Experimental evidence that vehicle traffic changes burrow architecture and reduces population density of ghost crabs on sandy beaches

T. A. Schlacher, S. Lucrezi

EXPERIMENTAL EVIDENCE THAT VEHICLE TRAFFIC CHANGES BURROW ARCHITECTURE AND REDUCES POPULATION DENSITY OF GHOST CRABS ON SANDY BEACHES

T. A. SCHLACHER [*], *S. LUCREZI*

Faculty of Science, University of the Sunshine Coast, Maroochydore DC, Q-4558, Australia
* Corresponding author: tschlach@usc.edu.au

RECREATIONAL ECOLOGY
ORV IMPACTS
OCYPODE
ECOLOGICAL INDICATORS
PULSE DISTURBANCE

ABSTRACT. – Driving of off-road vehicles on beaches and coastal dunes is part of the recreational activity spectrum in many coastal areas. Although this practice can cause environmental harm, controlled experiments to test specific ecological impacts of vehicles are rare on high-energy shores. Here we use an experimental approach, where sections of a beach were repeatedly driven over by a vehicle, to demonstrate effects on ghost crabs (Genus *Ocypode*) inhabiting a beach in eastern Australia. Vehicle traffic caused a significant reduction in crab burrow density by 66 % and the remaining burrows were smaller by 22 %, suggesting impacts on both population size and structure. Crabs also responded behaviourally to vehicle disturbance by altering their burrow architecture to simpler and deeper forms. Experimental data from this study not only add to a growing body of evidence highlighting deleterious environmental effects resulting from recreational vehicle use, but clearly demonstrate that environmental harm is a direct and undisputable consequence of vehicle traffic on beaches. This brings into focus the need to implement visitor management strategies that meet conservation targets without dismissing the social, cultural and economic dimensions of vehicle-based recreation.

INTRODUCTION

Driving of vehicles on beaches and dunes is today part of the recreational activity spectrum in many coastal areas and can, arguably, bring economic benefits for some local communities (Silberman & Andereck, 2006). However, the widespread practice of four-wheel driving along coastlines has repeatedly raised concerns about its environmental impacts (Hosier 1980, Wolcott & Wolcott 1984, Priskin, 2003a, Williams *et al.* 2004, Moss & McPhee 2006, Thompson & Schlacher 2008, Sheppard *et al.* 2009).

Ghost crabs of the genus *Ocypode* are semi-terrestrial animals, being generally widespread and abundant on tropical and sub-tropical beaches and coastal dunes. Ghost crabs have a semi-fossorial life habit, excavating extensive burrows, where they spend most of the day, switching to surface activity at night (Barrass 1963, Lucrezi *et al.* 2009a). Burrows provide shelter against predators, extreme weather conditions, co-specifics, and incoming tides; they are also critical for successful courtship, mating, egg development, and moulting (Vannini 1980, Schober & Christy 1993, Chan *et al.* 2006). Ghost crabs are often the top invertebrate predator on beaches, but their diet is equally catholic, ranging from scavenging on wreck to active predation on turtle and bird hatchlings (Wolcott 1978, Christoffers 1986)

Ghost crabs (Genus *Ocypode*) are amongst the invertebrates most heavily affected by vehicles, because their distribution overlaps with traffic (Schlacher & Thompson 2007), and because the crabs get crushed by cars both inside their burrows and while active on the beach surface (Schlacher *et al.* 2007b). In fact, ghost crabs have been shown to be ecological indicators of vehicle impacts on sandy beaches and coastal dunes, based on reductions in their density in areas open to traffic (Steiner & Leatherman 1981, Wolcott & Wolcott 1984, Moss & McPhee 2006, Foster-Smith *et al.* 2007, Hobbs *et al.* 2008).

Evidence for negative ecological impacts by vehicles on beach invertebrates is conventionally based on 'compare and contrast' designs, testing for differences in abundance between beaches of different traffic intensity (Moss & McPhee 2006, Schlacher *et al.* 2008a). While such mensurative experiments (*sensu* Hurlbert 1984) are illustrative of changes linked to vehicle traffic at specific beach locations, robust demonstration of environmental harm requires controlled experiments, where the putative agent of change can be isolated from potentially confounding drivers (Underwood 1997). Consequently, the chief objectives of this study was to test whether experimentally-controlled vehicle traffic on a sandy beach (1) leads to significant reductions in the density of ghost crabs, and (2) results in changes to the architecture of the crabs' burrows.

