide, either during stopovers on

migration or during the non-breeding period. These shorebirds remain in these environments for a considerable part of their lives, feeding on invertebrates in the sediments – an essential resource for their survival during these periods and for the continuity of their annual cycles (Evans 1976; Morrison 1984).

Many intertidal areas used by shorebirds during migration and in the non-breeding period are also used by humans (Bildstein *et al.* 1991). The presence of people in these areas may disturb foraging birds, decreasing the fitness of these individuals (Hill *et al.* 1997; Gill *et al.* 2001; Lafferty 2001). Many populations of migratory shorebirds are threatened globally (International Wader Study Group 2003) and are particularly vulnerable to human activities in coastal regions during the migratory and non-breeding periods (Myers *et al.* 1987; Bildstein *et al.* 1991). The extent of human interference of shorebirds and to their activities throughout their migratory routes require studies at the local level, at sites recognised as important for the migrating populations (Hill *et al.* 1997; Myers *et al.* 1987; Burton 2007). In this sense, it is necessary to investigate how the distribution and behaviour of birds within a specific area are affected by different human activities (Hill *et al.* 1997; Cornelius *et al.* 2001; Burton 2007; Gill 2007; Glover *et al.* 2011).

Humans use coastal regions known to be important to shorebirds for a range of purposes. Humans are the most common source of disturbance in many of these areas (e.g. Glover *et al.* 2011; Weston *et al.* 2012) and birds can respond differently to different types of human behaviour (i.e. stimuli). Two types of human activities that may affect shorebirds are activities associated with the exploitation of natural resources and the use of coastal areas for recreation. Human behaviour differs in these two types of activity and may cause different behavioural changes in shorebirds (e.g. Burger 1981; Smit and Visser 1993; Cornelius *et al.* 2001; Weston and Elgar 2007).

The manual collection of marine invertebrates for food (shellfishing) has been practiced by humans for more than 10 000 years, and is considered an important source of calories, proteins and minerals (Parkington 2003; Erlandson *et al.* 2008) and remains an important economic activity in many intertidal areas. However, the presence and number of people conducting this activity in intertidal areas may disturb foraging birds, reducing the quality of these habitats (e.g. Navedo and Masero 2007; Dias *et al.* 2008). In addition, the action of turning over the sediment during shellfishing may reduce invertebrate availability (e.g. Ferns *et al.* 2000; Masero *et al.* 2008) and thus the foraging efficiency of birds (e.g. Shepherd and Boates 1999). Thus, regulating invertebrate collection by people so that it is compatible with the conservation of migratory shorebirds is one of the challenges of managing coastal areas worldwide (Stillman *et al.* 2001; Goss-Custard *et al.* 2004; Navedo and Masero 2007; Dias *et al.* 2008).

The use of coastal areas by humans for activities associated with tourism has also dramatically threatened biodiversity in these areas (Gray 1997; Defeo *et al.* 2009). In north-eastern Brazil, coastal development, pollution and tourism represent more than 50% of the overall sources of pressure upon coastal biodiversity (review in Prates *et al.* 2007). The use of the Brazilian coast for tourism has increased in recent decades, encouraged by government policies and financial incentives, especially in the north-east (de Araujo and Bramwell 2002; Oliveira 2002, 2003).

The Baía de Todos os Santos, in north-eastern Brazil, is an important non-breeding stopover site for Nearctic charadriid and scolopacid shorebirds in South America (Antas 1983; Morrison and Ross 1989; Lunardi *et al.* 2012), and is also a breeding area for Wilson's Plover (*Charadrius wilsonia*) (Lunardi and Macedo 2010). Shellfishing occurs over large intertidal areas of the bay, as do recreational activities. The invertebrates collected are bivalve molluscs and crustaceans (crabs), which are gathered manually at low tide. This artisanal activity has been practiced for over 500 years by traditional coastal communities in this region of Brazil (Sousa 1851), and is currently regulated and subsidised by the Bahia state government (see <http://www.bahiapesca.ba.gov.br>, accessed 27 January 2009). However, it is not known whether human presence or activities in this intertidal area disturb birds in distinct ways.

In this study we investigated use of an intertidal area as a source of invertebrate food by shorebirds and a human community on the west coast of the Baía de Todos os Santos. This same area is also used for human recreation. We compared the behaviour of foraging birds under three conditions, using both a descriptive and an experimental approach: the absence of humans, the presence of humans collecting shellfish manually, and the presence of humans engaged in recreational activities. Specifically, our aims were to investigate if: (1) shorebirds respond similarly to both humans collecting shellfish and those engaged in recreational activities; (2) foraging efficiency is lower in the presence of humans, irrespective of the type of human activity (shellfishing or recreation), and (3) shorebirds prefer to forage in undisturbed sediments of the intertidal areas compared with sediment that has been recently overturned by shellfishers.

Materials and methods

Study area

This study was conducted on the western coast of the Baía de Todos os Santos, Bahia state, north-eastern Brazil (12°44'S, 38°44'W), in the municipality of Saubara. This is the second largest bay in Brazil, covering a maximum area of 1223 km² at equinoctial spring tide. Intertidal areas cover ~210 km² of the bay at low tide, and are mainly sandy-clay sediments, often associated with mangroves (Cirano and Lessa 2007). Since 1999, the Baía de Todos os Santos, including the water, coast and islands, has been designated an environmental protection area with the objective of preserving mangroves and associated fauna, especially migratory bird fauna (*Bahia State Decree 7595*, Brazil).

