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Emma Vanderzon, Ryan Baring & Diane Colombelli-Négrel

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Both human activities and environmental conditions influence foraging oystercatchers on urban beaches

Emma Vanderzon, Ryan Baring and Diane Colombelli-Négrel 

College of Science and Engineering, Flinders University, Adelaide, Australia

ABSTRACT

In developed coastal areas, shorebirds utilising sandy beaches as their primary habitat are often disturbed by human activities. Shorebird responses to human activities can have fitness consequences, through changes in their behaviour. In this study, we investigated whether human activities (number of people, presence of dogs) and environmental factors (air temperatures, wind speeds) influenced the abundance and the percentage of foraging birds for two urban shorebird species; *Haematopus longirostris* (Pied Oystercatcher) and *Haematopus fuliginosus* (Sooty Oystercatcher). We found that the number of oystercatchers (abundance) was lower when many people and dogs were present. However, a higher percentage of oystercatchers were observed foraging when people were present in high numbers and when dogs were present, a pattern that seems to be driven by Sooty Oystercatchers rather than Pied Oystercatchers. We also found that oystercatcher abundance and the percentage of foraging birds showed a negative relationship with air temperature and a positive relationship with wind speed. We discuss these results in the context of our study sites and the implications they may have for oystercatcher foraging habits, reinforcing the idea that multiple factors need to be investigated when assessing the potential impacts of human activities on shorebirds.

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Introduction

Shorebirds play an important role in ecosystems as key predators, consuming prey across multiple trophic levels and heavily contributing to mass and energy fluxes across food webs (Burger 1991; Moreira 1997; Dugan *et al.* 2003; Schlacher *et al.* 2007; Ramli and Norazlimi 2017). Shorebirds have been proposed as indicators of environmental health and biodiversity, making them model organisms for understanding ecological processes between land and sea (Defeo *et al.* 2009; Gregory and van Strien 2010; Schlacher *et al.* 2014; Bakker *et al.* 2021). Sandy beaches provide critical nesting and foraging habitat for shorebirds, particularly along coastlines with dissipative type beach systems (i.e. wide, flat beaches characterised by fine sediment and extensive surf zones). These beaches are generally abundant in food sources, such as molluscs, crustaceans, and annelids (Hubbard and Dugan 2003; Defeo and McLachlan 2005; Jones *et al.* 2007; Defeo *et al.* 2009) and are important migration stopover and overwintering sites for migratory shorebirds (Lunardi and Macedo 2014). Yet many beaches in Australia are heavily used for human activities, particularly recreational use (Defeo *et al.* 2009; Petch *et al.* 2018; Schneider *et al.*

2020; van der Kolk *et al.* 2022), which are expected to cause disturbance to shorebird behaviour (i.e. disrupt an animal's behaviour or physiological functioning; Nisbet 2000; Ellenberg *et al.* 2006; Schlacher *et al.* 2013). Thus, it is important to understand how human activities may alter the regular behaviours and survival of shorebirds, particularly in urban environments where risks from human interaction are greater (Burger 1991; Burger *et al.* 2010; Fitzpatrick and Bouchez 2010; Schlacher *et al.* 2013; Lunardi and Macedo 2014; Ramli and Norazlimi 2017).

Human activities on beaches have been found to adversely affect shorebird behaviours that are crucial for their survival and reproduction, such as foraging, breeding, roosting and migration (Verhulst *et al.* 2001; Coleman *et al.* 2003; Rodgers and Schwikert 2003; Baudains and Lloyd 2007; Burger *et al.* 2010). Behavioural modifications can include increased time spent in vigilance, flushing in response to people/dogs/cars approaching (Guinness *et al.* 2019; Timmis *et al.* 2022), delayed arrival and earlier departure from foraging and roosting sites, shifts in preferred foraging sites (Thomas *et al.* 2003; Fitzpatrick and Bouchez 2010; Schlacher *et al.* 2013; Ramli and Norazlimi 2017), higher

than normal energy expenditure and reduced time spent on foraging (Burger 1981; Verhulst *et al.* 2001; Stillman and Goss-Custard 2002; Coleman *et al.* 2003; Thomas *et al.* 2003; Defeo *et al.* 2009). Such disruption in foraging can reduce the ability of shorebirds to conserve energy for migration and breeding (Spencer 2010) and, hence, have long-term consequences for individual fitness and overall population trends (Hockin *et al.* 1992; Pfister *et al.* 1992; Schummer and Eddleman 2003).

Regardless of humans and their activities, shorebirds foraging on sandy beaches may also be influenced by environmental factors, such as air temperature and wind speed. For example, Western Sandpipers (*Calidris mauri*) alter their foraging behaviour at low air temperatures by increasing the frequency of their probing behaviour (i.e. burrowing of the bill into the sand). This is because ambient temperatures affected the burying depth of their invertebrate prey (Nebel and Thompson 2005), causing the sandpipers to probe deeper or more often to find prey, often leading to higher energy expenditure. Unfavourable weather conditions can also increase the energy costs linked with thermoregulation in shorebirds, especially during periods of low air temperatures and high wind speeds (Davidson 1981; Stillman and Goss-Custard 2002; Collop *et al.* 2016; González-Medina *et al.* 2020; Ryeland *et al.* 2021). Thus, environmental conditions that act as stressors may affect the tolerance of shorebirds towards human activities as they often need to increase their time foraging (and thus decrease their time spent in vigilance) when energetic requirements are high (Davidson 1981; Ydenberg and Dill 1986; Fernandez-Juricic *et al.* 2002).

South Australia is home to two species of oystercatchers currently under threat: the Pied Oystercatcher (*Haematopus longirostris*) and the Sooty Oystercatcher (*Haematopus fuliginosus*). Australian Oystercatchers are a conspicuous group of shorebirds predominantly seen along the western and south-eastern coastline of mainland Australia and in Tasmania (Lauro and Nol 1995; Taylor *et al.* 2014; Jones 2016; Wooding 2019). Both species have similar foraging habits and bill size, predominantly foraging on hard-shelled prey along estuaries, sandy beaches and rocky coastal areas (Lauro and Nol 1995; Jones 2016). Compared to the Eurasian Oystercatcher (*Haematopus ostralegus*), both Australian species have been under-represented in previous studies and many aspects of their ecology and factors impacting their survival are poorly understood (Taylor *et al.* 2014; Wooding 2019). The IUCN conservation status for both species is listed as 'least concern' at the national level in mainland Australia (Hansen *et al.* 2014; Taylor *et al.* 2014). However, the Pied

Oystercatcher is listed as 'endangered' in the state of New South Wales (Office of Environment & Heritage 2021) and both Australian oystercatcher species are listed as rare species in South Australia (South Australia National Parks and Wildlife, NPW Act 1972). Current threats to Australian Oystercatchers include disturbance from human recreational activities, coastal development, habitat loss, introduced and overabundant native predators, competition for their food sources via recreational and commercial fishing and global climate change (Taylor *et al.* 2014; Jones 2016). Therefore, understanding how human activities impact important foraging behaviours and, thus, fitness of these two declining species is critical for their management.

