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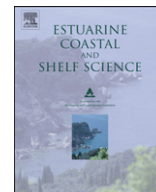
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## Human recreation alters behaviour profiles of non-breeding birds on open-coast sandy shores

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### ABSTRACT

Sandy beaches are primarily valued for their amenity and property values rather than for their ecological functions and properties. Some human usage of beaches potentially conflicts with the conservation and management of wildlife, such as beach-dwelling birds, on sandy shorelines. Because responses by birds to environmental change, including disturbance by humans, often involve behaviours that carry fitness costs, we quantify behaviour profiles of birds in relation to human occurrence along 200 km of sandy shoreline in Eastern Australia, including the large conservation area of Fraser Island. Disturbance to birds on these shores was considerable: 1) birds encountered motorized vehicles (cars, trucks, buses etc.) during 80% of focal bird observation bouts, 2) birds were flushed in over half (up to 86% in individual species) of all bouts, and 3) individuals spent, on average, one-third of their time on disturbance-related behaviours; this was particularly prevalent for Crested Terns (*Thalasseus bergii*) which were alert 42% of the time and spent 12% of their time escaping from human stimuli. Overall, this study demonstrated that motorized traffic is the prime agent of disturbance to birds on these beaches, resulting in frequent and time-consuming escape behaviours. These findings also emphasize that management of vehicle-based recreation on beaches needs to be re-aligned to meet conservation requirements in addition to providing leisure opportunities in National Parks and beyond; we identify some salient issue for this development: a) encouragement of social norms that promote environmentally benign beach use not involving motor vehicles, b) creation of spatial refuges for beach wildlife from traffic and other non-compatible uses, and c) investment in developing complementary management actions such as effective set-back distances.

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### 1. Introduction

Sandy shorelines form critical habitats that are essentially non-replaceable for bird breeding, foraging and roosting on beaches (Dowling and Weston, 1999; Maslo et al., 2011). Populations of many coastal birds are in decline, driven by expanding coastal cities, escalating beach use by humans and habitat loss (Defeo et al., 2009; Foster et al., 2009; Wilson et al., 2011). Humans can directly degrade sandy shore habitat quality by altering beach dimensions and stability, reducing structural diversity of vegetation on dunes, and decreasing food availability through harvesting and incidental crushing of fauna by vehicles (Defeo et al., 2009). In addition, sea level rise is predicted to impact coastal birds substantially (Galbraith et al., 2002). The nature of coastal development could also effectively fragment linear coastlines in a manner

analogous to the fragmentation of continuous terrestrial habitats such as woodlands (Weston et al., 2009).

Humans can also have indirect effects on fauna, for example by creating disturbance, whereby fauna respond to the presence of humans in a way which disrupts their normal activity (Hockin et al., 1992). This can result in 'conflict' between humans and birds on beaches, especially when peak holiday times coincide with the breeding season of birds, creating the potential for negative people–wildlife interactions (Lafferty, 2001a,b; Stillman and Goss-Custard, 2002; Weston and Elgar, 2007). Disturbance by humans could represent a particularly insidious threat, because it is subtle and rarely managed.

Human expectations of beaches are often more complex and multidimensional than a dual focus on recreation and real estate would suggest. Beach-use is influenced by a plethora of factors (e.g. demographics, ethnicity, opportunities for activities, education, etc.) and it encompasses an extraordinary breadth of different use types (Wolch and Zhang, 2004). People also have a very broad range of values and attitudes regarding beaches, not all of them being

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compatible with existing uses. For example, in eastern Australia, people want birds and other wildlife on beaches, but at the same time desire to maximize their recreational opportunities, including walking their dogs on beaches and driving their cars (Maguire et al., 2011). However, high levels of human use, dogs and vehicles are generally not compatible with supporting abundant and diverse birds and other fauna on beaches (Melvin et al., 1994; Weston and Elgar, 2005a,b, 2007). Beach recreation varies regionally, partly in relation to local regulations and cultures, although surprisingly, actual human behaviour on beaches remains poorly documented worldwide. Similarly, response of wildlife to humans is poorly documented, especially on beaches, and greater documentation of disturbance rates and contexts has been flagged as a research priority (Hockin et al., 1992). In particular, human activity and the response of wildlife to it, remains particularly poorly documented on subtropical and tropical beaches.

Disturbance by humans to birds on open-coast beaches is often seen as a major threat and hence poses a conservation challenge (Buick and Paton, 1989; Lafferty, 2001a,b). Disturbance of birds by humans impacts a range of ecological functions and individual fitness, including reproductive success. If disturbance levels are high, birds are excluded from energetically favourable habitats, their feeding rate declines, or both (Thomas et al., 2003; Weston and Elgar, 2005a,b; Maslo et al., 2012). Birds escaping from a threat by fleeing (e.g. by flying) also incur considerable metabolic costs (Torre-Bueno and Larochelle, 1978). More recently, disturbance has been viewed as a factor which decreases habitat quality, and potentially reduces carrying capacities of those habitats (Weston et al., 2012).

Of particular conservation concern are effects of human disturbance on the reproductive fitness of shorebirds, particularly for populations of threatened species (Dowling and Weston, 1999). Diminished breeding success in relation to disturbance usually involves one or more of the following mechanisms: 1) disruption to incubation or brooding (e.g. less parental attentiveness) resulting in thermal stress; 2) separation of chicks from parents and alarm behaviour causing failure of defence and/or attraction of predators, and 3) reduced foraging time or efficiency, or increased energy expenditure, resulting in energetic stress (Ruhlen et al., 2003; Weston and Elgar, 2005a,b; Goss-Custard et al., 2006; Baudains and Lloyd, 2007). The limited information available on the impact of human disturbance, in particular disturbance by vehicles, on coastal birds has focussed on breeding birds (Flemming et al., 1988; Williams et al., 2004; McGowan and Simons, 2006). However, the non-breeding period is also a crucial life history phase, especially where breeding is seasonal and breeders are long-lived, and animals (including immature ones) need to survive and enter the next breeding period in suitable condition (Drake et al., 2001). However, the effects of disturbance, including vehicles on coasts, on non-breeding birds have been poorly studied.

Under some circumstances, the effects of disturbance are also not confined to local populations or habitats. The consequences of disturbance can be transmitted over large geographic distances, as demonstrated by migrating birds that consistently select undisturbed sites irrespective of geographic location of habitat type (Vegvari et al., 2011). Disturbance-displaced birds can also increase competition in undisturbed habitats, ultimately resulting in lowered energy intake and even survival (West et al., 2002).