MATERIALS AND METHODS

Study area: North Stradbroke Island is a barrier island forming the eastern border of Moreton Bay (Fig. 1). The island is a popular tourist destination: most visitors come to the ocean-exposed sandy beaches where recreational driving of off-road
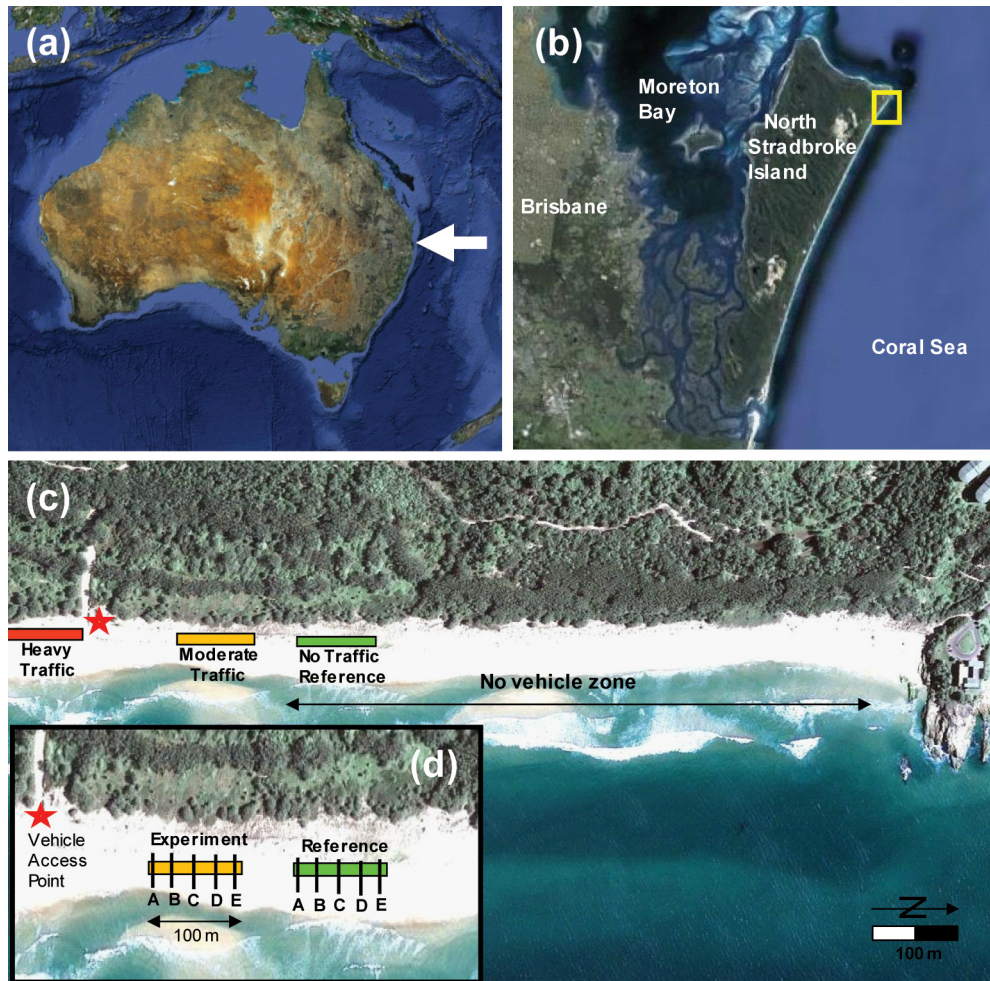
Fig. 1. – Location of the study site in eastern Australia (a), the northernmost part of the ocean-exposed Main Beach on North Strad-broke Island (b). Crab burrows were surveyed in three zones differing in vehicle traffic intensity from heavy (south of the access point marked with a star) to moderate and nil north of the access corridor cut through the dunes (c). Experimental vehicle passes were applied to a 100 x 2 m strip in the moderate traffic zone which formed the experimental site (d).

vehicles (ORVs) on the beaches causes considerable traffic (Schlacher & Morrison 2008). The number of cars driving on the island's eastern beaches can exceed 500 vehicles per day during peak tourist times (Schlacher *et al*. 2007b, Schlacher & Thompson 2008).