Here, we recorded the total numbers seen (abundance) and number of birds foraging of Pied and Sooty Oystercatchers along ten urban beaches (i.e. within 200 m of human habitations) in the southern-eastern Fleurieu Peninsula of South Australia. We also recorded key environmental conditions (e.g. air temperatures, wind speeds) and human activities (e.g. number of people, presence of dogs) that occurred on the beach at the same time with the aim to assess their influence on the abundance and foraging of oystercatchers. We focused on the number of people present on the beach and the presence of dogs because both are recognised as important disturbances to shorebirds (Burger *et al.* 2004; Heredia-Morales *et al.* 2024). Numerous studies have found that the presence of people on beaches can disturb and displace foraging shorebirds (Burger and Gochfeld 1991; Burton 2007; Weston and Elgar 2007; Glover *et al.* 2011; Ramli and Norazlimi 2017) as well as increase the time non-breeding shorebirds spend being vigilant, thus decreasing the overall time shorebirds spend foraging (Burger 1991; Verhulst *et al.* 2001; Schlacher *et al.* 2013). People walking with dogs are also perceived as a greater threat by shorebirds than people without dogs (Burger 1981; Lafferty 2001; Lord *et al.* 2001; Glover *et al.* 2011; Murchison *et al.* 2016), resulting in shorebirds flying away (Burger *et al.* 2004) and/or decreasing their time spent foraging in the presence of dogs (Thomas *et al.* 2003). Dogs have also been found to predate oystercatcher eggs and chicks on beaches in Australia (Maguire *et al.* 2019). We therefore hypothesised that the presence and foraging behaviour of oystercatchers at our study sites would be influenced by humans and dogs present on the beach.

Regardless of human activities, we also hypothesised that environmental conditions (temperature and wind speed) could be influencing oystercatcher presence and foraging behaviour. Similar to previous studies, and because undisturbed beaches would allow birds to spend more time on foraging, we predicted that (1)

oystercatchers would be present and foraging in significantly smaller numbers in the presence of dogs or when many people are on the beach (see Verhulst *et al.* 2001; Schlacher *et al.* 2013; Ramli and Norazlimi 2017) and alternatively (2) we would observe significantly greater numbers of oystercatchers (and many more birds foraging) when human activities were low or absent (see also Coleman *et al.* 2003; Jones 2016). We also predicted that oystercatchers would be present and foraging in smaller numbers in (1) lower air temperatures where prey availability is likely reduced (Rao *et al.* 2023) and (2) higher wind speeds during unfavourable weather conditions where there are increased costs of foraging (Collop *et al.* 2016).

Materials and methods

Study sites

Between December 2021 and June 2022, we surveyed a 400 m length of ten beaches to observe oystercatcher numbers (total seen and numbers foraging) as well as human activities (number of people, presence of dogs). These beach lengths were measured using GIS software to gain boundary coordinates during site visits prior to data collection. We also obtained data on air temperatures (°C) and wind speeds (km/h) for the time of our observations at each site from the Bureau of Meteorology (<http://www.bom.gov.au/>). Our sites were grouped into three broader locations: Middleton Beach (sites 1–5), Goolwa Beach (sites 6–8) and the Murray Mouth Estuary near Hindmarsh Island (sites 9 and 10) (Figure 1). These sites were selected as they have been confirmed as important foraging sites for oystercatchers during previous surveys conducted by Jones (2016) between 2011 and 2015. The Goolwa beach region is a recreational cockle (*Donax deltooides*) fishing area during the Australian summer and autumn period (November to May) (Ferguson and Mayfield 2006). Cockles are a known food source for oystercatchers at the sites we surveyed (Jones 2016); however, information regarding food availability for other prey items at all sites is unknown, although foraging success was regularly observed during our surveys (Vanderzon *et al.*, unpublished data). Cockle fishers were occasionally observed during our surveys; however, they were not recorded separately and are included in the ‘total number of people’ at each site (see Methods for abundance and foraging observations). All sites offer direct access to the beach, whether by walking from an adjacent car park (sites 1–4, 6, 9–10), driving along the beach (sites 6–8), or following a footpath through

the coastal dunes (sites 7–8). All beach sites were also similar in width (90–100 m) at low tide when observations were made (observational, author 1). During our study, we only accessed sites by walking from the nearest carpark.

General field methods

We selected data collection days randomly to include weekdays, weekends, and public holidays to capture human activities across all day types as we expected human activity to be higher on weekends and public holidays compared to weekdays (Weston and Stankowich 2014). We randomised the order in which we visited each site to avoid sampling bias and minimise the chances of seeing the same oystercatcher individuals if they moved between adjacent sites between observation periods. At every site, each bird was treated as a new individual since we could not track individual bird movement (i.e. the birds were not banded or visually tagged in any way). All observations were conducted at low tide or first light when low tide was earlier than sunrise, as shorebirds predominantly forage on sandy beaches at low tide when most of the beach is exposed (Spencer 2010). Surveys took on average between 2.5–3 hours total including transportation between sites. For sites that allowed beach access (sites 1, 2, 3, 4, 6, 7, 8, 9, 10), we observed the oystercatchers directly on the beach. For site(s) with no immediate beach access (site 5), we made our observations from the closest lookout point within 20 m of the beach. To avoid any bias, all observations were done by a single researcher (author 1) with birds observed by scanning the 400 m beach area using Nikon (Nikon Australia Pty Ltd) 8 × 42 binoculars. During each abundance and foraging behaviour survey at each site, we recorded (i) the total number of individuals identified per oystercatcher species, (ii) the number of people, and (iii) whether dogs were present or absent (both on and off leash). All observations were made and recorded immediately upon arrival to the site (i.e. we did not record numbers over a set period that could include new arrivals) as a count of the entire group present at that site, rather than focal observations per individual.

Abundance observations

We recorded counts for oystercatcher abundance once per month at all ten sites (Figure 1). The observations were split over two consecutive days (five sites observed on one day, and five sites observed on the second day) to ensure that observations were made at similar tidal