The study area comprised an intertidal flat of ~350 ha, partly delimited with wooden stakes and boundaries determined using GPS (Garmin Etrex 10, UTM SAD69, Garmin International, Olathe, KS, USA). This area is used by a traditional community for shellfishing and recreation (Fig. S1 in the Supplementary material). The main bivalve extracted by humans is *Anomalocardia brasiliana*, one of the most abundant and economically important species in the intertidal flats of the Baía de Todos os Santos (Soares *et al.* 2011). This bivalve is collected manually, by scraping at the surface layer of sediment (which is ~1–3 cm deep) with a flat, metal tool (length ~5–10 cm, width ~2–6 cm). The portions of overturned soil are irregularly shaped and vary widely in size (Fig. S1). Shellfish are usually collected by a single woman or small groups of women and children (2–3 people). Recrea-

tional activities on the intertidal area are mainly walking and soccer. Shellfishing occurs mainly on weekdays, whereas recreational activity takes place mainly on weekends and holidays. Three exclusive conditions of human activity were analysed: (1) no human presence or activity; (2) recreational activity, consisting of use of the intertidal area by people engaged in recreation, such as walking, and (3) shellfishing, in which individuals or small groups manually collect bivalve molluscs from the exposed intertidal sediments. There were no dogs or other domestic animals associated with the three conditions (dogs can cause large responses in shorebirds; e.g. Weston and Elgar 2005).

Overall sampling methodology

Field work was conducted on 161 days, between September 2007 and March 2008, during low tide (2 h either side of official low tide time; tidal predictions from Centro de Previsões de Tempo e Estudos do Clima, <http://www.cptec.inpe.br>, accessed 28 August 2007), and under similar environmental conditions (no rain, wind-speed between 1 and 3 on the Beaufort scale). We conducted the following observations and experiments: (1) survey of numbers of birds and humans (total days of surveys: $n = 31$ when no humans were present in the study area, $n = 70$ when humans were present and engaged exclusively in shellfishing and $n = 60$ when humans were present and engaged exclusively in recreational activity); (2) followed by a 2-min focal sample of human movement (total humans sampled: $n = 100$ (within the 70 days when exclusive shellfishing occurred), and $n = 100$ (within the 60 days of exclusive recreational conditions)); (3) followed by a 2-min focal sample of foraging shorebirds (total individuals sampled: $n = 103$ Semipalmated Plovers and $n = 122$ Semipalmated Sandpipers, with 3–6 focal samplings in each study day) and (4) followed by a flight-response experiment (total experiments: $n = 31$, with one on each day in the absence of humans, $n = 53$ with one on each day of recreation, and $n = 70$, with one on each day of shellfishing). In 68 days of shellfishing, we also conducted observations of paired (undisturbed *v.* recently overturned) intertidal sediments to compare the intensity of foraging activity (peck marks, footprints and faeces) by shorebirds. In addition to the 161 days described above, we conducted observations of shorebirds in the intertidal flat to compare the numbers of visits and agonistic encounters among shorebirds in overturned and undisturbed flats, in 20 different days of shellfishing.

The data were collected in different days when exclusive conditions were present: absence of humans, presence of humans in recreation or presence of humans in shellfishing. Data collected on days when more than one of these conditions occurred were not used in analyses.

Surveys of birds and humans

On each sampling day ($n = 161$), we conducted three surveys of ~20 min during the low tide, counting all birds and humans within the study area. We observed and recorded the birds and humans from fixed, inconspicuous points inside the mangrove forest, from where it was possible to observe the intertidal study area using one pair of 10 × 50-mm binoculars (Bushnell PowerView, Philippines) and a 20–60 × 65-mm spotting scope with tripod (Bushnell NatureView Spotting Scope, China). We classified the data obtained on each sampling day, for both birds and humans,

in the three exclusive human activity conditions analysed in this study. The data from the three surveys on each sampling day were combined and values averaged.

Index of human movement

As an index for the extent of human movement, we undertook 2-min focal sampling ($n = 200$) of individual people in the study area at low tide over the course of the study. The focal samplings were conducted after the surveys, only in days when humans were detected in the intertidal area. We recorded the number of steps taken by a person, who was chosen randomly, within the 2-min period to approximate travel distance for comparison of the intensity of human movement in two conditions of human activity, recreation and shellfishing.

Flight-initiation distance and flight length in response to different human activities