Vehicles enter the beach via designated access points, and most traffic occurs on the middle and upper shore above the effluent line (Schlacher & Thompson 2007). All 34 km of Main Beach are open to vehicle traffic, except for a 600 m section at the northernmost part of the beach; this vehicle exclusion zone was designated as the '*No traffic zone*' for the purpose of this study (Fig. 1). All vehicles access the beach via a corridor cut through the dunes and most cars then head south, with much fewer cars turning north. Therefore, the southern section was treated as the '*heavy traffic zone*' (Fig. 1). Some traffic is also present north of the access point in the area of the beach separat-ing the exclusion zone from the heavy traffic zone: this area was referred to as the '*moderate traffic zone*' (Fig. 1).

Experimental design for vehicle effects on burrow dimen-sions and crab density: In each of the three traffic zones, bur-

row casts were made in a 100 m long and 2 m wide strip, run-ning parallel to the base of the dunes. Casting occurred over three days before (29-31 Jan. 2009) and after (4-6 Feb. 2009) the experimental application of vehicle passes in the moderate traffic zone (see below). Casts were made of every burrow in the experimental 100 x 2 m strips in each of the three zones by pouring a mix of Cornice Cement (Gyprock[tm]) and water into the burrow opening. Cornice Cement was chosen because it is a fast-setting and non-toxic type of plaster. The mix was prepared by adding 1 kg of plaster to 2 liters of freshwater until a smooth blend was obtained.

After the plaster had set (approximately 30 min), the casts were dug out by carefully removing the sediment around them by hand, or with a small trowel. After measuring their depth, casts were labeled and taken back to the laboratory. In the labo-ratory, each cast was photographed and the following measure-ments were made: shape (Y, U, I, J, Spiral, Multi-branched), length and diameter of the main shaft, diameter of the opening (taken as the width of the main shaft ca. 1 cm below the sur-face), angle of inclination, and weight (proxy for volume); diameter measurements were made at the widest and narrowest
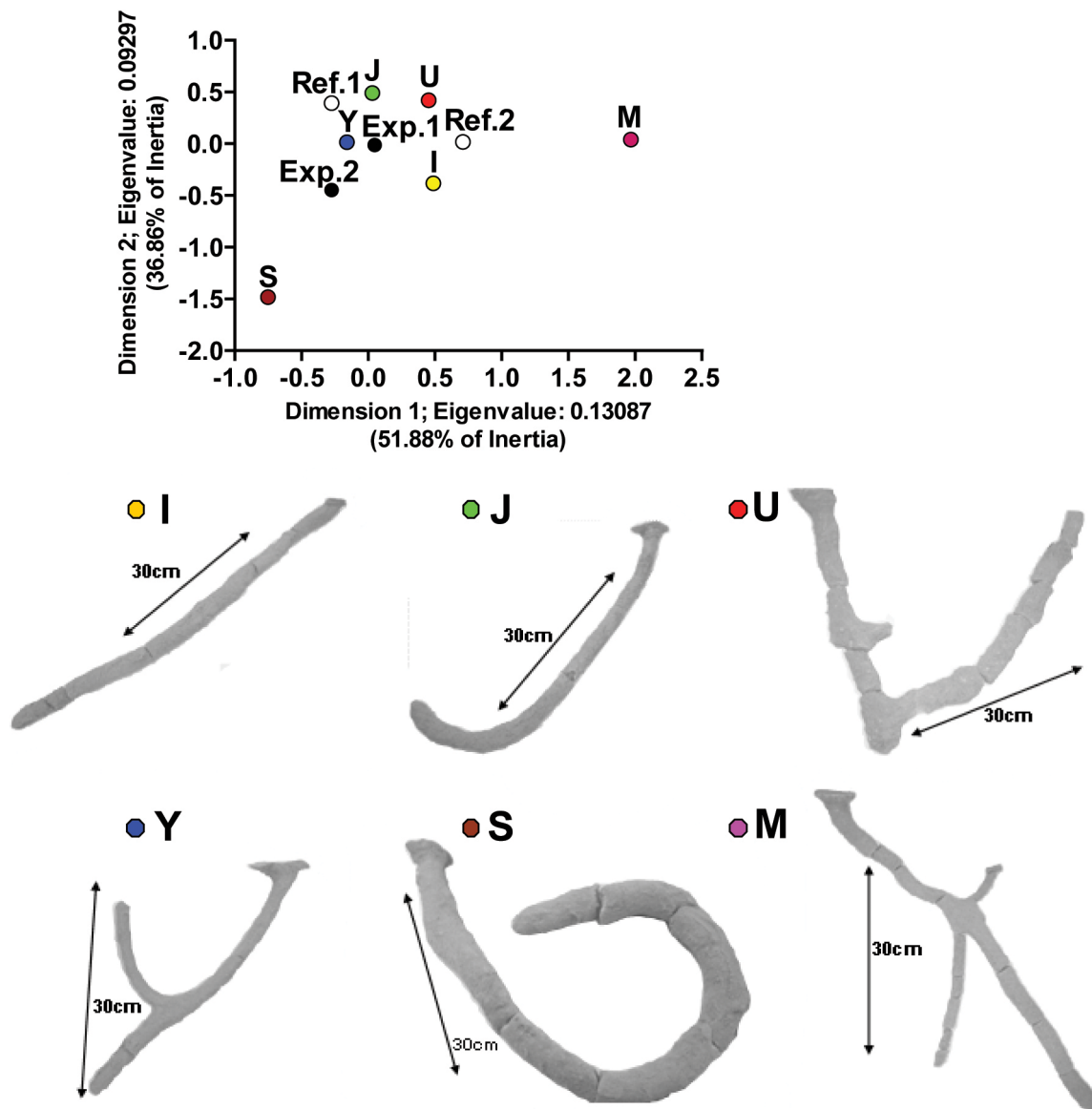
Fig. 2. – Correspondence Analysis (top panel) of the distribution of frequencies of ghost crab burrow shapes (I, M, J, Y, U, S) in the experimental (Exp.) and reference site (Ref.) before (Ref.1, Exp.1) and after (Ref.2, Exp.2) the experimental application of vehicle impacts. Middle and bottom panels are illustrations of different burrow shapes (I, J, U, Y, S, M), where letter symbols match those in the correspondence analysis above.