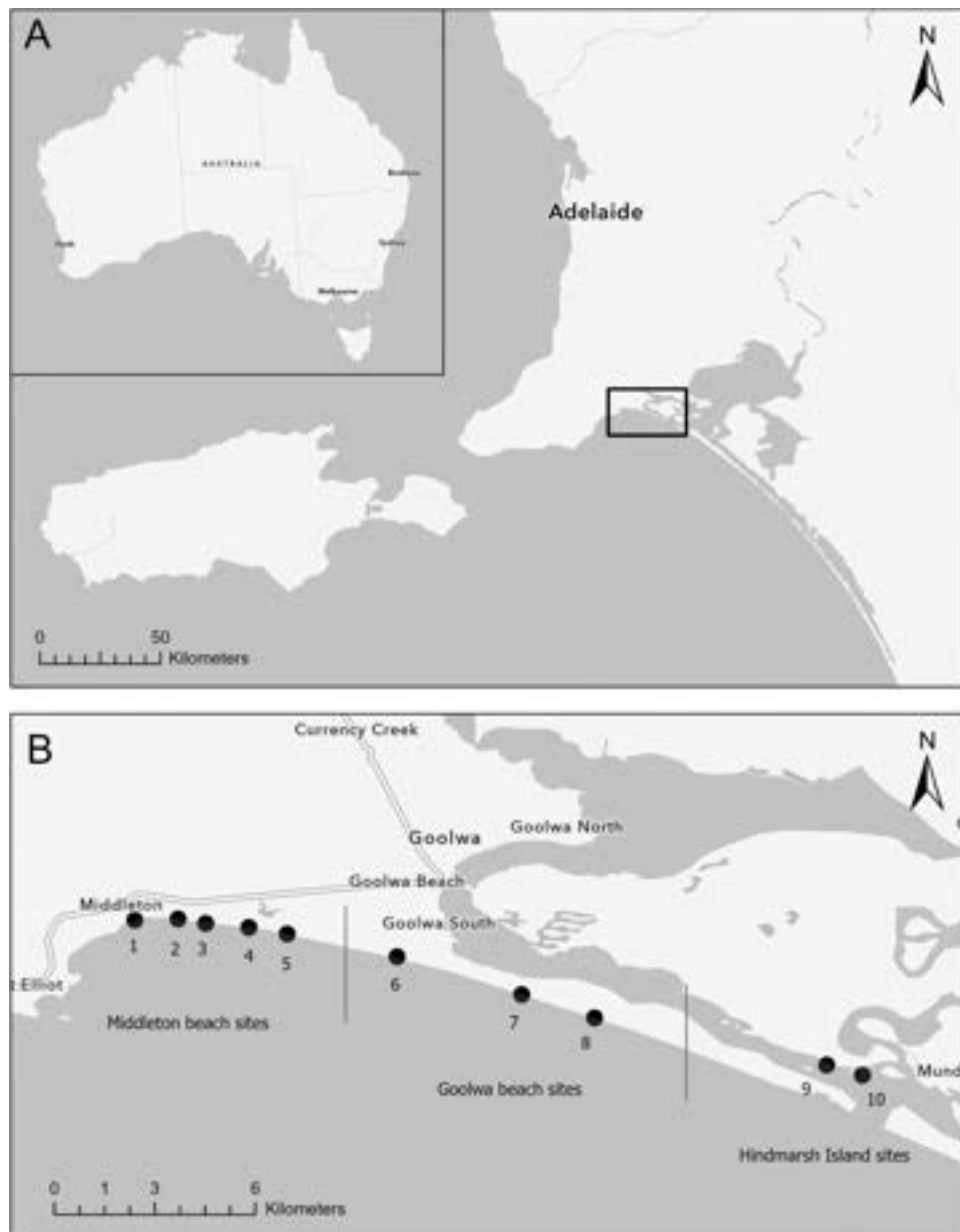


Figure 1. (A) Map of the Fleurieu Peninsula, South Australia, indicating the study area ($35^{\circ}31'23.7''\text{S}$ $138^{\circ}46'20.0''\text{E}$). (B) Exact locations of the 10 sites used in this study to observe oystercatcher abundance (sites 1–10) and foraging behaviour (sites 3, 7, 10) in relation to human activities and environmental conditions (adapted from Jones 2016). The top left corner indicates the location of the Fleurieu Peninsula within Australia.

states. At each site, we recorded (i) the total number of oystercatchers per species and (iii) people and dogs as described in the ‘general field methods’.

Foraging behaviour observations

We observed and recorded oystercatcher foraging behaviour three times per month (independent to the abundance surveys) at three sites only, due to time constraints: sites 3, 7 and 10 (i.e. one site per broader location as described in the study site

section, randomly selected; Figure 1). At each site, we recorded (i) the total number of oystercatchers per species and (ii) the number of oystercatchers foraging per species (as per Supplementary Table S1; see also Figure 2) and (iii) people and dogs as described in the ‘General field methods’. All observations were made and recorded instantaneously upon arrival to the site (i.e. we did not record the percentage of birds foraging over a set period). All oystercatchers observed during this study were foraging on sand.



Figure 2. Examples of oystercatcher foraging behaviours observed during surveys on the south-eastern Fleurieu Peninsula: (A) searching and probing behaviour by Pied Oystercatchers, and (B–D) cockle handling by Pied and Sooty Oystercatchers.

Statistical analysis

We performed all statistical analyses in RStudio v. 2022.7.1.554 (Team 2020). ‘Site’ (sites 1 through 10) and ‘Julian date’ were assigned as random factors in all models. Foraging data were analysed as the percentage of birds foraging rather than total number of birds foraging to correct for the total number of oystercatchers present at each site. Variance inflation factors were < 2 , confirming no collinearity between our predictors (Zuur *et al.* 2009; Fox *et al.* 2015) and low correlation between variables (< 0.3). All residual model diagnostics were checked visually for normality, homogeneity or dispersion to ensure all statistical assumptions were met.

To analyse oystercatcher abundance, we used the R package ‘lmer4’ and generalised linear mixed models (GLMM) (model 1) with a negative binomial distribution and a logit link function to reduce overdispersion. Models included the following fixed continuous predictor variables: ‘wind speed’, ‘air temperature’, ‘people’, ‘dogs’ and ‘species’. The analyses were not separated by species as both Pied and Sooty oystercatchers regularly forage together in flocking groups at our study sites. We, therefore, included ‘species’ as a fixed continuous predictor in our models (for abundance and foraging) to account for differences between the two oystercatcher species in our dataset.

To analyse oystercatcher foraging behaviour, we used zero-inflated GLMMs (model 2) with a Poisson distribution and a logit link function with the R package ‘glmmTMB’ (Brooks *et al.* 2017) and single zero-inflation parameter applied to all observations

($ziformula = \sim 1$). A Poisson distribution was used rather than a negative binomial as it was the best model fit and reduced overdispersion. Models included the following fixed continuous predictor variables: ‘wind speed’, ‘air temperature’, ‘people’, ‘dogs’ and ‘species’.

Off-road vehicles seen parked or in motion at sites were recorded during surveys and originally analysed as fixed factors in both models. Vehicle driving is only permitted at sites 6–8 and was found to be correlated with ‘people’ and ‘dogs’ at these sites and not significant in all model outputs ($p > 0.05$) during preliminary data analyses. Therefore, vehicles as a factor was excluded from the final model outputs

Results

Oystercatcher abundance

Across 70 abundance surveys, we recorded a total of 774 oystercatcher sightings (557 Pied Oystercatchers and 217 Sooty Oystercatchers). Both species were present at the same time during 10 of the 70 surveys (14.3%); each species was present during 20 surveys (29% of surveys per species; Supplementary Table S2).

People were observed in 62 out of 70 (89%) surveys, and oystercatcher abundance decreased as the number of people increased (Table 1; Figure 3(A)). Dogs were present in 41 out of 70 (59%) surveys and were always accompanied by at least one person walking them. Oystercatcher abundance was also lower when dogs were present compared to when no dogs were observed (Table 1; Figure 3(B)). Oystercatcher abundance showed a negative relationship with air temperature and

Table 1. Output from the generalised linear mixed models assessing whether ‘people’, ‘dogs’, ‘air temperature’, ‘wind speed’ and ‘species’ predicted the abundance (model 1) and foraging (model 2) of Pied and Sooty Oystercatchers.

Fixed Factors	Estimate	Standard Error	z-value	P-value
Model 1 (Abundance data)				
Intercept	−0.37	0.002	−146.62	<0.001
People	−0.08	0.002	−31.58	<0.001
Dogs [present]	0.44	0.002	174.39	<0.001
Air temperature	−0.04	0.002	−16.28	<0.001
Wind speed	0.04	0.002	19.26	<0.001
Species [Sooty]	−0.09	0.002	−36.92	<0.001
Model 2 (Foraging data)				
Intercept	3.92	0.38	10.40	<0.001
People	0.03	0.01	3.72	<0.001
Dogs [present]	0.61	0.08	−7.48	<0.001
Air temperature	−0.09	0.02	−4.04	<0.001
Wind speed	0.04	0.01	6.25	<0.001
Species [Sooty]	0.18	0.05	3.17	0.001

Statistically significant (≤ 0.05) values are marked in bold text.