To measure the behavioural responses of foraging shorebirds to human approach within each of the three conditions of human activity, we conducted a standardised experiment in which mixed flocks of Semipalmated Plover (*Charadrius semipalmatus*) and Semipalmated Sandpiper (*Calidris pusilla*) were approached while they were foraging along the water's edge at low tide. Mixed flocks containing only these two species were chosen because they represent a type of assemblage often observed during the three conditions of human activity conditions investigated. We defined a flock as an assemblage of individuals foraging close to one another (all nearest neighbours within 20 m). To standardise sampling, we selected only flocks of 10–20 individuals for the experiment. Experimental procedures consisted of a single observer (V. O. Lunardi, wearing the same type and colour of clothing) approaching the birds at a steady pace ($0.5\text{--}1\text{ steps s}^{-1}$) perpendicular to the best approximation of the long axis of the flock (Blumstein *et al.* 2003). The starting distance, the distance at which an approach begins, is usually positively related to flight distance (Weston *et al.* 2012), so we standardised the starting distance at 230–250 m, with the observer starting the approach from the interior of the mangrove forest. We recorded two variables: (1) flight-initiation distance, defined as the approach distance that caused displacement, running or flight of at least 90% of the individuals present, and (2) flight-length, the distance travelled by the flock as a result of the response, from the initial point to the first point where at least 90% of the flock landed (see Beale and Monaghan 2004; Yasué 2006). The experimental approach ended as soon as the observer caused displacement. This experiment was conducted only once on each sampling day (except for 7 of 60 recreation days, when we had technical problems, $n = 53$). We measured flight length and flight-initiation distances directly, using string, wooden stakes and a tape measure. On days when there were no people in the intertidal areas, the experiment was conducted after the bird surveys.

Foraging rates in response to human activities

We conducted 2-min focal sampling of individuals among mixed flocks of foraging Semipalmated Plovers and Semipalmated Sandpipers under the three human activity conditions. The focal sampling during shellfishing activities classified

foraging either as: (1) in substrate overturned by shellfishers, or (2) in undisturbed substrate. For Semipalmated Plovers we measured the number of pecks in the sediment and the number of prey ingested. For Semipalmated Sandpipers we recorded only the number of pecks in the sediment, as it was impossible to observe the exact number of prey ingested by individuals of this species. These records were expressed as rates per 2 min: NPecks (number of pecks in 2 min) and NPrey (number of prey ingested in 2 min).

Use of undisturbed v. recently overturned intertidal sediments

We estimated the intensity of foraging activity by shorebirds in areas where sediments had been overturned by shellfishers v. intact sediments (e.g. Ferns *et al.* 2000; Pomeroy *et al.* 2006; Robar and Hamilton 2007). Data were collected on survey days when shellfishing had taken place ($n=68$ days), ~1 h after official low tide, after shellfish gatherers had already overturned portions of sediment and the birds had subsequently foraged in those areas. On each field day when shellfishing was observed, one intertidal area overturned by shellfishers was selected at random. We delimited a rectangular plot divided into subplots of 50×50 cm in parts of the intertidal area overturned by shellfishers. The sizes of the plots were different because the areas disturbed by shellfishers were variable and each control plot was designed to match each area overturned by shellfishers. As a control, we demarcated an adjacent plot of the same area, also divided into 50×50 -cm subplots, covering undisturbed sediment. Each control (undisturbed) plot was on the north side of the overturned plot, had the same area as the disturbed adjacent plot and shared a common edge. Each area was marked out using wooden stakes, string and tape measure and location recorded with GPS and a compass was used to mark out the plots (Brunton 70M Professional Mirrored Compass, Riverton, WY, USA). The density (number m^{-2}) of peck marks, footprints and faeces in each plot was recorded (see Ferns *et al.* 2000; Pomeroy *et al.* 2006; Robar and Hamilton 2007; Fig. S1). Overlapping peck marks and footprints were considered as single records of each type. Each pair of sediment plots was analysed only once in the study ($n=68$ from 70 days of shellfishing, with no paired plots analysed on the 2 days when we had technical problems).

As a second estimate of foraging intensity, we conducted behavioural observations in another 20 areas recently overturned by shellfishers. In each of these areas, we delimited a 5×5 -m plot ($25 m^2$) using wooden stakes, string, tape measure and compass, in which we conducted 10-min observations of foraging birds. In each observation period, we recorded the number of birds and species that entered the plot (number of visits) and the number of agonistic encounters among birds (one individual chased another) within the plot. A control plot of the same size was delimited in undisturbed sediment ~10 m from each plot of overturned sediment, and observations conducted using the same methods as the plot of overturned sediment. The observations of the two plots were always done on the same day, with observations of the plot recently overturned by shellfishers always made first, followed by observations of the plot of undisturbed sediment. Each plot was analysed once. These

observations were conducted within ~40 min after official low tide, after shellfishers had already overturned portions of sediment. These behavioural observations were also undertaken on different days to all the other fieldwork.

The areas were regarded as spatially independent, as they were separated from one another by at least 120 m. Furthermore, our observations suggest that individual shorebirds rarely moved between them during an observation period. We also saw no consistent distributional pattern of sites overturned by shellfishers, and each the plots in a pair of overturned and undisturbed plots was within 10 m of the other. Thus, it is unlikely that our comparisons of the paired plots would have been affected by broadscale variation of invertebrate density within the intertidal study area.

Statistical analyses

The counts of birds and people and index of movements of people (steps per 2 min) obtained under the three human activity conditions were compared using Kruskal–Wallis one-way analysis of variance (ANOVA) for ranks test (Zar 1999), with a Monte-Carlo exact test as a correction for random data (confidence level = 99%, number of resamples = 10 000; see Adams and Anthony 1996), and Tamhane's T2 (Tamhane 1979) for *post hoc* multiple comparisons (based on 5000 bootstrap samples). We used the same statistical procedure to compare the flight-initiation distances and the foraging rates of Semipalmated Plovers and Semipalmated Sandpipers (including in overturned and undisturbed sediments when shellfishing had taken place) under the three different human activity conditions. Flight length was analysed using one-way ANOVA (Zar 1999) and Gabriel's method of multiple comparisons of means (Gabriel 1978) based on 5000 bootstrap samples.