While a range of physiological and biochemical changes are associated with wildlife response to threatening stimuli, behavioural measurements of response offer a feasible indicator of a species' response; consequently, behavioural responses have been used in the majority of studies of wildlife disturbance (Weston et al., 2012; Weston and Stankowich, *in press*). While many studies have focussed on one or several behaviours thought to be

related to demographically relevant parameters (e.g. parental care assumed to influence reproductive success), few studies examine decisions regarding time budgeting i.e. the allocation of resources between behaviours critical for survival. Here we quantify behaviour profiles of birds (i.e. the proportion of time birds dedicate to different activities) in relation to human disturbance on open-coast sandy beaches. There are four principal reasons for our choice of biological response variable (behaviour), our choice of stressor (disturbance by humans), and our choice of habitat (exposed sandy shores): 1) Many responses by birds to environmental change are in the first instance behavioural (Stillman et al., 2007); 2) Recreational use of beaches is often intense, creating high-frequency and high intensity disturbance stimuli (Schlacher and Thompson, 2012); 3) Disturbance carries fitness costs for animals (Houston et al., 2012), and 4) Beach ecosystems and their wildlife face unprecedented conservation and management challenges (Dugan et al., 2010).

## 2. Methods

### 2.1. Study area

Bird behaviour in relation to human disturbance was quantified on ocean-exposed beaches in Eastern Australia, extending from Fraser Island to south of Double Island Point (Figure Appendix A1). The beaches in the region, including the study sites, are important areas for shorebird roosting, breeding and/or foraging (Fisher et al., 1998; Meager et al., 2012). Our study sites are within the Great Sandy Strait Ramsar site that supports at least 18 of 24 migratory wader species listed under the Japan–Australia Migratory Bird Agreement (JAMBA) and the China–Australia Migratory Bird Agreement (CAMBA). The beaches and dunes also provide critical habitat for several resident (i.e. Australian breeding) shorebird species, and concerns have been raised about the impacts of recreation on these species on these beaches (McFarland, 1993; Fisher et al., 1998).

The eastern, sandy beaches of Fraser Island, the world's largest sand barrier island (Thompson and Schlacher, 2008), are included in this study. The island, and the beaches to the south, are very popular tourist destinations, where driving of four-wheel drive vehicles, fishing in the surf zone, and camping in the coastal dunes are among the main recreational activities (Hockings and Twyford, 1997). Tourists visit the island and beaches to the south also in off-road tour buses and in small aircraft that land on the beach (Hockings, 1998). All these activities constitute considerable motorized traffic on the beaches, and in the coastal dunes abutting the beaches (Schlacher et al., 2008a,b, 2011).

### 2.2. Recording bird behaviour and disturbance

Focal observations of behaviour and recordings of disturbance events were made by two observers (TAS, TN) from a vehicle. Initially, birds were sequentially selected for sampling as they were encountered while driving along the beach. Since this would cluster data points at the margins of a linear beach habitat, we improved spatial dispersion of records by three complementary strategies: 1) alternating field days between Fraser Island and Inskip Beach, 2) randomly choosing different starting points for observations along each beach on different days, and 3) selecting birds in sections of each beach where no previous records were made (Figure Appendix A1). Because focal observations were well separated in space and time, we assume that they represent largely independent observations and that the likelihood of re-sampling the same individuals within a short period is low.

Most birds were observed on the lower part of the beach and we usually positioned the vehicle on the upper shore near the dunes to minimize any observer disturbance. The distance to focal flocks was never closer than 50 m, but usually around 100 m or more. Birds appeared relaxed and were not directly disturbed by the observation vehicle. Flock size was not standardised as this would have been logistically impossible. However, within a species, there was little variation in flock size across the focal observations. In a few instances where birds started to become alert, the observation was abandoned and we moved quickly away. Similarly, we did not approach highly vigilant, alarmed, or nesting birds. Observations were made over ten days from January 8th to 18th, 2011. This period usually coincides with the peak holiday season and maximum traffic on beaches. However, in January 2011 severe and prolonged flooding of roads prevented most people from accessing the beaches and hence the reported levels of disturbance are likely to be much higher in years of normal weather conditions. A longer period of observation would have improved the temporal dispersion of replicates (though no temporal variation in responses was evident or likely), but would have incurred much higher costs of data acquisition. We therefore designed the field program to optimize resources by increasing spatial dispersion within an intense

window of field work. Observations were made usually within 3–4 h of low tide on each day.

We focused on six species: 1) *Thalasseus bergii* (Crested Tern), 2) *Chroicocephalus novaehollandiae* (Silver Gull), 3) *Haematopus longirostris* (Australian Pied Oystercatcher), 4) *Sternula albifrons* (Little Tern), 5) *Vanellus miles* (Masked Lapwing), and 6) *Charadrius ruficapillus* (Red-capped Plover); these species comprise 83% of the total number of shorebirds counted on ocean-exposed sandy beaches in the region (Schlacher and Nielsen unpubl. data).

Each observation bout lasted 10 min, and used a mixed focal animal and scan sampling approach. We observed focal birds with binoculars and recorded their behaviour at 10 s intervals using a stopwatch with a repeat timer. Thus, each 10-minute focal observation bout comprised 60 instantaneous recordings of bird behaviour. For flocks of birds (most commonly for terns, occasionally for gulls) we selected a random subgroup of 5–8 individuals within the field of view of the binoculars, and observations were recorded for each individual. Twenty-one types of behaviour were seen (Table 1).

Birds encountered several natural and anthropogenic stimuli; those which evoked a response at least once are henceforth termed 'disturbance triggers'. Disturbance triggers were classified as: a) People (walking), b) Dogs (approaching), c) Cars (passing,