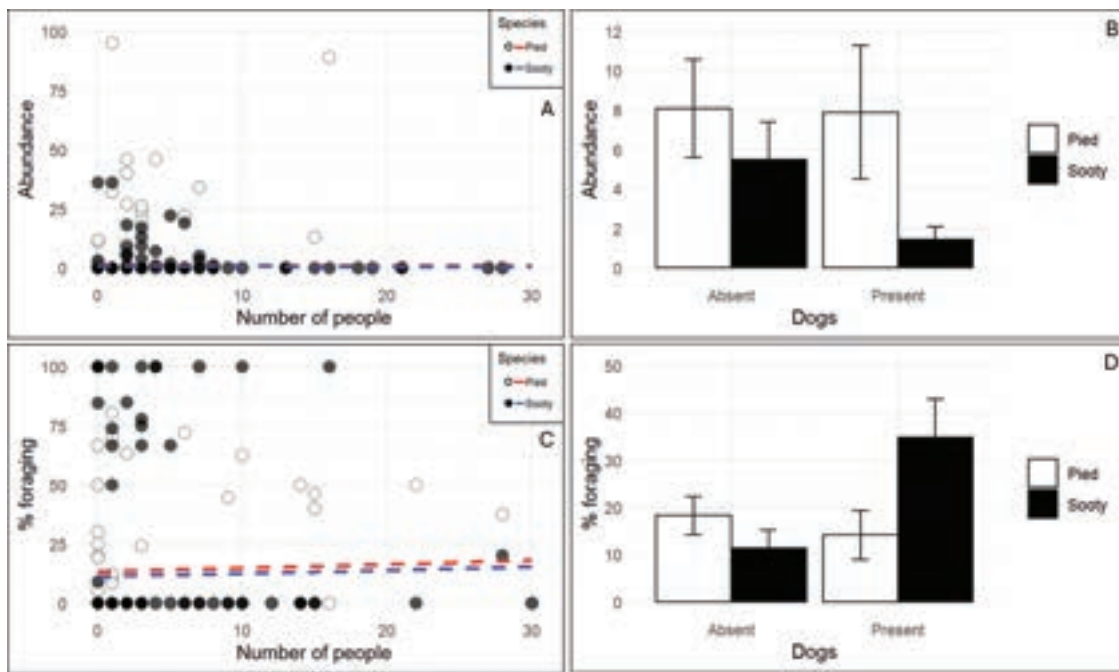


Figure 3. Abundance (number of birds present) (A, B) and percentage (%) of birds foraging (C, D) for Pied and Sooty Oystercatchers in relation to the number of people (A, C) and the presence of dogs (present vs absent) (B, D) recorded on surveys. Model predictions (dashed lines) plotted for both species.

a positive relationship with wind speed (Table 1; Figure 4). Overall, the abundance of Sooty Oystercatchers was lower (on average 3.10 ± 7.45 birds per survey) than Pied Oystercatchers (on average 7.96 ± 18.5 birds per survey; Table 1). An average of 11 oystercatchers (11.06 ± 20.55) were counted at each site during surveys.

Foraging behaviour

We conducted 84 foraging surveys and obtained a total of 1023 sightings of oystercatchers foraging (774 Pied

Oystercatchers and 249 Sooty Oystercatchers). Pied Oystercatchers were present for 36 of these surveys (43%) and Sooty Oystercatchers were present for 31 surveys (37%). An average of five oystercatchers (4.76 ± 9.07) were seen foraging at each site during surveys (Pied Oystercatchers 3.24 ± 8.37 ; Sooty Oystercatchers 1.52 ± 3.93). On average at each site, few individuals were seen engaged in behaviours other than foraging such as resting (Pied Oystercatchers 2.90 ± 8.97 ; Sooty Oystercatchers 0.58 ± 1.70) or in vigilance (Pied Oystercatchers 2.77 ± 9.83 ; Sooty Oystercatchers 0.88 ± 3.30). Of the surveys conducted, oystercatchers were

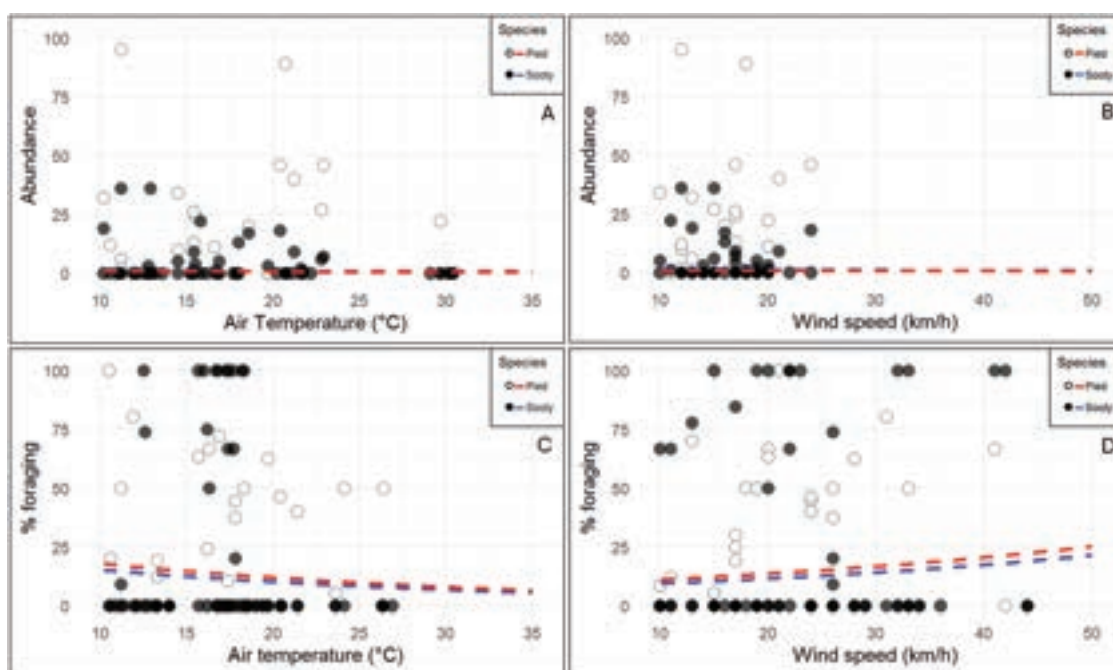


Figure 4. Abundance (number of birds present) (A, B) and percentage (%) of birds foraging (C, D) for Pied and Sooty Oystercatchers in relation to air temperature (°C) (A, C) and wind speeds (km/h) (B, D) recorded on surveys. Model predictors (dotted lines) plotted for both species.

observed foraging in 33% of surveys, whereas 67% of surveyed oystercatchers were engaged in other behaviours (Supplementary Table S2). Both species were seen present together during 16 of the 84 foraging surveys (19%).