We used parametric *t*-tests (Zar 1999) to compare foraging activity (density of peck marks, footprints and faeces combined in sampling plots), and the frequency of agonistic encounters and number of visits in sampling plots with undisturbed and overturned sediments. This statistical procedure was also used to test the difference between the number of people that used the intertidal area on days of recreational activity and days when shellfishing occurred, and to test if people engaged in recreation moved more than did the shellfishers (steps per 2 min). Mann–Whitney *U*-tests (Zar 1999), with Monte-Carlo exact test as a correction for random data (confidence level = 99%, number of resamples = 10 000) was used when the assumptions of the parametric tests were not met. Numbers of people and their intensity of movement, the frequency of agonistic encounters, the density of peck marks, footprints and faeces, and the number of visits were \log_n transformed before analysis. Mean values of raw data are presented with standard deviations unless otherwise indicated. A significance level of $\alpha < 0.01$ (bilateral test) was used for all statistical analyses. The *P*-values presented in Kruskal–Wallis and Mann–Whitney *U*-test results were obtained from Monte-Carlo exact tests.

Results

Human activity and number of foraging shorebirds

The mean number of people that used the intertidal area on days of recreational activity (7.17 ± 5.76 people, $n=60$ days) was not

significantly different from that recorded on shellfishing days (5.5 ± 4.28 , $n = 70$; $t = 1.72$, $P = 0.088$), although the difference was close to significant. In contrast, people engaged in recreation moved significantly more than shellfishers (recreational activity = 27.3 ± 25.5 steps per 2 min, shellfishing = 7.9 ± 12.7 steps per 2 min, $n = 100$ for both, $t = -6.5$, $P < 0.001$). The birds recorded in the surveys were four species of Charadriidae, the Grey Plover (*Pluvialis squatarola*), Semipalmated Plover, Collared Plover (*Charadrius collaris*) and Wilson's Plover, and five species of Scolopacidae, the Whimbrel (*Numenius phaeopus*), Willet (*Tringa semipalmata*), Ruddy Turnstone (*Arenaria interpres*), Sanderling (*Calidris alba*) and Semipalmated Sandpiper.

Compared with abundance in the absence of people, the presence of shellfishers or people engaged in recreation did not significantly affect the abundance of foraging Semipalmated Plover on the intertidal area (Kruskal–Wallis test: $H = 5.73$, d.f. = 2, $P = 0.057$). The abundance of Collared Plover ($H = 37.69$, d.f. = 2, $P < 0.001$), Wilson's Plover ($H = 33.50$, d.f. = 2, $P < 0.001$), Sanderling ($H = 49.76$, d.f. = 2, $P < 0.001$), Semipalmated Sandpiper ($H = 108.82$, d.f. = 2, $P < 0.001$), Ruddy Turnstone ($H = 14.03$, d.f. = 2, $P = 0.001$) and Grey Plover ($H = 42.51$, d.f. = 2, $P < 0.001$) was significantly negatively affected by the presence of people engaged in recreational activity but not by people engaged in shellfishing (compared with absence of people; Fig. 1). However, two species were negatively affected by both human activities compared with the absence of people: Whimbrel ($H = 46.97$, d.f. = 2, $P < 0.001$) and Willet ($H = 33.12$, d.f. = 2, $P < 0.001$) (Fig. 1).

Flight-initiation distance and flight length in response to different human activities

Mixed flocks of Semipalmated Plover and Semipalmated Sandpiper responded differently to the standardised disturbance experiment under the three conditions of human activity (no people, recreational activity and shellfishing). Flight-initiation distance was significantly lower in response to shellfishing activity than absence of people or recreation ($H = 23.08$, $P < 0.001$). However, flight length was greater in response to recreational activity than under absence of people or shellfishing activity ($F_{2,151} = 36.19$, $P < 0.001$) (Fig. 2).

Foraging rates in response to different human activities

Foraging rate of Semipalmated Sandpipers was different among the analysed conditions (absence of humans, humans engaged in recreation and shellfishing (in overturned and undisturbed sediments); $H = 199$, d.f. = 3, $P < 0.001$). Sandpipers foraging rate during shellfishing activity was lower in undisturbed sediment when compared with foraging that occurred in the absence