**Table 1**  
Categories and types of behaviour recorded for birds on open-coast sandy shores in this study.

Behaviour type	Description	Reference (examples)
1. Foraging		
1.1. Food searching	Birds walk/run along the shore in search of benthic food items.	(Burger, 1991, 1994; Weston and Elgar, 2005a,b, 2007; Weston, 2007; Tarr et al., 2010; Maslo et al., 2012)
1.2. Probing	Birds probe/peck the sediment in search of food items.	(Yasué et al., 2003; Zharikov and Skilleter, 2003, 2004)
1.3. Prey capture	Prey items caught in bill.	(Zharikov and Skilleter, 2003, 2004; Yasue et al., 2008)
1.4. Prey handling	Manipulation of prey with bill or feet before swallowing.	(Zharikov and Skilleter, 2004a,b; Yasue et al., 2008)
1.5. Swallowing	Visible movement of prey items through the oesophagus.	(Yasué et al., 2003; Zharikov and Skilleter, 2003; Yasue, 2005; Yasue et al., 2008)
1.6. Drinking	Birds drink from small freshwater pools or creeks that run across the beach from the dunes to the swash.	(Morrier and McNeil, 1991)
2. Inter- and intraspecific interactions		
2.1. Antagonistic behaviour/aggression	Aggressive behaviour displayed towards other birds, either same or different species (e.g. fight for food).	(Morrier and McNeil, 1991; Weston and Elgar, 2007; Tarr et al., 2010)
2.2. Courtship	Behaviour leading to, or initiating, mating or pair formation.	(Lack, 1940)
3. Resting, preening, miscellaneous		
3.1. Resting (roosting)	Birds sit/crouch with minimal motion or they sleep on the beach.	(Morrier and McNeil, 1991; Zharikov and Skilleter, 2004a,b; Weston and Elgar, 2007; Tarr et al., 2010)
3.2. Maintenance/preening	Preening, bathing or stretching.	(Morrier and McNeil, 1991; Weston and Elgar, 2007; Tarr et al., 2010)
3.2. Swash avoidance	Birds that roost or forage on the dry sand move rapidly up-shore to escape incoming swashes.	This study
3.4. Locomotion (general)	Birds walk, run or fly without an obvious, immediate or apparent stimulus identified by human observers.	(Morrier and McNeil, 1991; Tarr et al., 2010)
3.5. Vocalisation	Birds make a sound.	(Burger and Gochfeld, 1993; Stolen, 2003)
3.6. Defecate	Birds discharge waste from the cloaca.	
3.7. Thermoregulation	Birds aim to lower body temperature by standing on the shore with bills open.	(Visser and Ricklefs, 1993)
4. Disturbance-related response behaviours		
4.1. Vigilance/scan/alert	Birds are clearly alert, often with heads raised and directed towards human/dog/vehicles/raptors, and/or continuously scan their environment.	(Burger, 1991, 1994; Stolen, 2003; Yasué et al., 2003)
4.2. Flush/escape – run	Birds run away from a disturbance trigger.	(Burger, 1991; Lafferty, 2001a,b; Stolen, 2003; Lafferty et al., 2006; Weston and Elgar, 2007; Weston et al., 2011)
4.3. Flush/escape – flight	Birds take flight in response to a disturbance stimulus/trigger.	(Lafferty, 2001a,b; Stolen, 2003; Beale and Monaghan, 2004; Weston and Elgar, 2005a,b; Lafferty et al., 2006; Weston and Elgar, 2007; Glover et al., 2011; Weston et al., 2011)
5. Foraging associations with fishermen and bait collectors ('Kleptoparasitism')		
5.1. Waiting for food	Birds wait close to humans for potential feeding opportunities.	(Thompson, 1986; Steele and Hockey, 1990)
5.2. Scouting for food	Birds walk around humans to search for food scraps/items.	(Thompson, 1986; Steele and Hockey, 1990)
5.3. Feeding	Birds feed on food scraps and/or bait discarded by fishermen and bait collectors.	(Thompson, 1986; Steele and Hockey, 1990)

approaching), d) Buses (passing, approaching), e) Trucks (passing, approaching), f) Aircraft (overhead, landing), g) Motorbike (passing, approaching), or h) Raptors (overhead, dunes). For each encounter between birds and a stimulus, three temporal metrics were recorded: 1) time taken to first disturbance response within a 10 min focal observation bout, 2) the duration of each disturbance response, and 3) the return time after the response (i.e. time taken for birds to resume pre-disturbance activity). We measured beach dimensions (total beach width, swash zone width, beach-face slope), and weather conditions (wind speed, direction, temperature, rain) on site after each focal observation.

### 2.3. Data analyses

Differences in multivariate behaviour spectra between species were tested with Permutational Analysis of Variance, PERMANOVA (Anderson, 2001). 'Species' was the fixed factor in the PERMANOVA design. The underlying similarity matrix was based on Bray–Curtis resemblance coefficients, calculated from square-root transformed proportional time allocations to each of the 21 behaviour types listed in Table 1. Thus, our analysis of behaviour is conceptually analogous to the classic species x sample analysis based on abundance/biomass data in community ecology: in our analysis of behaviour profiles, 'samples' are the individual focal observations, 'species' are the 21 different types of behaviour (Table 1), and 'abundance/biomass data' are the proportional time allocations to each of the behaviour types (Table 2). PERMANOVA was

complemented with classification (group-average clustering) and ordination (non-metric multidimensional scaling, NMDS) techniques to display relationships between species in terms of their behavioural profiles (sensu Clarke and Gorley, 2006).

The relationship between variation in time allocated by individuals to the full suite of different behaviours and potential environmental and human predictors was explored with distance-based linear models, DISTLM (McArdle and Anderson, 2001). The method partitions multivariate variation according to a multiple regression (Anderson et al., 2008). Variability in behaviour was calculated as Bray–Curtis dissimilarities of square-root transformed data of relative time spent engaged in each type of behaviour (Clarke et al., 2006).

The criterion to evaluate the 'performance' of models was the corrected Akaike information criterion (AICc) (Burnham et al., 2011; Symonds and Moussalli, 2011). The contribution of individual predictor variables in models was evaluated based on a multi-model inference approach (Anderson, 2008). Here, model Akaike weights were summed across all models in which a variable was included. These summed AIC weights ( $w_+$ ) provide relative probabilities of variable importance; variables with  $w_+ < 0.3$  are likely to be of little or no importance (Burnham and Anderson, 2002).

The initial full set of predictors for DISTLM encompassed 19 variables in four thematic groups: 1) seven environmental predictors (i.e. temperature, rainfall, cloud cover, wind speed and direction, width and slope of the shore), 2) flock size of the birds for each focal observation, 3) seven human-associated disturbance

**Table 2**  
Proportion of time allocated to different types of behaviour by six common species of birds on ocean-exposed shores investigated in this study.