part (excluding chambers) and the mean value was used in subsequent analysis.

Counts of burrow openings were made in each traffic zone at sunrise on six days in the austral summer of 2009 (31st January, 1st, 3rd, 4th, 5th, 6th February). Burrow counts were made in 100 contiguous quadrats (2 x 1 m) laid in a line along the beach 3 m seawards from the base of the dune. Counts were followed by a series of vehicle passes in the moderate traffic zone, resulting in a pulsed impact (*sensu* Glasby & Underwood 1996): 20 vehicle passes after the first burrow count on day 1, 6 after the second, 7 after the third, 7 after the fourth, and 12 after the fifth. The number of passes was adjusted to limit environmental damage to a reasonable degree of physical disturbance of the beach surface, which was evident as deep (~20 cm) ruts that covered most of the experimental area. The total number of experimental vehicle

passes done during this study is well below normal traffic levels during peak holiday periods (Schlacher & Thompson, 2007). The passes were performed with a Toyota Hilux (weight 1200 kg, tyre width: 20.5 cm) which is one of the most common vehicle types on eastern Australian beaches. No experimental traffic was applied to the vehicle exclusion zone to the north, or the heavy traffic zone to the south which continued to receive normal beach traffic (Fig. 1). The potential for recovery of ghost crab populations following heavy vehicle traffic was gauged by conducting burrow counts one week after the last experimental vehicle pass on two consecutive days (11th and 12th February. 2009).

After the last series of experimental vehicle passes in the moderate traffic zone, and following the sixth burrow count, each area where the counts had been made was divided into five transects (A-E) spaced 25 m apart along the shore (Fig. 1).

Table I. – Distribution of burrow shapes in three beach sections differing in traffic intensity, before (Time 1) and after (Time 2) the experimental application of additional vehicle passes in the moderate traffic zone.

Burrow Shape	Time 1: before vehicle impact						Time 2: after vehicle impact					
	Heavy Traffic		Moderate Traffic		No Traffic		Heavy Traffic		Moderate Traffic		No Traffic	
Y	15	(44%)	22	(65%)	26	(76%)	5	(29%)	21	(75%)	10	(48%)
I	18	(53%)	7	(21%)	0	(0%)	9	(53%)	4	(14%)	5	(24%)
U	0	(0%)	1	(3%)	1	(3%)	0	(0%)	0	(0%)	1	(5%)
J	1	(3%)	4	(12%)	7	(21%)	2	(12%)	1	(4%)	3	(14%)
M	0	(0%)	0	(0%)	0	(0%)	1	(6%)	0	(0%)	2	(10%)
S	0	(0%)	0	(0%)	0	(0%)	0	(0%)	2	(7%)	0	(0%)
Total	34		34		34		17		28		21	