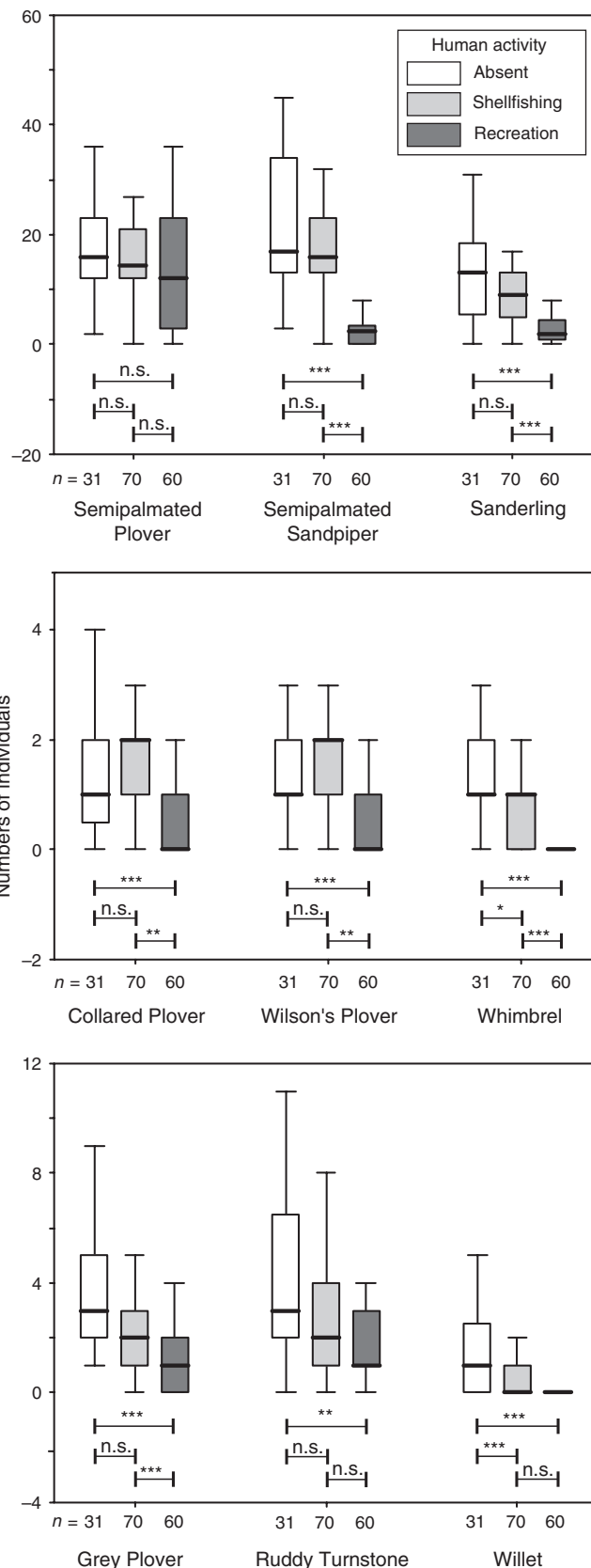


Fig. 1. Numbers of individuals of nine shorebird species foraging in intertidal area of the Baía de Todos os Santos in three conditions: absence of humans, presence of humans engaged in shellfishing, and presence of humans engaged in recreational activity. Asterisks indicate significance level in comparisons between types of activity and absence of such (Tamhane's T_2 *post hoc* comparisons, based on 5000 bootstrap samples; see Methods): ***, $P < 0.001$; **, $0.001 \leq P < 0.009$; *, $P = 0.037$; n.s., $P \geq 0.05$. Boxplots show median, inter-quartile ranges, and minimum and maximum values; n is number of days of observation of that human activity condition.

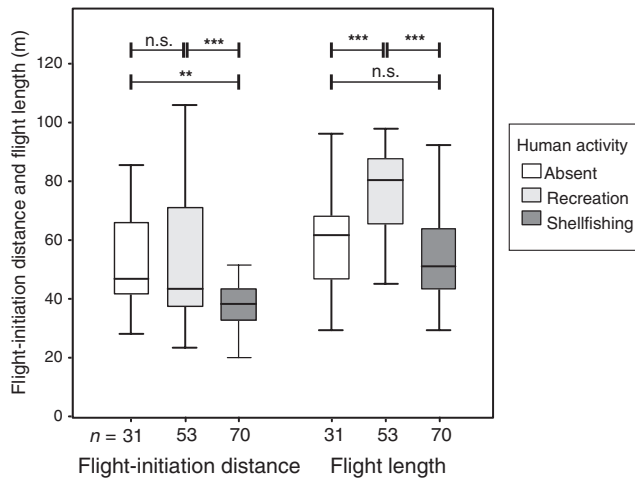


Fig. 2. Flight-initiation distance and flight length after human approach of mixed flocks of Semipalmated Plovers and Semipalmated Sandpipers foraging in the intertidal area of the Baía de Todos os Santos, in the absence of humans, presence of humans engaged in shellfishing and presence of humans engaged in recreational activity. Asterisks indicate levels of significance in the comparisons between types of activity and absence of such (Tamhane's T_2 *post hoc* comparisons, based on 5000 bootstrap samples): ***, $P < 0.001$; **, $P = 0.001$; n.s., $P \geq 0.05$. Boxplots show median, inter-quartile ranges, and minimum and maximum values; n is number of days of observation of that human activity condition.

of humans. However, foraging rate was higher when the sandpipers foraged in sediment overturned by shellfishers when compared with the total absence of humans (Fig. 3). In Semipalmated Plovers, rates of foraging (NPecks: $H = 168.37$, d.f. = 3, $P < 0.001$) and ingestion (NPrey: $H = 173.63$, d.f. = 3, $P < 0.001$) were both lower under the recreational condition and higher under the shellfishing condition in sediment overturned by shellfishers. In comparison, in undisturbed sediment, the foraging and ingestion rates were statistically similar to those obtained in the absence of people (Fig. 3).