	<i>Thalasseus bergii</i> (Crested Tern)		<i>Chroicocephalus novaehollandiae</i> (Silver Gull)		<i>Haematopus longirostris</i> (Australian Pied Oystercatcher)		<i>Charadrius ruficapillus</i> (Red-capped Plover)		<i>Vanellus miles</i> (Masked Lapwing)		<i>Sternula albifrons</i> (Little Tern)		All species	
No. obs./no. individuals	30/164		14/50		13/31		9/21		9/17		14/114		90/398	
Behaviour type	Mean	(se)	Mean	(se)	Mean	(se)	Mean	(se)	Mean	(se)	Mean	(se)	Mean	(se)
1. Foraging	0.005	(0.005)	0.481	(0.103)	0.362	(0.111)	0.642	(0.090)	0.340	(0.129)	0.004	(0.004)	0.231	(0.037)
1.1 Food searching	0.005	(0.005)	0.394	(0.083)	0.303	(0.096)	0.527	(0.069)	0.269	(0.105)	0.004	(0.004)	0.190	(0.030)
1.2 Probing	0.000	(0.000)	0.076	(0.042)	0.017	(0.006)	0.099	(0.037)	0.057	(0.032)	0.000	(0.000)	0.030	(0.009)
1.3 Prey capture	0.000	(0.000)	0.012	(0.012)	0.009	(0.005)	0.016	(0.011)	0.011	(0.007)	0.000	(0.000)	0.006	(0.002)
1.4 Prey handling	0.000	(0.000)	0.000	(0.000)	0.032	(0.022)	0.000	(0.000)	0.002	(0.002)	0.000	(0.000)	0.005	(0.003)
1.5 Swallowing	0.000	(0.000)	0.000	(0.000)	0.002	(0.001)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
1.6 Drinking	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.001	(0.001)	0.000	(0.000)	0.000	(0.000)
2. Inter- and intraspecific inter	0.000	(0.000)	0.025	(0.015)	0.007	(0.007)	0.019	(0.016)	0.000	(0.000)	0.004	(0.002)	0.008	(0.003)
2.1 Antagonistic behaviour	0.000	(0.000)	0.020	(0.012)	0.007	(0.007)	0.019	(0.016)	0.000	(0.000)	0.004	(0.002)	0.007	(0.003)
2.2 Courtship	0.000	(0.000)	0.005	(0.003)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.001	(0.001)
3. Resting, preening, miscellaneous	0.452	(0.055)	0.179	(0.069)	0.496	(0.113)	0.205	(0.074)	0.397	(0.101)	0.644	(0.072)	0.412	(0.035)
3.1 Resting (Roosting)	0.115	(0.044)	0.068	(0.051)	0.186	(0.082)	0.014	(0.012)	0.082	(0.053)	0.149	(0.077)	0.110	(0.024)
3.2 Maintenance/preening	0.267	(0.043)	0.067	(0.031)	0.248	(0.100)	0.142	(0.081)	0.301	(0.087)	0.430	(0.063)	0.246	(0.028)
3.3 Swash avoid	0.026	(0.010)	0.003	(0.002)	0.025	(0.018)	0.019	(0.012)	0.002	(0.002)	0.040	(0.016)	0.021	(0.005)
3.4 Locomotion, general	0.008	(0.003)	0.041	(0.018)	0.033	(0.019)	0.031	(0.020)	0.012	(0.007)	0.013	(0.009)	0.021	(0.005)
3.5 Vocalisation	0.000	(0.000)	0.000	(0.000)	0.005	(0.004)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.001	(0.001)
3.6 Defecate	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
3.7 Thermoregulation	0.036	(0.020)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.011	(0.010)	0.013	(0.007)
4.0 Disturbance-related behaviour	0.542	(0.054)	0.211	(0.079)	0.135	(0.048)	0.134	(0.056)	0.264	(0.101)	0.348	(0.071)	0.333	(0.033)
4.1 Vigilance and scan	0.417	(0.054)	0.130	(0.061)	0.058	(0.026)	0.116	(0.051)	0.257	(0.101)	0.265	(0.058)	0.252	(0.029)
4.2 Flush/escape – run	0.011	(0.006)	0.017	(0.013)	0.038	(0.015)	0.016	(0.008)	0.006	(0.004)	0.009	(0.006)	0.015	(0.004)
4.3 Flush/escape – flight	0.115	(0.046)	0.063	(0.062)	0.015	(0.012)	0.002	(0.002)	0.001	(0.001)	0.074	(0.060)	0.061	(0.021)
5. 'Kleptoparasitism'	0.000	(0.000)	0.104	(0.072)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.016	(0.012)
5.1 Waiting for food	0.000	(0.000)	0.024	(0.018)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.004	(0.003)
5.2 Scouting for food	0.000	(0.000)	0.051	(0.047)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.008	(0.008)
5.3 Feeding	0.000	(0.000)	0.029	(0.024)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)	0.005	(0.004)

triggers (e.g. cars, buses, trucks, motorbikes, aircraft, people, and dogs), and 4) four other disturbance triggers (raptors, high swash, birds other than raptors, unknown).

To avoid overfitting of models we first culled variables which were correlated with other variables, setting a criterion for multicollinearity of  $r \geq 0.45$  (Sokal and Rohlf, 1995; Zar, 1996). Individual variables retained from multicollinear sets were those that explained the highest proportion of variance in marginal tests of DISTLM. We also combined cars, buses, trucks, motorbikes and aircraft into a single category 'motorized craft' to reduce the number of predictors relative to sample size. For collinear environmental variables, we retained those that were measured on a ratio scale over those measured on an ordinal scale, circular scale, or based on visual estimates (e.g. temperature over percentage cloud cover, wind speed over wind direction). The final set of predictors used for DISTLM included six predictors: 1) air temperature, 2) wind speed, 3) shore width, 4) flock size, 5) number of motorized craft, and 6) number of people.

### 3. Results

#### 3.1. Characterisation of behaviours

Twenty-one types of behaviour were observed in five broad categories: 1) foraging, 2) inter- and intra-specific interactions, 3) resting, 4) disturbance-related behaviours, and 5) associations with fishermen and bait collectors (Table 1).

Across all species, birds allocated most of their time to resting and preening, which together accounted for 41% of time (Table 2). Preening was particularly prevalent in Little Terns (43% of all behaviour records). Behaviours related to disturbance (i.e. alerts and flushes) were the second-highest ranked activity in terms of

time allocated by individuals (Table 2). When averaged over all species, one-third of the birds' time budget was expended on activities directly related to disturbance; this was particularly high in Crested Terns which were alert 42% of the time and spent 12% of their time escaping from disturbance stimuli (Table 2). Similarly, Little Terns displayed vigilance behaviour (i.e. alert and scans) for 27% of the time and escaped from disturbance for close to one-tenth of their time (Table 2). Terns generally feed in and beyond the surf-zone, and hence foraging was only sporadically observed in these species. Conversely, Silver Gulls, Red-capped Plovers, Masked Lapwings and Australian Pied Oystercatchers spent up to 64% of their time foraging (Table 2). Most other forms of behaviour accounted for only small (<5%) proportions of time allocated by birds, the exception being Silver Gulls that were close to fishermen and bait collectors to obtain food scraps and discards (Table 2).

#### 3.2. Interspecific differences in behaviour

Bird species using exposed sandy beaches differed significantly in their multivariate behaviour spectra (PERMANOVA, Pseudo- $F = 5.86$ ,  $P < 0.001$ ), falling into two distinct groups: terns and other beach birds (Fig. 1). The clear separation between terns and other species in terms of their overall behavioural profile results from the different strategies in habitat use: terns use the ocean beaches primarily to rest and preen between foraging bouts in the surf-zone and beyond; the gull species and shorebirds we sampled also forage on the non-vegetated beach landwards of the swash zone. Accordingly, a substantially larger time allocation to foraging in non-terns, juxtaposed with a stronger prevalence of preening and roosting on the beach in terns, separate these two groups. While this separation is primarily a result of their different ecologies, it is also driven by considerably higher time investment responding to disturbance by