People were observed in 55 out of 84 (64%) surveys, while dogs were observed in 31 out of 84 (39%) surveys. A higher percentage of oystercatchers were observed foraging when people were present in higher numbers (Table 1; Figure 3(C)) and when dogs were present (Table 1; Figure 3(D)). The percentage of oystercatchers foraging showed a negative relationship with air temperature and a positive relationship with wind speed (Table 1; Figure 4). The percentage of birds foraging was higher for Sooty Oystercatchers ($19.94 \pm 4.05\%$ of birds per survey) compared to Pied Oystercatchers (on average $16.72 \pm 3.17\%$ of birds per survey; Table 1).

Discussion

Non-breeding shorebirds tend to change their abundance and behaviours in areas frequently visited by people and dogs (Lafferty 2001; Coleman *et al.* 2003; Fitzpatrick and Bouchez 2010; Schlacher *et al.* 2013; Ramli and Norazlimi 2017), and human activities are known to alter the behaviour of foraging shorebirds on sandy beaches (Burger 1991; Burger and Gochfeld 1991;

Schlacher *et al.* 2013). Here, we found that, while the abundance of oystercatchers decreased with the number of people and presence of dogs, the percentage of birds foraging increased. This relationship could indicate that, while oystercatchers are in smaller numbers, those present at these beaches surveyed are very tolerant of people and dogs. Such tolerance by oystercatchers to human presence may also be explained by the regular attendance of recreational cockle fishers at our study sites. While people fishing on beach shorelines may impact shorebirds by reducing overall food availability (Ferns *et al.* 2000; Masero *et al.* 2008; Lunardi and Macedo 2014), oystercatchers could also be using cockle fishers as an indicator of foraging sites with abundant prey items or to scavenge undersized cockles that have been left behind. Similar relationships have been found for Semipalmated Plovers (*Charadrius semipalmatus*) and Semipalmated Sandpipers (*Calidris pusilla*) in north-eastern Brazil, where they appeared to prefer foraging through sediments that had been overturned by shellfishers compared to undisturbed sediments (Lunardi and Macedo 2014). Lunardi and Macedo (2014) suggested that these shorebirds may have adopted a foraging strategy to utilise human fishing practises as an indicator for their food source, rather than perceiving them as a disturbance. Thus, future studies should investigate possible competition for food resources

between fishers and oystercatchers at the study sites we surveyed but also across their distributional range.

Oystercatcher responses to human activities can be species-specific, despite both species utilising the same habitat and being exposed to the same activities. In our study, both species differed in abundance and percentage of birds foraging but in opposite trends. In addition, we observed different patterns of responses to dogs between the two species. Sooty Oystercatchers were present in greater numbers when dogs were absent from beaches, while Pied Oystercatcher numbers hardly changed in the presence or absence of dogs (Figure 3). These results could suggest that Sooty Oystercatchers may be more sensitive and less tolerant towards dogs than Pied Oystercatchers. Alternatively, Pied Oystercatchers may not recognise dogs as a potential disturbance, especially if the perceived value of their resource (i.e. the feeding/roosting location) is high (Yasué 2005; Glover *et al.* 2011). Glover *et al.* (2011) has shown that Pied Oystercatchers do discriminate between people walking, jogging, and people with dogs, and that Sooty Oystercatchers have longer flight initiation distances compared to Pied Oystercatchers. Another explanation is that Pied Oystercatchers may have habituated to human activities, such as dog walking, while Sooty Oystercatchers have not, as the capacity to habituate can vary greatly between closely related species (Sutton *et al.* 2021). Habituation generally occurs when individuals are repeatedly exposed to non-lethal disturbances, leading individuals to lower their response (e.g. by not flushing or spending less time in vigilance) (Whittaker and Knight 1998; Glover *et al.* 2011; Schlacher *et al.* 2013). Experimental studies, such as testing flight initiation distances (Blumstein *et al.* 2003; Fitzpatrick and Bouchez 2010; Glover *et al.* 2011; Lunardi and Macedo 2014), may help in disentangling these hypotheses further.

The opposite patterns between Pied and Sooty Oystercatchers observed in our study could also be attributed to variation in group size and beach use by each species, and the differences in human activities occurring at those sites. While both species were often observed together in flocking or foraging groups, Pied Oystercatchers accounted for most of the observations and were often in large groups (particularly at Goolwa beach and the Murray Mouth) across wider areas on the beaches (i.e. closer to the shoreline when foraging and higher up on the beach when resting). Sooty Oystercatchers were also generally seen in smaller groups than Pied Oystercatchers at the Middleton beach sites, particularly site 1 where they would be seen foraging near, or roosting, upon the rocky point. Group size can be associated with disturbance responses

to people, where larger flock sizes will have increased feeding rates and reduced response to humans, or 'potential threats', compared to smaller flocks (Yasué 2005; Shuai *et al.* 2024) since each individual bird spends less time in vigilance to scan for threats (Barnard 1980). Hence, smaller groups of Sooty Oystercatchers (i.e. compared to the larger groups of Pied Oystercatchers) could therefore be more prone to human disturbance. Of the three site locations, Middleton beach had the highest densities of people and dogs present, especially during the summer months. Yet we sometimes observed no oystercatchers at this site even when there were no – or very few – people. The lack of birds could indicate that there are other factors, such as food availability and benthic fauna assemblages that play a role in determining where oystercatchers prefer to forage or rest (Bakker *et al.* 2021). The connectedness between beach sites could also play a role, as birds may be foraging in 'disturbed' areas because they can escape to connected foraging sites. Alternatively, it could be that birds are foraging at 'disturbed' sites simply because this is their only option and the risks do not yet outweigh the benefits (Radvan *et al.* 2023). In future, understanding the availability of alternative sites and the specific ways that each species uses these sites (i.e. the relationship between oystercatcher abundance, benthic fauna prey and habitat use or connectivity) could assist in explaining the differences between Pied and Sooty Oystercatcher abundances.

The foraging behaviour of shorebirds can be affected by low air temperatures and high wind speeds, which are both known to affect prey distribution and the energy needs of the foraging birds (Goss-Custard 1969; Smith 1975; Burger 1991). Our results showed that both abundance and percentage of birds foraging decreased with increasing air temperature and increased with increasing wind speeds. The negative relationship with rising air temperatures was not unexpected as shorebirds are capable of regulating their body heat at higher optimal temperatures when resting, to retain energy for foraging activities (Davidson 1981). However, it is generally assumed that foraging would decrease with increasing wind speeds due to the increased energy cost of thermoregulation (González-Medina *et al.* 2020). Jones (2016) found that south-west winds during summer and autumn indirectly influence the presence of Sooty Oystercatchers because the winds bring sea grass (e.g. beach-cast wrack) onto the beach, which is rich in food resources, such as crustaceans and molluscs (Baring *et al.* 2014). Similar observations were made in this study, where Sooty Oystercatchers would occasionally be seen foraging on accumulated seagrass at the Middleton beach sites. It is also possible that Pied and

Sooty Oystercatchers are still able to forage efficiently when wind speeds are high, especially if some sites are protected from direct wind gusts (e.g. by large dunes or rocky headlands), such as site 10 in our study. Varying environmental conditions also have the potential to alter disturbance responses in shorebirds (McBlain *et al.* 2020) as birds need to trade-off between food acquisition and the cost of avoiding people and dogs (Carr and Lima 2012; Timmis *et al.* 2022; Gutiérrez *et al.* 2023), which can result in shorebirds taking greater risks when disturbed, such as allowing humans to approach closer while foraging (Gutiérrez *et al.* 2023). Therefore, it is possible that oystercatchers in our study continue to forage despite high wind speeds and greater human disturbances, especially if the energy costs of disturbance avoidance are greater during weather conditions with high wind speeds. The increased foraging by oystercatchers with increasing wind speeds could also be explained by a reduction in human disturbance when wind speeds are high if this is a favourable trade-off. Overall, our results highlight that multiple factors should be considered when assessing shorebird abundance and foraging behaviour, even when human activities are expected to be the predominant cause of disturbance.