Use of intertidal areas: undisturbed v. overturned sediments

The plots containing sediment recently overturned by shellfishers showed higher densities of peck marks, footprints and a higher number of faeces than adjacent undisturbed sediment plots (Table 1). Semipalmated Plovers, Wilson Plovers, Ruddy Turnstones, Semipalmated Sandpipers and Sanderlings made more visits to plots with recently overturned sediment than to plots in undisturbed sediment (Table 2). However, there was no significant difference in use of overturned and undisturbed plots by Collared Plovers (Mann–Whitney test: $U = 174$, $P = 0.316$). The mean number of agonistic encounters between birds was higher in plots with overturned sediment (6.95 ± 4.02 , $n = 20$ observation periods) than in those with undisturbed sediment (1.75 ± 1.20 , $n = 20$; $t = -6.12$, d.f. = 39, $P < 0.001$).

Discussion

In this study we investigated the behavioural responses of shorebirds to human recreational and shellfishing activities in an

intertidal area of the Baía de Todos os Santos, Brazil, and also assessed the variation in behaviour between the absence and presence of people. The presence–absence comparison is one of the most widely suggested and most widely used parameters for studying the influence of human activities on biodiversity (e.g. Burton *et al.* 2002; Burton 2007; Navedo and Masero 2008; see review in Gill 2007). The different patterns of use of the intertidal area by shellfishers and people engaged in recreation resulted in different behavioural responses by shorebirds.

It is assumed that behavioural responses of animals to human presence and activities may be species-specific (Blumstein *et al.* 2003) and can vary with the intensity of the human stimulus (Weston *et al.* 2012). We found that recreational activity had a negative influence on the abundance of eight of the nine species of shorebird recorded in the intertidal area, whereas shellfishing had a negative influence on only two of the nine species. Because the number of people observed gathering shellfish was not significantly different to that engaged in recreational activity on days of those activities, we suggest that some species of shorebirds assess risk and make judgements based on the different human behaviours. That shellfishers move less than people engaged in recreation, the different speeds at which people move in these two activities may explain this result. Burger (1998) reported that more Common Terns (*Sterna hirundo*) left their nests when watercraft approached a breeding colony at high speeds compared with watercraft approaching at lower speeds. Indeed, the intense movement of people may represent a greater threat to animals than individuals moving at slower speeds (Burger 1981). However, this does not apply to all species (review in Ydenberg and Dill 1986; Frid and Dill 2002). For example, different speeds of travel by humans (e.g. walker, joggers) caused different behavioural responses in some species of shorebirds but not in others (Glover *et al.* 2011). Running caused less disturbance to Snowy Plovers (*Charadrius nivosus*) than walking (Lafferty 2001), and static humans are likely to cause more incubation disturbances than mobile humans in Hooded Plovers (*Thinornis rubricollis*) (Weston *et al.* 2011).

The two largest shorebirds in the Baía de Todos os Santos (range in body mass: Willet 199–264 g (Lowther *et al.* 2001); Hudsonian Whimbrel 310–450 g (Skeel and Mallory 1996)) were less abundant under both shellfishing and recreational activities. Other studies also show that large shorebirds tend to be more sensitive to human presence than small species (de Boer and Longamane 1996; Burton *et al.* 2002; Dias *et al.* 2008) and flight-initiation distance in birds is directly related to body mass (e.g. Blumstein 2006; Weston *et al.* 2012). The possible explanations are related to differences between species in varying combinations of energetic costs of fleeing, conspicuousness, evolutionary history with humans and visual abilities (review in Glover *et al.* 2011). Relative brain size is thought not to influence flight distance (Guay *et al.* 2013).

We expected foraging efficiency to be lower in the presence of humans, irrespective of the type of activity (shellfishing or recreation). Shorebirds detect humans primarily as predators (Frid and Dill 2002), and the investment in anti-predator behavioural responses in the presence of humans may reduce foraging rates in animals (Gill *et al.* 2001; Frid and Dill 2002; Cresswell 2008). The foraging rates of Semipalmated Plover and Semipalmated Sandpiper, as well as the ingestion rates of Semipalmated

Plover in overturned sediment by shellfishers, were higher than during recreational activity and also higher in overturned sediment than in undisturbed sediment. These results suggest that shellfisher activity *a priori* does not reduce the short-term foraging success of these two species during their non-reproductive period in the Baía de Todos os Santos (see also Pierce *et al.* 1993) and likely does not alter survival or accumulation of energy required for the next migratory period. However, we do not know if a small increase in shellfishing activity can exclude shorebirds from this area for long periods. It is also not known whether traditional shellfishing activity can promote prey reduction in the long-term.

We examined whether shorebirds would prefer to forage in intertidal areas with recently overturned sediment (by shellfishers) rather than in undisturbed sediment. Previous studies suggest that shorebirds are vulnerable to foraging reductions when the first few centimetres of intertidal sediment are overturned (Shepherd and Boates 1999; Ferns *et al.* 2000; Kaiser *et al.* 2001; Griffiths *et al.* 2006; Masero *et al.* 2008). Charadriid and scolopacid shorebirds search for prey using visual and tactile cues, selecting foraging sites based mainly on the type and permeability of the sediment and the availability of their main prey (Myers *et al.* 1980; Pienkowski 1983; Hicklin and Smith 1984; Kalejta and Hockey 1994). When the first centimetres of intertidal sediment are overturned, visual and tactile cues used by shorebirds to detect prey can be modified (Wynberg and Branch 1994; Shepherd and Boates 1999; Griffiths *et al.* 2006). In this study we found that shorebirds preferred to use sediments that had been overturned by shellfishers compared with intact sediments. Higher foraging rates were also recorded for Semipalmated Plover and Semipalmated Sandpiper in areas with overturned sediment. These results suggest that shorebirds adopt foraging strategies that may be dependent on human fishing practices in the Baía de Todos os Santos, with some shorebird species profiting opportunistically by using the sediment as soon as it is overturned by shellfishers.