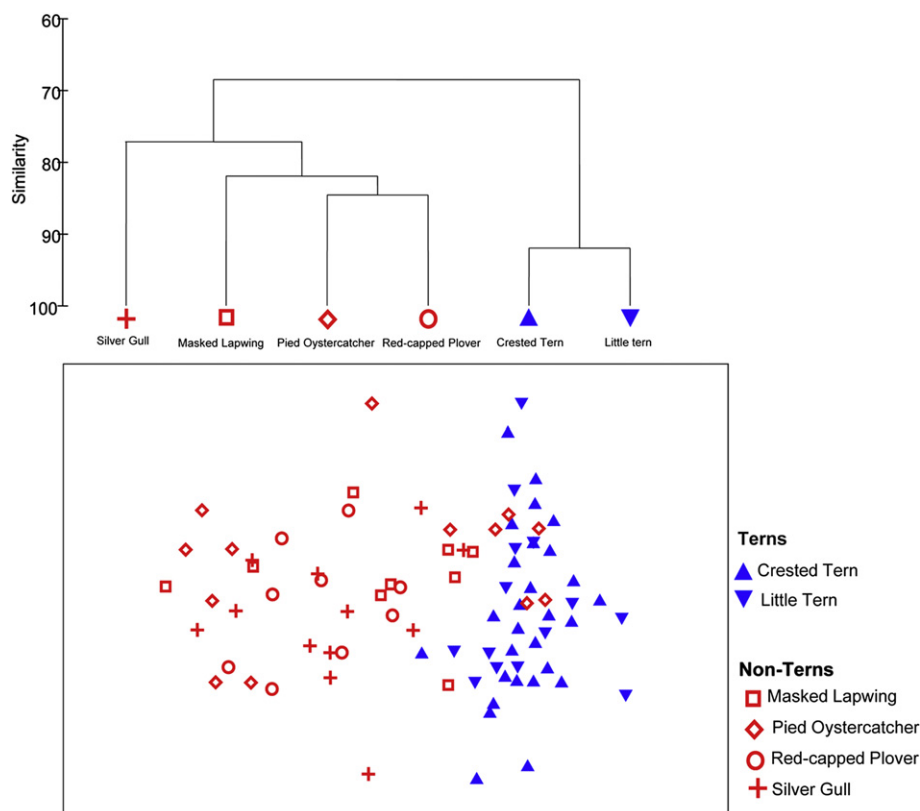


Fig. 1. Classification (cluster analysis, top) and ordination (NMDS, bottom) of multivariate behavioural profiles among six species of birds observed on open-coast sandy beaches.

terns (Table Appendix A1). Terns were observed to be alert for 37% of time compared with 12% in other species. Terns, who generally are lower on the beach near the swashline, also spent 10% of their time in flight after having been flushed, while escape flights accounted for 2% of time in other species (Table Appendix A1).

### 3.3. Disturbance to birds: characterising stimuli and responses

Disturbance to birds was considerable (Table 3). Birds were flushed in 55% of all focal observations (Table 3). Flushing was most prevalent in Little Terns (86%) and substantial in all other species, except Masked Lapwings which were not observed to flee from humans, cars or other triggers (Table 3). On average, 1.34 disturbance events were observed per 10 min of focal observation, ranging from 0.33 events in Red-capped Plovers to 2.32 in Little Terns (Table 3). It usually took less than 3 min after starting a focal observation for birds to take flight in response to a disturbance trigger, usually a car (Table 3).

Cars, all of them off-road capable four-wheel drives (4WDs), were the most commonly encountered human-related disturbance stimulus during the study (Table 4). Except for focal observations on Silver Gulls, cars driving along the beach were encountered by birds in over 80% of all focal bird observations on the shore (Table 4). All other anthropogenic disturbance stimuli were less frequent; these included trucks, buses, motorbikes, small aircraft landing on the beach, dogs and people (Table 4).

All human-associated disturbance stimuli had a similar likelihood of flushing birds (Table Appendix A2). After birds had encountered a motorized craft (i.e. car, truck, bus, aircraft), they took flight at least once in two-thirds of focal observation bouts (Table Appendix A2). This ‘flushing rate’ was similar to dogs (75%) and people (58%), but sample sizes are low for these types of stimuli as the most common type of human interaction with beach birds on these beaches involves vehicles.

Disturbed birds escaped by running or by taking flight (Figure Appendix A2). Both species of terns routinely escaped by taking flight (Figure Appendix A2). Crested Terns allocated 18-times more time to escapes involving flight than to running away from a threat; Little Terns invested 9 times more into flight response than into running in response to disturbance (Figure Appendix A2). Conversely, Silver Gulls moved away from threats mainly by running. Red-capped Plovers and Australian Pied Oystercatchers employed both strategies, with more time spent escaping on foot (Figure Appendix A2).

After birds had been flushed and had responded by either escape flights or runs, they resumed pre-disturbance behaviour, on average, within 16.6 s ( $se = 0.9$ ,  $n = 106$ ). Mean return times did not differ significantly between species ( $F_{3,99} = 1.79$ ,  $P = 0.15$ ). There was, however, a trend ( $F = 2.96$ ,  $P = 0.16$ ) for individuals to resume

their pre-disturbance behaviour quicker if they got flushed repeatedly within the same focal observation (Fig. 2). This relationship between the time it took for birds to resume pre-disturbance behaviour and the number of flush events was pronounced for Australian Pied Oystercatchers ( $r = -0.99$ ,  $P = 0.01$ ) and Silver Gulls ( $r = -0.89$ ,  $P = 0.04$ ), but weak for the two species of terns (Crested Tern:  $r = -0.35$ ,  $P = 0.49$ ; Little Tern:  $r = -0.49$ ,  $P = 0.32$ ; Table Appendix A3).

### 3.4. Drivers of multivariate behavioural profiles

Modelling of the relationship between multivariate variation in behaviour and several potential predictors indicated that both environmental conditions and human triggers influenced how birds allocated time to different behaviour types (Table 5). The frequency of disturbance by cars, buses, trucks, motorbikes and aircraft shaped the overall behavioural spectrum of Crested Terns, Little Terns and Australian Pied Oystercatchers in concert with habitat properties (i.e. shore width), weather, and flock size. Terns spent less time roosting at higher temperatures (Fig. 3), and the time spent by birds on disturbance-related behaviours (i.e. vigilance, flush runs, escape flights) increased with greater numbers of motorized craft encountered by three of the species (Fig. 3).

## 4. Discussion

### 4.1. Impacts of vehicles on birds on beaches

Death caused by vehicles results from fatal collisions with post-fledging birds, and the crushing of eggs or flightless young (Buick and Paton, 1989; Melvin et al., 1994). In our study area, vehicle strikes with birds are not uncommon, particularly for Australian Pied Oystercatchers and Crested Terns (McFarland, 1993; Fisher et al., 1998). Optimal escape theory suggests that birds respond most readily and strongly to stimuli where the cost of non-response is particularly high (Ydenberg and Dill, 1986; Cooper and Frederick, 2007). On beaches with vehicle traffic birds must first and foremost avoid collisions with traffic: this would explain the high rates of vigilance we observed and the frequent occasions when roosting birds, especially terns, have to take flight to escape vehicles. These responses were, however, not always successful: we have encountered several bird carcasses in tyre ruts, apparently killed in collisions with vehicles (Fig. 4).