While human activities are a well-known source of stress that can lead to decreased fitness and reproductive success for individuals (Sih *et al.* 2011), they do not always have survival consequences if the availability of suitable alternative habitats outweighs the fitness costs of the disturbance. It is often assumed that the impacts of human activities are more serious when behavioural responses are stronger (Gill *et al.* 2001); however, Stillman and Goss-Custard (2002) found that oystercatchers responded more to human activities when they were better able to compensate for lost foraging time associated with the response to people. This suggests that human activities alone may not be the biggest driver to shorebird fitness, but should be considered along with other factors, such as habitat availability and use by shorebirds, environmental conditions and population dynamics. The unexpected trends found in our study between oystercatcher abundance, foraging and human activities could indicate that the birds utilise multiple foraging and roosting locations to avoid high levels of human disturbances or that habituation may have occurred. However, there is still a possibility that flushing or periodically changing foraging sites in response to disturbance is energetically costly for the oystercatchers when human activities fluctuate seasonally. Thus, it is important to understand the level of potential disturbance that might possibly result in dispersal of oystercatchers to other available alternative

habitats (Coleman *et al.* 2003). To define these relationships in the context of our study, experimental testing on the tolerance of oystercatchers to human disturbance activities and developing a clear understanding of the distribution range and movements of the oystercatcher populations is required. Our study highlights that disruption of foraging by human activities is only one key factor shaping the abundance and foraging habits of oystercatchers on South Australian beaches. In addition, we also identified the importance of environmental conditions (e.g. temperature and wind speeds) on oystercatcher presence and foraging, thereby underscoring the existing complexity of these interactions. Future complementary studies of manipulative in-situ human disturbances alongside long-term records of response to variations in environmental conditions would contribute to identifying the real risks of human and oystercatcher interactions.

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Author contributions

Emma Vanderzon: Conceptualisation, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualisation, Writing – original draft. **Ryan Baring:** Conceptualisation, Funding acquisition, Methodology, Project administration, Resources, Writing – review & editing. **Diane Colombelli-Négrel:** Conceptualisation, Funding acquisition, Methodology, Project administration, Resources, Visualisation, Writing – review & editing.

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ORCID

Diane Colombelli-Négrel  <http://orcid.org/0000-0002-9572-1120>

Ethics statement

This study was conducted under the Flinders University Animal Ethics permit number AEC BIOL4269 and scientific permit M27089.

References

- Bakker, W., B. J. Ens, A. Dokter, H.-J. van der Kolk, K. Rappoldt, M. van de Pol, *et al.* (2021). Connecting foraging and roosting areas reveals how food stocks explain shorebird numbers. *Estuarine Coastal and Shelf Science* **259**, 107458. doi:10.1016/j.ecss.2021.107458
- Baring, R. J., P. G. Fairweather, and R. E. Lester. (2014). Storm versus calm: Variation in fauna associated with drifting macrophytes in sandy beach surf zones. *Journal of Experimental Marine Biology and Ecology* **461**, 397–406. doi:10.1016/j.jembe.2014.09.011
- Barnard, C. (1980). Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Animal Behaviour* **28** (1), 295–309. doi:10.1016/S0003-3472(80)80032-7
- Baudains, T. P., and P. Lloyd. (2007). Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation* **10**(3), 400–407. doi:10.1111/j.1469-1795.2007.00126.x
- Blumstein, D. T., L. L. Anthony, R. Harcourt, and G. Ross. (2003). Testing a key assumption of wildlife buffer zones: Is flight initiation distance a species-specific trait? *Biological Conservation* **110**(1), 97–100. doi:10.1016/S0006-3207(02)00180-5
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**(2), 378–400. doi:10.32614/RJ-2017-066
- Burger, J. (1981). The effect of human activity on birds at a coastal bay. *Biological Conservation* **21**(3), 231–241. doi:10.1016/0006-3207(81)90092-6
- Burger, J. (1991). Foraging behavior and the effect of human disturbance on the piping plover (*Charadrius melodus*). *Journal of Coastal Research* **7**, 39–52.
- Burger, J., and M. Gochfeld. (1991). Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). *The Condor* **93**(2), 259–265. doi:10.2307/1368941
- Burger, J., M. Gochfeld, C. D. Jenkins, and F. Lesser. (2010). Effect of approaching boats on nesting Black skimmers: Using response distances to establish protective Buffer zones. *The Journal of Wildlife Management* **74**(1), 102–108. doi:10.2193/2008-576
- Burger, J., C. Jeitner, K. Clark, and L. J. Niles. (2004). The effect of human activities on migrant shorebirds: Successful adaptive management. *Environmental Conservation* **31**(4), 283–288. doi:10.1017/S0376892904001626
- Burton, N. H. K. (2007). Landscape approaches to studying the effects of disturbance on waterbirds. *Ibis* **149**, 95–101. doi:10.1111/j.1474-919x.2007.00658.x
- Carr, J. M., and S. L. Lima. (2012). Heat-conserving postures hinder escape: A thermoregulation–predation trade-off in wintering birds. *Behavioral Ecology* **23**(2), 434–441. doi:10.1093/beheco/arr208
- Coleman, R., N. A. Salmon, and S. Hawkins. (2003). Sub-dispersive human disturbance of foraging Oystercatchers *Haematopus ostralegus*. *Ardea* **91**, 263–268.
- Collop, C., R. A. Stillman, A. Garbutt, M. G. Yates, E. Rispin, and T. Yates. (2016). Variability in the area, energy and time costs of wintering waders responding to disturbance. *The Ibis* **158**(4), 711–725. doi:10.1111/ibi.12399
- Davidson, N. C. (1981). 'Survival of Shorebirds (*Charadrii*) During Severe Weather: The Role of Nutritional Reserves.' (Springer: US.) doi:10.1007/978-1-4613-3318-0_18
- Defeo, O., and A. McLachlan. (2005). Patterns, processes and regulatory mechanisms in sandy beach macrofauna: A multi-scale analysis. *Marine Ecology Progress Series* **295**, 1–20. doi:10.3354/meps295001
- Defeo, O., A. McLachlan, D. S. Schoeman, T. A. Schlacher, J. Dugan, A. Jones, *et al.* (2009). Threats to sandy beach ecosystems: A review. *Estuarine Coastal and Shelf Science* **81**(1), 1–12. doi:10.1016/j.ecss.2008.09.022
- Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. (2003). The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine Coastal and Shelf Science* **58**, 25–40. doi:10.1016/S0272-7714(03)00045-3
- Ellenberg, U., T. Mattern, P. J. Seddon, and G. L. Jorquera. (2006). Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation* **133**(1), 95–106. doi:10.1016/j.biocon.2006.05.019
- Ferguson, G., and S. Mayfield. (2006). The South Australian goolwa cockle (*donax deltoidea*) fishery. *SARDI Research Report Series* **150**, 30.
- Fernandez-Juricic, E., M. D. Jimenez, and E. Lucas. (2002). Factors affecting intra- and inter-specific variation in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology* **80** (7), 1212–1220. doi:10.1139/z02-104
- Ferns, P., D. Rostron, and H. Siman. (2000). Effects of Mechanical cockle harvesting on intertidal communities. *The Journal of Applied Ecology* **37**(3), 464–474. doi:10.1046/j.1365-2664.2000.00509.x
- Fitzpatrick, S., and B. Bouchez. (2010). Effects of recreational disturbance on the foraging behavior of waders on a rocky beach. *Bird Study* **1**(2), 157–171. doi:10.1080/00063659809461088
- Fox, G. A., S. Negrete-Yankelevich, and V. J. Sosa. (2015). 'Ecological Statistics: Contemporary Theory and Application.' (Oxford University Press: USA)
- Gill, J. A., K. Norris, and W. J. Sutherland. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* **97**(2), 265–268. doi:10.1016/S0006-3207(00)00002-1
- Glover, H. K., M. A. Weston, G. S. Maguire, K. K. Miller, and B. A. Christie. (2011). Towards ecologically meaningful and socially acceptable buffers: Response distances of shorebirds in Victoria, Australia, to human disturbance. *Landscape and Urban Planning* **103**(3–4), 326–334. doi:10.1016/j.landurbplan.2011.08.006
- González-Medina, E., J. Cabello-Vergel, N. Playà-Montmany, A. Villegas, M. Parejo, J. M. Abad-Gómez, *et al.* (2020). Going to sleep with a full belly: Thermal substitution by