Whether there are positive or negative effects of shellfishing upon shorebird foraging may depend on the behaviour of the main type of prey consumed (e.g. the intrinsic prey mobility and speed) and the birds' foraging strategies and diet (review in Navedo and Masero 2008). For example, the intertidal flat disturbance by manual shellfishing did not affect the foraging success of Eurasian Curlews (*Numenius arquata*) in a wintering area in northern Spain, possibly because their main prey (the crab *Carcinus maenas*) may have been more active after sediments were overturned, making it more visible and thus more suscep-

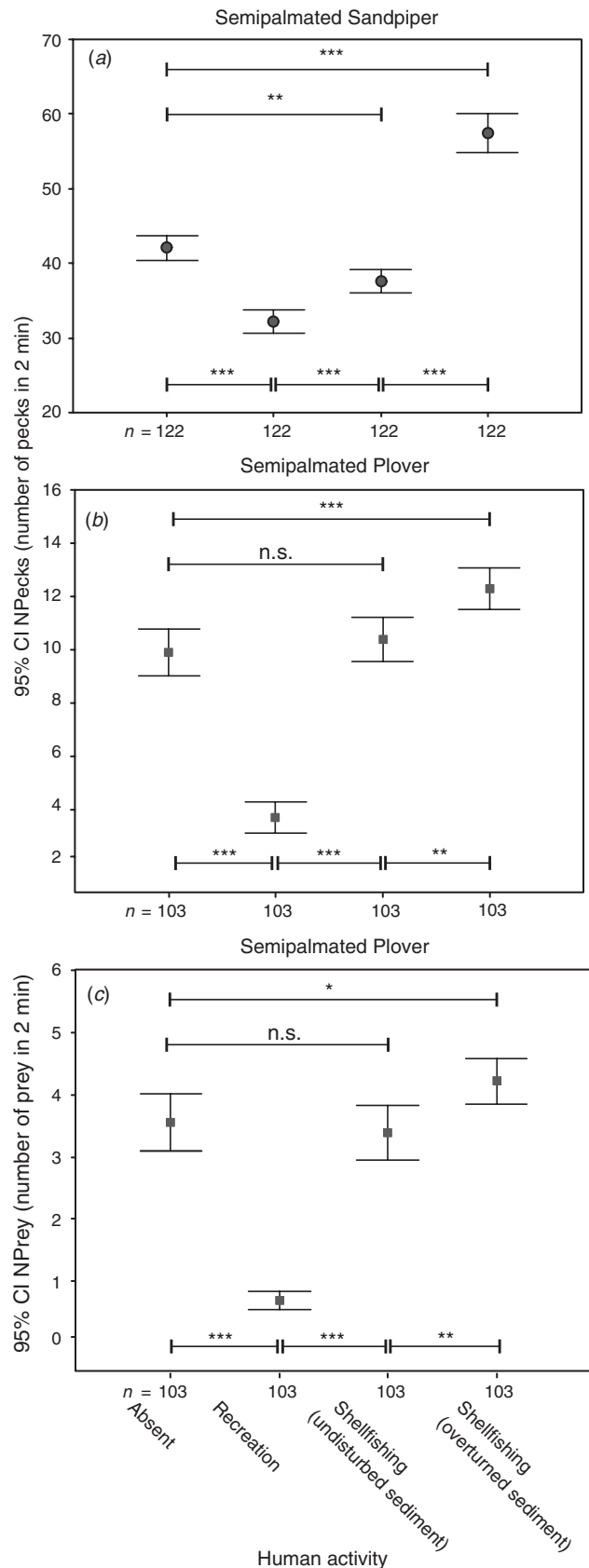


Fig. 3. Foraging rates of Semipalmated Sandpipers and Semipalmated Plovers in the intertidal area of the Baía de Todos os Santos, in the absence of humans, presence of humans engaged in recreational activity, and presence of humans manually shellfishing; the latter condition was sampled separately for substrate overturned by shellfishers and undisturbed substrate. (a) Number of pecks by Semipalmated Sandpipers; (b) number of pecks by Semipalmated Plovers and (c) number of prey caught by Semipalmated Plovers. Plots show means and 95% confidence intervals. Asterisks indicate levels of significance in the comparisons between types of activity and absence of such (Tamhane's T_2 *post hoc* comparisons, based on 5000 bootstrap samples): ***, $P < 0.001$; **, $0.001 \leq P \leq 0.006$; *, $P = 0.042$; n.s., $P \geq 0.05$; n is focal samplings.