Apart from direct mortality, frequent disturbance by vehicles can also displace birds from their preferred feeding and roosting sites (Tarr et al., 2010; Meager et al., 2012). The position along the intertidal gradient where birds feed or roost is important in determining their susceptibility to vehicles. Traffic on exposed sandy beaches in the region is mostly concentrated on the wet part

**Table 3**  
Summary statistics of disturbance events measured by three complementary metrics: A – the frequency at which responses to disturbance stimuli (“disturbance events”) occurred across all focal observations, B – the rate at which responses were recorded per 10 min of focal observations, and C – the time it took for the first disturbance response to occur after focal observations had started.

Species	A – Frequency of encounters			B – Incident rate of disturbance		C – Time to first disturbance event	
	No. focal obs. (n)	No. focal obs. with disturb. events (n)	(%)	Mean no. responses per 10 min (n)	(se)	Mean lag (s)	(se)
<i>Charadrius ruficapillus</i> (Red-capped Plover)	9	2	(22%)	0.33	(0.24)	145	(95)
<i>Haematopus longirostris</i> (Australian Pied Oystercatcher)	13	9	(69%)	1.63	(0.41)	114	(56)
<i>Chroicocephalus novaehollandiae</i> (Silver Gull)	15	7	(47%)	0.93	(0.39)	251	(76)
<i>Sternula albifrons</i> (Little Tern)	14	12	(86%)	2.32	(0.47)	181	(43)
<i>Thalasseus bergii</i> (Crested Tern)	29	19	(66%)	1.69	(0.56)	191	(31)
<i>Vanellus miles</i> (Masked Lapwing)	9	0	–	–	–	–	–
All Species	89	49	(55%)	1.34	(0.23)	181	(22)

**Table 4**

Frequency of occurrence of human-related disturbance stimuli during focal bird observations on open-coast sandy shores for six common bird species investigated in this study.

Species	Cars	Trucks	Buses	Motor bikes	Aircraft	Dogs	People
<i>Charadrius ruficapillus</i> (Red-capped Plover)	●●●●	●	●●	—	—	—	—
<i>Haematopus longirostris</i> (Australian Pied Oystercatcher)	●●●●●	●	●	●	—	—	●
<i>Chroicocephalus novaehollandiae</i> (Silver Gull)	●●●	—	—	—	—	●	●●
<i>Sternula albifrons</i> (Little Tern)	●●●●●	●	●	—	●	—	●
<i>Thalasseus bergii</i> (Crested Tern)	●●●●	—	●	●	—	—	●
<i>Vanellus miles</i> (Masked Lapwing)	●●●●	●	—	—	—	—	—
All species	●●●●	●	●	●	●	●	●

● <20%; ●● 20–40%; ●●● 41–60%; ●●●● 61–80%; ●●●●● >81%.

of the beach, just upshore of the swashline, and vehicles ‘migrate’ up and down the beach-face with rising and falling tides (Schlacher and Thompson, 2007). Unfortunately, birds do the same. Terns usually roost in flocks near the swashline and oystercatchers and gulls forage mostly in the shallow swash or the wet sand above it (Fig. 4, unpubl. obs.); this places roosting and foraging birds in the path of vehicle traffic. The consequences of this ‘spatial overlap’ between vehicle traffic and shorebirds are frequent disturbance events and collisions between birds and cars (see also Fisher et al., 1998). Vehicles are also driven on the beach at night and this may be particularly problematic as birds are stunned by headlights and can be killed in this manner (unpubl. obs.).

Negative impacts from disturbance are amplified in situations where food sources for birds are low (Goss-Custard et al., 2006). On the beaches studied by us, high volumes of vehicle traffic have been linked to substantial reductions in the abundance and diversity of benthic invertebrates, the principal, or a major, component of the food of Australian Pied Oystercatchers, Silver Gulls and Red-capped Plovers (Schlacher et al., 2007a,b, 2008a,b; Schlacher and Morrison, 2008; Schlacher and Lucrezi, 2010a,b). Thus, the consequence of disturbance to shorebirds by motorized craft, the dominant disturbance trigger in this study, are potentially most severe in areas where recreational traffic also lowers resource levels for shorebirds by reducing the abundance and diversity of their invertebrate prey. Thus, vehicles produce strong cumulative impacts that are unlikely to be exhibited by other stimuli such as walkers.

Vehicles can significantly depress foraging rates of birds by decreasing the time birds spend foraging and increasing the time spent being vigilant or responding to disturbance stimuli (Stolen, 2003). The effects of vehicles on bird feeding can also be larger

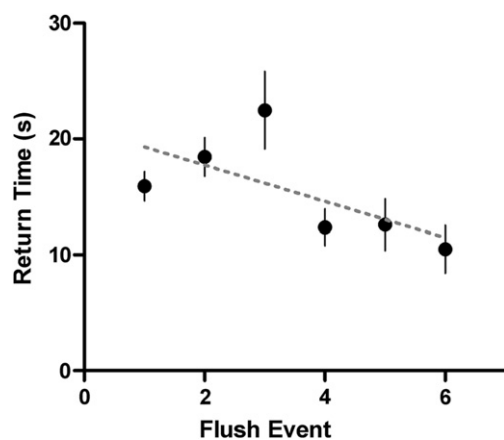
than those caused by people, presumably because birds perceive motorized vehicles as a bigger threat due to their larger size, speed and more noise (Maslo et al., 2012). Off-road vehicles also allow fishermen, other beach visitors and their pets (where allowed) to reach relatively remote beaches that would normally be too distant from access points to be easily reached on foot (Priskin, 2003). Thus, vehicles effectively extend the footprint of human disturbance into bird habitats that have traditionally offered a spatial refuge from human threats because of their isolation (Williams et al., 2004). This is the case for the beaches of Fraser Island studied by us where visitors in off-road vehicles reach nearly every exposed beach on the island, spreading human disturbance effects to over 100 km of the shoreline and its bird habitats (Thompson and Schlacher, 2008).

Our study did not test the possibility that sandy shores which are heavily disturbed by vehicles might represent an ecological trap, whereby apparently suitable habitat selected by birds might actually represent a population sink, perhaps through direct mortality, decreased fitness, or both (Schlaepfer et al., 2002). In particular, any scavenging bird attracted to human waste (e.g. bait) may inadvertently occur in an area where it risks death or frequent responses to disturbance, possibly to the extent that its lifetime fitness is reduced. Ecological traps are insidious because they can cause the extinction of populations over short time frames, and because they are difficult to detect and therefore difficult to manage (Battin, 2004). While our study did not address this possibility, further work may reveal that ecological traps occur on Australian beaches that are heavily modified or used by humans.