- specific dynamic action in shorebirds. *Comparative Biochemistry & Physiology Part A Molecular & Integrative Physiology* **244**, 110689. doi:10.1016/j.cbpa.2020.110689
- Goss-Custard, J. (1969). The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**(3), 338–356. doi:10.1111/j.1474-919X.1969.tb02549.x
- Gregory, R. D., and A. van Strien. (2010). Wild bird indicators: Using composite population trends of birds as measures of environmental health. *Ornithological Science* **9**(1), 3–22. doi:10.2326/osj.9.3
- Guinness, S., W. F. Van Dongen, P. J. Guay, R. W. Robinson, and M. A. Weston. (2019). Evaluating how the group size of domestic, Invasive dogs affect Coastal Wildlife responses: The case of flight-initiation distance (FID) of birds on southern Australian beaches. In 'Impacts of Invasive Species on Coastal Environments: Coasts in Crisis'. (Eds C. Makowski, and C. W. Finkl.) pp. 413–424. (Springer International Publishing: Cham.) doi:10.1007/978-3-319-91382-7_12
- Gutiérrez, J. S., T. Catry, M. Espinosa-Colín, J. A. Masero, and J. P. Granadeiro. (2023). Heat stress increases risk taking in foraging shorebirds. *Functional Ecology* **37**(4), 1005–1019. doi:10.1111/1365-2435.14288
- Hansen, B. D., C. D. Minton, A. E. Harrison, and R. Jessop. (2014). Conservation assessment of the Sooty Oystercatcher *Haematopus fuliginosus*. *International Wader Studies* **20**, 161–172.
- Heredia-Morales, A., E. Palacios, and M. E. Reiter. (2024). Evaluating the response of nonbreeding shorebirds to rate and agents of human disturbance. *Waterbirds* **47**(2), 1–11. doi:10.1675/063.047.0210
- Hockin, D., M. Ounsted, M. Gorman, D. Hill, V. Keller, and M. A. Barker. (1992). Examination of the effects of disturbance on birds with reference to its importance in ecological assessments. *Journal of Environmental Management* **36** (4), 253–286. doi:10.1016/S0301-4797(08)80002-3
- Hubbard, D. M., and J. E. Dugan. (2003). Shorebird use of an exposed sandy beach in southern California. *Estuarine Coastal and Shelf Science* **58**, 41–54. doi:10.1016/S0272-7714(03)00048-9
- Jones, A., W. Gladstone, and N. Hacking. (2007). Australian sandy-beach ecosystems and climate change: Ecology and management. *The Australian Zoologist* **34**(2), 190–202. doi:10.7882/AZ.2007.018
- Jones, G. K. (2016). 'Changes in distribution and abundance of Australian pied and Sooty Oystercatchers on highly disturbed beaches of the south-eastern Fleurieu Peninsula.' (Stilt: South Australia.)
- Lafferty, K. (2001). Birds at a southern California beach: Seasonality, habitat use and disturbance by human activity. *Biodiversity and Conservation* **10**(11), 1949–1962. doi:10.1023/A:1013195504810
- Lauro, B., and E. Nol. (1995). Feeding behavior, prey selection, and Bill Size of Pied and Sooty Oystercatchers in Australia. *The Wilson Bulletin* **107**, 629–640.
- Lord, A., J. R. Waas, J. Innes, and M. J. Whittingham. (2001). Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation* **98**(2), 233–240. doi:10.1016/S0006-3207(00)00158-0
- Lunardi, V. O., and R. H. Macedo. (2014). Shorebirds can adopt foraging strategies that take advantage of human fishing practices. *Emu - Austral Ornithology* **114**(1), 50–60. doi:10.1071/MU12097
- Maguire, G. S., K. K. Miller, and M. A. Weston. (2019). Only the strictest rules apply: Investigating regulation compliance of beaches to minimize Invasive dog impacts on threatened shorebird populations. In 'Impacts of Invasive Species on Coastal Environments: Coasts in Crisis'. (Eds C. Makowski, and C. W. Finkl.) pp. 397–412. (Springer International Publishing: Cham.) doi:10.1007/978-3-319-91382-7_11
- Masero, J., M. Castro, S. Estrella, and A. Páez-hurtado. (2008). Evaluating impacts of shellfish and baitworm digging on bird populations: Short-term negative effects on the availability of the mudsnail *Hydrobia ulvae* to shorebirds. *Biodiversity and Conservation* **17**(4), 691–701. doi:10.1007/s10531-005-3434-0
- McBlain, M., K. A. Jones, and G. Shannon. (2020). Sleeping Eurasian Oystercatchers adjust their vigilance in response to the behaviour of neighbours, human disturbance and environmental conditions. *Journal of Zoology* **312**(2), 75–84. doi:10.1111/jzo.12812
- Moreira, F. (1997). The importance of shorebirds to energy fluxes in a food web of a South European Estuary. *Estuarine Coastal and Shelf Science* **44**(1), 67–78. doi:10.1006/ecss.1996.0112
- Murchison, C. R., Y. Zharikov, and E. Nol. (2016). Human activity and habitat characteristics influence shorebird habitat use and behavior at a Vancouver Island migratory stopover site. *Environmental Management* **58**(3), 386–398. doi:10.1007/s00267-016-0727-x
- Nebel, S., and G. J. Thompson. (2005). Foraging behaviour of western sandpipers changes with sediment temperature: Implications for their hemispheric distribution. *Ecological Research* **20**(4), 503–507. doi:10.1007/s11284-005-0061-x
- Nisbet, I. C. T. (2000). Disturbance, habituation, and management of waterbird colonies. *Waterbirds: The International Journal of Waterbird Biology* **23**, 312–332.
- Petch, N., G. S. Maguire, T. A. Schlacher, and M. A. Weston. (2018). Motivations and behavior of off-road drivers on sandy beaches. *Ocean & Coastal Management* **163**, 82–91. doi:10.1016/j.ocecoaman.2018.05.021
- Pfister, C., B. A. Harrington, and M. Lavine. (1992). The impact of human disturbance on shorebirds at a migration staging area. *Biological Conservation* **60**(2), 115–126. doi:10.1016/0006-3207(92)91162-L
- Radvan, M., A. R. Rendall, and M. A. Weston. (2023). The habitat connectivity hypothesis of escape in urban woodland birds. *Behavioral Ecology* **34**(2), 297–305. doi:10.1093/beheco/arac127
- Ramli, R., and N. A. Norazlimi. (2017). The effects of disturbance on the abundance and foraging behaviour of shorebirds and waterbirds in the tropical mudflat areas. *Sains Malaysiana* **46**(3), 365–372. doi:10.17576/jsm-2017-4603-02
- Rao, G. B., S. Babu, and G. Quadros. (2023). Environmental factors and prey availability determine wintering habitat use by shorebirds along the west coast of India. *Regional Studies in Marine Science* **67**, 103219. doi:10.1016/j.rsma.2023.103219
- Rodgers, J. A., and S. T. Schwikert. (2003). Buffer zone distances to protect foraging and loafing waterbirds from disturbance by airboats in Florida. *Waterbirds: The*