Table II. – Summary of general linear model (Factorial ANOVA) contrasting dimensions of ghost crab burrows between different traffic zones (no vehicle traffic, moderate traffic, and heavy traffic) before and after the experimental application of vehicle passes in the moderate traffic zone (experimental site). Values of burrow diameter (cm) and weight (g) were log-transformed and values of angle of inclination (°) square-root transformed. Significant results are bolded. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Source of variation	Df	Depth (cm)		Length (cm)		Diameter (cm)		Weight (g)		Angle of inclination (°)	
		MS	F	MS	F	MS	F	MS	F	MS	F
Traffic Zone	2	3098.3	**3.96***	6242.8	**3.81***	0.01	0.01	3.63	**3.84***	9.95	**3.56 ***
Time	1	786.7	1.01	2083.2	1.27	0.08	0.87	0.72	0.76	28.20	**10.09 ***
Zone x Time	2	2258.2	2.88	3539.4	2.16	0.13	1.39	2.43	2.58	25.16	**9.00***
Error	162	782.7		1639.8		0.09		0.94		2.79	

Table III. – Comparison of ghost crab burrow dimensions between different beach zones (no vehicle traffic, moderate traffic, and heavy traffic) before (Time 1) and after (Time 2) the experimental application of vehicle passes in the moderate traffic zone (experimental site).

Vehicle use zone	Time	Vertical height (c)		Length (cm)		Diameter (cm)		Weight (g)		Angle of inclination (°)	
		N	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE
Heavy Traffic	1	34	39.35	5.85	57.72	8.76	2.81	0.13	645.76	106.74	23.79	2.21
Heavy Traffic	2	17	25.47	5.74	33.94	7.48	2.43	0.19	333.33	86.83	7.06	1.71
Moderate Traffic	1	34	42.07	4.35	62.97	7.00	2.57	0.13	638.57	100.85	22.26	2.03
Moderate Traffic	2	28	52.11	4.68	72.03	5.55	2.66	0.16	734.00	118.38	15.29	1.83
No Traffic	1	34	41.60	5.32	59.26	6.75	2.60	0.13	514.29	78.40	19.00	2.05
No Traffic	2	21	31.99	4.86	52.09	9.13	2.58	0.16	578.16	117.68	24.76	3.08

Each transect extended from the base of the dunes to the low water mark, and was divided into adjacent plots, 2 m long and 1 m across. For every plot, the number of active ghost crab burrow openings, their diameter, and their position with respect to the base of the foredune and relative to the band of tyre tracks (above, in, and below) was recorded to test for the effect of vehicle traffic on the across-shore distribution pattern of ghost crabs.

Only 'active' burrow openings were counted. Active burrows were recognised by either the presence of fresh tracks emanat- ing from the opening, or evidence of recent re-working of the burrows visible as small mounds of excavated sediment next to the entrance, or both. Two species of ghost crabs, *Ocypode ceratophthalma* and *Ocypode cordimana* occur on the beach, but their burrow openings cannot be distinguished with confidence. We therefore report all burrow counts at the genus level.

Data analysis: Correspondence Analysis was used to compare the distribution of different burrow shapes amongst beach zones before and after the experimental vehicle passes. Variation

Table IV. – Summary results of GLM (General Linear Model) contrasting burrow counts between the experimental and reference area during and after the application of vehicle passes. Significant results are bolded.

Source	df	SS	MS	F Value	P
Traffic Zone	1	1.488	1.488	**7.79**	0.0315
Time	1	0.172	0.171	0.90	0.3796
Time x Zone	1	1.744	1.744	**9.13**	0.0233
Error	6	1.146	0.190		

in burrow dimensions (weight, length, height, diameter, angle) and the density and diameter of burrow openings were analyzed with a General Linear Model (GLM) containing the fixed factors 'Beach Traffic Zone' (heavy, moderate, none) and 'Time' in relation to experimental application of vehicle passes (before *vs.* after) followed by Tukey HSD post-hoc tests (Zar 1996, Underwood 1997).