Table 1. Comparison of the density (number m⁻²) of peck marks, footprints and faeces in intertidal sediments of plots either undisturbed (*n* = 68) or overturned by shellfishers (*n* = 68)Independent samples test either *t*-test (two-tailed), or Mann–Whitney *U*-test (two-tailed); see Methods

	Mean density (number m ⁻²) ± s.e. (95% confidence intervals)		Independent samples test (<i>P</i>)
	Undisturbed	Overturned	
Peck marks	13.3 ± 1.9 (9.89–17.7)	27.8 ± 3.8 (21.4–35.6)	<i>t</i> = 5.16 (<i>P</i> = 0.001)
Footprints	25.6 ± 3.0 (20.2–32.5)	54.1 ± 6.6 (42.2–67.3)	<i>t</i> = 4.58 (<i>P</i> = 0.001)
Faeces	0.15 ± 0.05 (0.07–0.3)	0.28 ± 0.05 (0.2–0.4)	<i>U</i> = 1067.5 (<i>P</i> = 0.001)

Table 2. Comparison of the number of shorebirds occurring in plots either undisturbed (*n* = 20) or overturned by shellfishers (*n* = 20)

Species	Mean ± s.e. (95% confidence interval)		<i>t</i> (<i>P</i>)
	Undisturbed	Overturned	
Semipalmated Plover	11.1 ± 2.0 (7.3–15.3)	42.9 ± 3.4 (36.3–49.4)	–8.18 (<i>P</i> < 0.001)
Ruddy Turnstone	2.4 ± 0.6 (1.3–3.5)	6.6 ± 1.0 (4.6–8.7)	–4.19 (<i>P</i> < 0.001)
Semipalmated Sandpiper	12.2 ± 1.5 (9.2–14.9)	29.8 ± 4.7 (21.1–38.9)	–3.04 (<i>P</i> < 0.004)
Sanderling	1.0 ± 0.2 (0.6–1.4)	2.8 ± 0.5 (2.0–3.8)	–3.66 (<i>P</i> < 0.005)
Wilson's Plover	1.7 ± 0.2 (1.3–2.1)	2.2 ± 0.2 (1.8–2.6)	–1.50 (<i>P</i> < 0.001)

tible to capture by Curlews (Navedo and Masero 2008). Other species of intertidal invertebrates may also be more active after disturbance of sediments in intertidal areas, making them more vulnerable to predation (Zwarts and Esselink 1989; Brosnan and Crumrine 1994; Rippe and Dierschke 1997; Ambrose *et al.* 1998; Zharikov and Skilleter 2004). Although we did not examine the effect of shellfishing on the invertebrate intertidal community in the present study, we suggest that the artisanal shellfishing in the Baía de Todos os Santos provides a temporary increase in visible prey, soon after shellfishers overturn the intertidal sediments. In fact, shorebirds foraging visually occupied sites recently overturned by shellfishers in almost all field observations, even during shellfishing activity, often remaining only a few metres from shellfishers (V. O. Lunardi, pers. obs.). Small-scale prey-patch characteristics were found to be crucial in the choice of foraging habitat by avian marine predators (Benoit-Bird *et al.* 2013). In this sense, shorebirds in the Baía de Todos os Santos may quickly learn that temporarily available small-scale patches of sediment overturned by shellfishers represent increased availability of prey.

We found that mixed flocks of Semipalmated Plover and Semipalmated Sandpiper were more reluctant to move after a standard approach stimulus in the presence of shellfishers. Additionally, the distance travelled by the flocks after the stimulus was greater in the presence of recreational activity. These results provide yet additional evidence that shorebirds respond differently to shellfishing and recreational activity (Pierce *et al.* 1993; de Boer and Longamane 1996; Cornelius *et al.* 2001). Furthermore, these results allow us to infer that these shorebirds tolerate closer proximity of people during shellfishing because they perceive that this activity represents, at least temporarily, a foraging opportunity in the overturned sediment. Another non-exclusive explanation would be that short-term learning has occurred in response to the different stimulus represented by the slow moving shellfishers compared with the faster moving people involved in recreational activity (see also Weston *et al.* 2011, 2012).

Management implications

This study has shown that recreational activity can compromise the abundance and foraging success of shorebirds, at least in the short-term. These indicators must be considered in management and conservation proposals for the intertidal areas of this Brazilian bay. During the summer in the Baía de Todos os Santos, many intertidal areas receive an elevated number of tourists and shellfishers tend to avoid the areas with high densities of people as these hinder their work of turning over the sediment (V. O. Lunardi, pers. obs.). Thus, the limitation of intertidal areas for recreational activities can benefit both shellfishers and shorebirds. In comparison, behavioural responses of small shorebirds to traditional fishing practices presented here suggests that shorebirds adopt foraging strategies that utilise human artisanal fishing practices. Nonetheless, the influence of shellfishing should be considered with caution in management decisions of the Baía de Todos os Santos. Further studies of avian energy acquisition during foraging in sediment undisturbed and overturned by shellfishers in different sites and species are needed, as are studies of the effect of shellfishing on the intertidal invertebrate community. Investigations are also needed concerning the maximum density of shellfishers in the intertidal area that shorebirds can tolerate, without experiencing foraging disturbances (Zharikov and Skilleter 2004; Navedo and Masero 2007; Dias *et al.* 2008). An increase in the number of shellfishers in the intertidal area of the Baía de Todos os Santos may compromise the efficient feeding and survival of a large number of shorebirds (mainly the larger species) that inhabit this bay, and its invertebrate intertidal community. Thus, we suggest the creation of temporary foraging and resting zones for shorebirds, with the implementation of education, high levels of voluntary compliance, sustainable limits to public access (Gill 2007) and limited traditional gathering of invertebrates. This may be an important measure for reconciling shorebird conservation and the subsistence of the traditional community on the coast of this tropical bay.

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