- International Journal of Waterbird Biology* **26**(4), 437–443. doi:10.1675/1524-4695(2003)026[0437:BZDTPF]2.0.CO;2
- Ryeland, J., M. A. Weston, and M. R. E. Symonds. (2021). The importance of wetland margin microhabitat mosaics; the case of shorebirds and thermoregulation. *The Journal of Applied Ecology* **58**(2), 382–391. doi:10.1111/1365-2664.13769
- Schlacher, T. A., J. Dugan, D. S. Schoeman, M. Lastra, A. Jones, F. Scapini, et al. (2007). Sandy beaches at the brink. *Diversity and Distributions* **13**(5), 556–560. doi:10.1111/j.1472-4642.2007.00363.x
- Schlacher, T. A., T. Nielsen, and M. A. Weston. (2013). Human recreation alters behaviour profiles of non-breeding birds on open-coast sandy shores. *Estuarine Coastal and Shelf Science* **118**, 31–42. doi:10.1016/j.ecss.2012.12.016
- Schlacher, T. A., D. S. Schoeman, A. R. Jones, J. E. Dugan, D. M. Hubbard, O. Defeo, et al. (2014). Metrics to assess ecological condition, change, and impacts in sandy beach ecosystems. *Journal of Environmental Management* **144**, 322–335. doi:10.1016/j.jenvman.2014.05.036
- Schneider, T. J., G. S. Maguire, D. A. Whisson, and M. A. Weston. (2020). Regulations fail to constrain dog space use in threatened species beach habitats. *Journal of Environmental Planning and Management* **63**(6), 1022–1036. doi:10.1080/09640568.2019.1628012
- Schummer, M. L., and W. R. Eddleman. (2003). Effects of disturbance on activity and energy budgets of migrating waterbirds in South-Central Oklahoma. *The Journal of Wildlife Management* **67**(4), 789–795. doi:10.2307/3802686
- Shuai, L.-Y., F. Morelli, P. Mikula, Y. Benedetti, M. A. Weston, E. Ncube, et al. (2024). A meta-analysis of the relationship between flock size and flight initiation distance in birds. *Animal Behaviour* **210**, 1–9. doi:10.1016/j.anbehav.2024.01.013
- Sih, A., M. C. O. Ferrari, and D. J. Harris. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* **4**(2), 367–387. doi:10.1111/j.1752-4571.2010.00166.x
- Smith, P. C. (1975). 'A Study of the Winter Feeding Ecology and Behaviour of the Bar-Tailed Godwit (*Limosa lapponica*).' (Durham, England: Durham University.)
- Spencer, J. (2010). 'Migratory Shorebird Ecology in the Hunter Estuary, South-Eastern Australia.' (Sydney, New South Wales: Australian Catholic University.)
- Stillman, R. A., and J. D. Goss-Custard. (2002). Seasonal changes in the response of Oystercatchers *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology* **33**(4), 358–365. doi:10.1034/j.1600-048X.2002.02925.x
- Sutton, N. M., M. A. Weston, P. J. Guay, J. Tregoweth, and J. P. O'Dwyer. (2021). A bayesian optimal escape model reveals bird species differ in their capacity to habituate to humans. *Behavioral Ecology* **32**(6), 1064–1074. doi:10.1093/beheco/arab033
- Taylor, I. R., M. I. Newman, P. Park, B. D. Hansen, C. D. T. Minton, A. Harrison, and R. E. Jessop. (2014). Conservation assessment of the Australian Pied oystercatcher *Haematopus longirostris*. *International Wader Studies* **20**, 116–128.
- Team, R. (2020). 'RStudio: Integrated Development Environment for R.' (RStudio, PBC: Boston, MA.)
- Thomas, K., R. Kvitek, and C. Bretz. (2003). Effects of human activity on the foraging behavior of Sanderlings *Calidris alba*. *Biological Conservation - BIOL CONSERV* **109**(1), 67–71. doi:10.1016/S0006-3207(02)00137-4
- Timmis, A. D., M. R. E. Symonds, and M. A. Weston. (2022). The influence of resting posture and orientation on alertness and escape in shorebirds. *Journal of Ornithology* **163** (2), 509–521. doi:10.1007/s10336-021-01957-y
- van der Kolk, H. J., B. J. Ens, K. Oosterbeek, E. Jongejans, and M. Pol. (2022). The hidden cost of disturbance: Eurasian Oystercatchers (*Haematopus ostralegus*) avoid a disturbed roost site during the tourist season. *Ibis* **164**(2), 437–450. doi:10.1111/ibi.13035
- Verhulst, S., K. Oosterbeek, and B. J. Ens. (2001). Experimental evidence for effects of human disturbance on foraging and parental care in Oystercatchers. *Biological Conservation* **101**(3), 375–380. doi:10.1016/S0006-3207(01)00084-2
- Weston, M. A., and M. A. Elgar. (2007). Responses of incubating hooded plovers (*Thinornis rubricollis*) to disturbance. *Journal of Coastal Research* **23**, 569–576. doi:10.2112/04-0151.1
- Weston, M. A., and T. Stankowich. (2014). Dogs as agents of disturbance. In 'Free-Ranging Dogs and Wildlife Conservation'. (Ed M. E. Gompper.) pp. 94–116. (Oxford University Press Oxford: Oxford.)
- Whittaker, D., and R. L. Knight. (1998). Understanding wildlife responses to humans. *Wildlife Society Bulletin* **26**, 312–317.
- Wooding, L. (2019). A review of the Sooty oystercatcher on the Hunter Region coastline of New South Wales. *Australia the Whistler* **13**, 83–93.
- Yasué, M. (2005). The effects of human presence, flock size and prey density on shorebird foraging rates. *Journal of Ethology* **23**(2), 199–204. doi:10.1007/s10164-005-0152-8
- Ydenberg, R. C., and L. M. Dill. (1986). The economics of fleeing from predators. In 'Advances in the Study of Behavior. Vol. 16'. (Eds J. S. Rosenblatt, C. Beer, M.-C. Busnel, and P. J. B. Slater.) pp. 229–249. (Elsevier.)
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. (2009). 'Mixed Effects Models and Extensions in Ecology with R.' (Verlag, New York: Springer.)