#### 4.2. Behavioural plasticity and possible maladaptations

Reactions by animals to disturbance stimuli carry fitness costs (Goss-Custard et al., 2006). In situations where individuals experience repeated non-lethal disturbance, the theoretical expectation is that individuals should habituate to lower the fitness costs incurred by their responses to disturbance, provided that the stimulus is benign (Whittaker and Knight, 1998). In shorebirds, there is evidence for moderated response frequencies or distances, for some but not all species, in areas that receive more visitors and their dogs (Baudains and Lloyd, 2007; Glover et al., 2011), perhaps as a result of learning on the part of the birds (but see Weston et al., 2012). However, no study reports the absence of responses among birds in environments heavily used by humans, suggesting that even if habituation does occur, it is limited. Moreover, our study shows that vehicles are not benign stimuli (Fig. 4), and so responses to disturbance remain adaptive, at least to some extent, and complete habituation would be maladaptive.

Adaptive responses increase the survival and reproductive success, maladaptive ones do the opposite (Sih et al., 2011). Behavioural strategies that minimize contact with humans, dogs and vehicles (e.g. escape, avoidance) are likely to improve

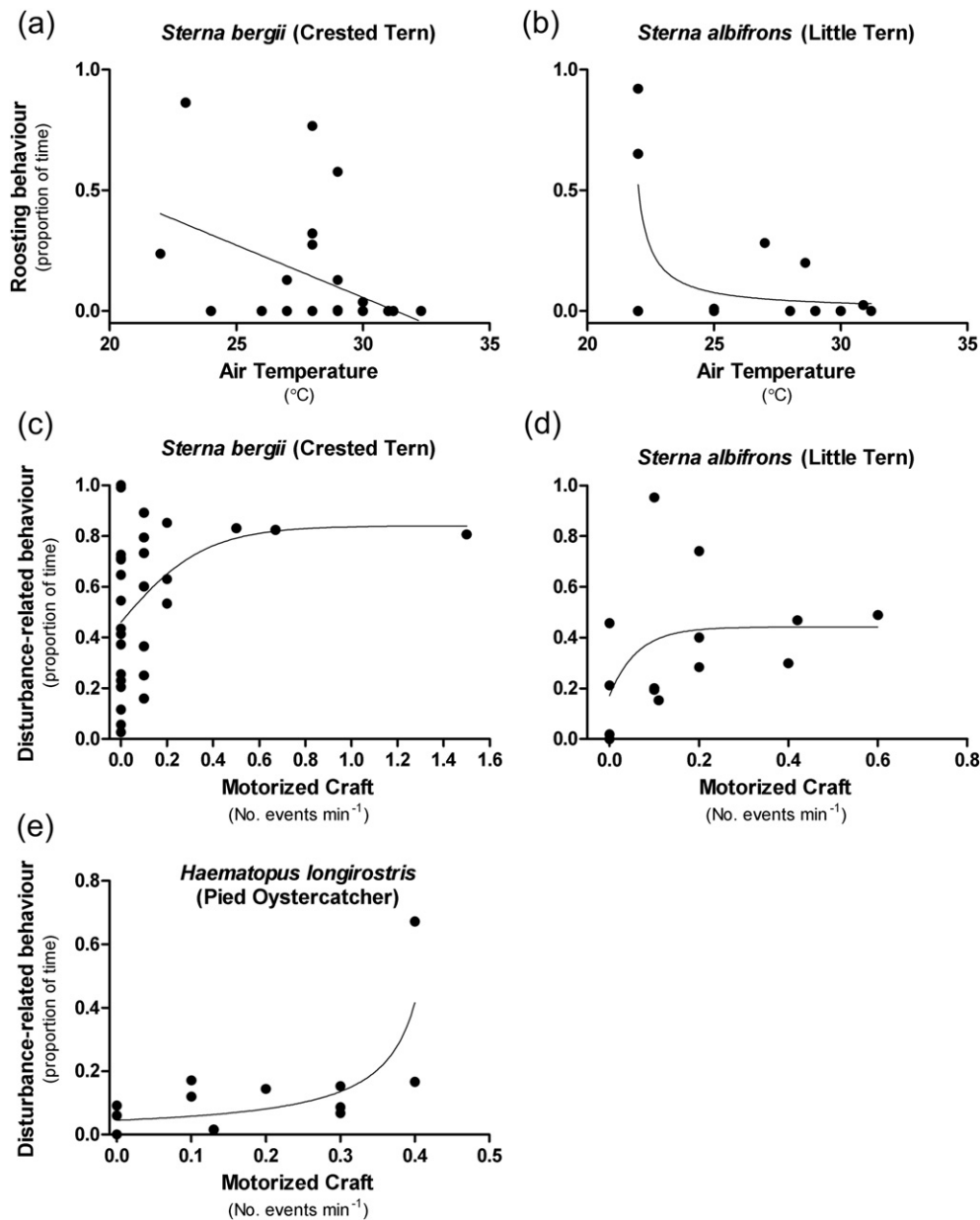


**Fig. 2.** Relationship between the time it took individuals to resume their pre-disturbance behaviour (return time, s, in seconds) and the number of the flush event during 10 minute-long focal observation bouts during which birds got repeatedly flushed.



**Table 5**  
Summary of variable weights (AICc w+) from distance-based linear models for each species, relating variation in the multivariate spectrum of behaviour to potential environmental predictors. Variables marked with \* are those included in the best model (using AICc as the criterion for model ranking) "na" denotes variables excluded from models because of zero variation for this predictor across all observational records for a species.

	<i>Thalasseus bergii</i> (Crested Tern)	<i>Sterna albifrons</i> (Little Tern)	<i>Haematopus longirostris</i> (Australian Pied Oystercatcher)	<i>Charadrius ruficapillus</i> (Red-capped Plover)	<i>Chroicocephalus novaehollandiae</i> (Silver Gull)
Temperature	0.55*	0.61*	0.31	0.31	0.33
Wind speed	0.34	0.18	0.37*	0.54*	0.31
Shore width	0.48	0.29	0.25	0.23	0.42*
Flock size	0.44	0.25	0.33	0.19	0.35
Motorized craft	0.32	0.33	0.26	0.14	na
People	0.35	0.22	na	na	0.02



**Fig. 3.** Relationship between the time allocated by birds to roosting/resting in relation to air temperature (a,b), and the time allocated to vigilance and flushes ('disturbance-related behaviour') in relation to the combined frequency of disturbance triggers by cars, buses, trucks, motorbikes and aircraft ('motorized craft') on open-coast beaches (c,d,e). Lines illustrate the general shape of the relations and represent best-fit (based on  $R^2$ ) linear and non-linear regression models for variables that we are included in the best (based on AICc) distance-based linear models (DISTLM, cf. Table 5).



**Fig. 4.** Examples of recreational beach traffic on beaches in the region (a), a flock of Crested Terns flushed by a car (b); badly injured (c) and dead Crested Tern inside tyre ruts on the beach (d), and dead Australian Pied Oystercatcher in tyre tracks (e,f). All photos: T.A. Schlacher.

individual fitness for birds on beaches in most cases. Conversely, maladaptive behaviours are possible. For example, we have frequently observed that Australian Pied Oystercatchers rest by crouching in the ruts made by vehicles in the sand. Presumably the birds roost in the ruts because they offer some shelter from wind, a thermoregulatory benefit. This behaviour of crouching down in ruts does, however, increase their risk of being run-over by vehicles, because it makes the birds less visible to drivers and because some drivers have a tendency to follow already formed tracks (Schlacher and Morrison, 2008) (Fig. 4). Such microhabitat preference may thus represent an ecological trap (sensu Schlaepfer et al., 2002).

Increased vigilance comes at the cost of other fitness-enhancing activities such as foraging (Sih et al., 2011) and is associated with internal responses such as increased hormonal and physiological activity (Weimerskirch et al., 2002; Walker et al., 2006). Because our study clearly shows large investments in vigilance following human disturbance, this behavioural change could be maladaptive (sensu Tuomainen and Candolin, 2011) if it does not carry survival or other benefits. A similar, energetically costly, response in the form of increased vigilance can occur in birds of prey on beaches. Raptors that scavenge on animal carcasses at the interface between the non-

vegetated part of the beach and the dunes are more vigilant on beaches with vehicle traffic and dogs (unpubl. obs.). Such vigilance is likely to be costly, as scavenging raptors are more likely to abandon carcasses and thereby decrease their food intake rates.

#### 4.3. Management and conservation aspects

The conservation status of two of the species investigated in this study (Little Tern and Australian Pied Oystercatcher) is formally recognized as 'endangered' under State law ([www.derm.qld.gov.au](http://www.derm.qld.gov.au); [www.environment.nsw.gov.au](http://www.environment.nsw.gov.au)). A fundamental step in designing conservation measures is to understand, in a robust and quantitative manner, the threats to target species. In this context, information on how human beach use alters the natural behaviour of birds is important. We show that both of these threatened species are affected by human disturbance: Little Terns spend, on average, 35% of their time on behaviours responding to disturbance, and Australian Pied Oystercatchers, 14% (Table 2).

Few beaches are currently managed specifically for wildlife or their biodiversity (Schlacher et al., 2006, 2007). There is, however, a fundamental social disconnect between traditional beach management that focuses on maximizing amenity potential, and

modern environmentally-focused aspirations of beach users. People want to have opportunities to view wildlife – values which are compromised by management that allows destructive and high-intensity use, such as the driving of vehicles on the shore: the majority (67%) of Australian beach users want vehicles banned from beaches and vehicle traffic deters many others (Maguire et al., 2011).

Management approaches to mitigate the negative effects of vehicles on wildlife encompass two basic techniques: 1) actions that disaggregate the cause of the impact (stressor) in space and time from the ecological features it impacts upon, 2) actions that reduce the magnitude and frequency of the stressor to environmentally acceptable limits (e.g. thresholds approach). Disaggregating stressors from wildlife requires the creation of spatial refuges (i.e. multiple use zoning that designates conservation areas from where vehicles are excluded (sensu Celliers et al., 2004) or designating temporary beach closures during times when wildlife is most vulnerable (e.g. Weston et al., 2011).

Beach closures have been shown to be highly effective in conserving birds on sandy shores (Williams et al., 2004), and invertebrates in sections closed to vehicles are also substantially more diverse and abundant (Schlacher et al., 2007a,b; Lucrezi and Schlacher, 2010; Schlacher and Lucrezi, 2010a,b). Beach closures in the region are, however, embryonic and small. On Fraser Island, 122 km (98%) of the 124 km long ocean-exposed sandy shoreline is open to vehicles. Similarly, in the Cooloola part of the Great Sandy National Park to the south of Fraser Island, vehicles are permitted to drive on 72 km (or 94%) of the 77 km long sandy shoreline, whereas traffic exclusion zones extend for only 5 km. Thus, motorized traffic is present along 94% of the 201 km long sandy shoreline in one of Australia's premier coastal conservation areas. A mere 7 km of beach are free from cars, but most of the vehicle exclusion zones are used as bathing reserves and dog exercise areas. Hence, current zonation offers virtually no protection to shorebirds and other wildlife. This lack of explicit management actions to protect beach ecosystems appears paradoxical given the region is a declared National Park (the Great Sandy National Park, [www.derm.gov.au](http://www.derm.gov.au)), and is listed as 'World Heritage' by UNESCO (<http://whc.unesco.org/en/list/630>).

Besides spatial zoning of uses, reducing the size of the stressor (i.e. lower traffic volumes) and removing the stressor (i.e. temporary beach closures) during ecologically sensitive periods (e.g. breeding periods of shorebirds) are complementary strategies to conserve beach wildlife. There are no limits on the number of vehicles allowed on beaches and the beaches are open to vehicles all year round, the only exception being temporary closures when cyclonic or other storm conditions present a safety risk.

Designing conservation measures that reduce the magnitude and frequency of the stressor to levels where ecological effects are no longer deemed 'significant' is more challenging for two main reasons: 1) the approach is based on an inherent requirement to define an 'acceptable' level of impact, a complex value judgement shaped by social and cultural norms (Stern, 2000), and 2) notwithstanding these complexities, there is very limited information on thresholds of impacts caused by vehicles to beach fauna; what is available shows that comparatively few vehicle passes (<100) produce measurable changes to the environment, and even fewer vehicles (<50 passes) cause significant mortalities and sublethal effects in beach invertebrates (Schlacher et al., 2008a,b; Sheppard et al., 2009). These figures on traffic volumes in relation to their impacts on beach invertebrates probably should not be extrapolated to set limits on the number of vehicles with regards to conserving birds. Rather, specific research is required to measure the shape of the response curve between traffic volume and its effects on birds (e.g. time spent escaping, reductions in reproductive

fitness, etc.). Such work should also examine the effects of variables that are, theoretically, amenable to be included in regulations aimed at reducing 'conflicts' between birds and vehicles: distance between vehicles and birds/flocks ('buffers' or 'set-backs'), speed of vehicle approaching roosting birds, noise level of vehicles, time of the day, tidal height, and beach width (see also Tarr et al., 2010; Glover et al., 2011).

Because perceptions, attitudes and actions of people are a major determinant of wildlife conservation outcomes, education and awareness training can, theoretically, make positive contributions to conservation (Williams et al., 2009), including beach birds (Dowling and Weston, 1999). Motorized recreation is, however, always and invariably harmful to beach and dune environments, impacting a broad range of ecosystem components (Hosier et al., 1981; Wolcott and Wolcott, 1984; Groom et al., 2007; Schlacher and Lucrezi, 2010a,b). It is therefore doubtful whether driver education can make a meaningful contribution to lowering the large and widespread impacts that vehicles cause on habitats, species and ecological assemblages on beaches (Schlacher and Thompson, 2008). It is also untested whether there are real conservation outcomes of driver education campaigns. At worst, brief information and training sessions may be misguided, factitious, and counter-productive to conservation by imparting a sense of 'justification' or absolution for driving cars on beaches when in reality the practice is never defensible on environmental grounds.

## Acknowledgements

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2012.12.016>.

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