RESULTS

Burrows resembled the letters I, Y, J, U, M (multi-branched), and S (spiral). In the two beach sections with vehicle traffic, most burrows were of the Y shape (29-75 %) and the simpler I shape (14-53 %; Table I). J-shaped burrows were most abundant in the no-traffic zone where they comprised up to 21 % of all burrows compared to fewer burrows of this shape in vehicle-impacted zones (Table I). More complex burrow shapes (U, M, S) were rare in all sections during both times. Experimental vehicle impacts shifted the frequency distribution in the impact zone towards fewer I-shaped burrows (T1: 21 %, T2:14 %) and fewer J-shaped ones (T1:12 %, T2: 4 %; Table I). Burrows became deeper, longer, wider and steeper in the impact zone after the experimental vehicle passes (Tables II & III).

Burrow densities varied significantly over time, linked to the experimental application of vehicle disturbance (Table IV; Fig. 3). After the initial 20 vehicle passes, the number of burrows in the experimental zone decreased by 40 %. A further 6 passes on the next day reduced the remaining burrows by 24 %, and an additional 7 passes caused a further reduction by 79 %; after the last set of experimental vehicle impacts (T2) mean burrow numbers were two-fifth of the pre-impact values at T1 (Fig 3a; Tukey HSD test P = 0.016). By the end of the study (T3), burrow numbers had recovered, but not to the pre-impact values (Fig. 3a). Experimental vehicle passes caused a significant decrease in the mean opening diameter of ghost crab burrows (Tukey HSD test P < 0.001; Fig. 3b), a pattern of temporal variation that was not recorded in the reference zone (Fig. 3b).

Vehicle traffic also changed the distribution of burrows across the beach (Fig. 4). After the experimental application of traffic, burrow density was significantly (paired t-test, t = 4.17, df = 7, P = 0.004) lower where tyre tracks

had substantially rutted the beach on the upper part of the shore in the experimental area (Fig. 4).

DISCUSSION

Burrow forms resembled the letters I, Y, J, U, M, and S. These forms represent different transitional stages of the same burrow-making process, with increasing complexity (Chakrabarti 1981). Burrow shapes also vary with crab age. Typical juvenile burrow shapes are I, J, U, and sometimes Y, while adult shapes include J, Y, and spiral burrows (S) or 'copulation burrows' (Vannini 1980, Chan *et al.* 2006). I-shaped burrows were dominant in the heavy traffic zone, whilst more complex burrow forms such as the Y- and U shapes were more abundant in the vehicle exclusion zone and moderate traffic zone. Interestingly, U-shaped burrows were no longer present at the experimental site after the application of vehicle passes. Due to the frequent physical disruption of the sediment, crabs inhabiting heavily-driven beaches may have to reg-
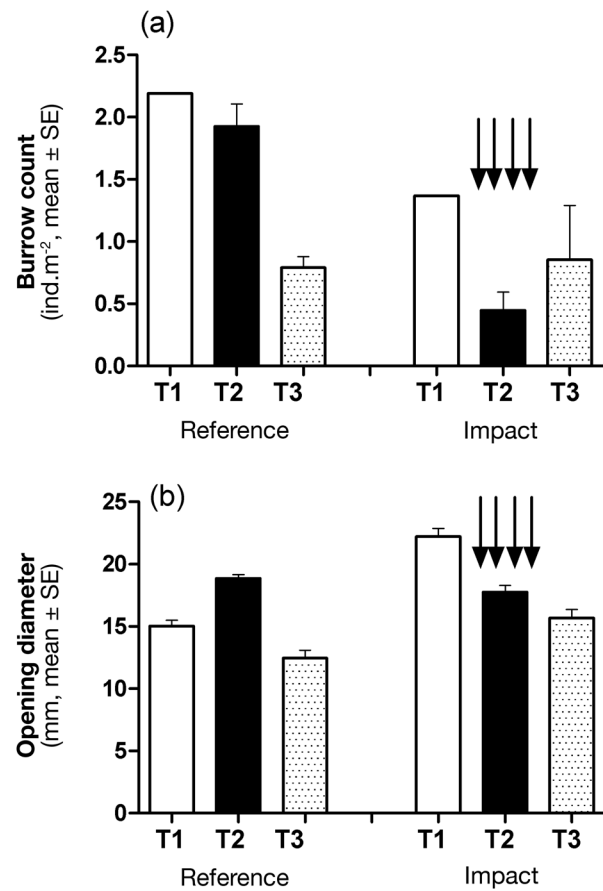

Fig. 3. – Comparison of burrow density (a) and burrow opening diameter (b) before (T1) during (T2) and one week after (T3) the experimental application of vehicle passes at the experimental site (impact) compared with the no-traffic zone (reference). Arrows illustrate the vehicle passes.
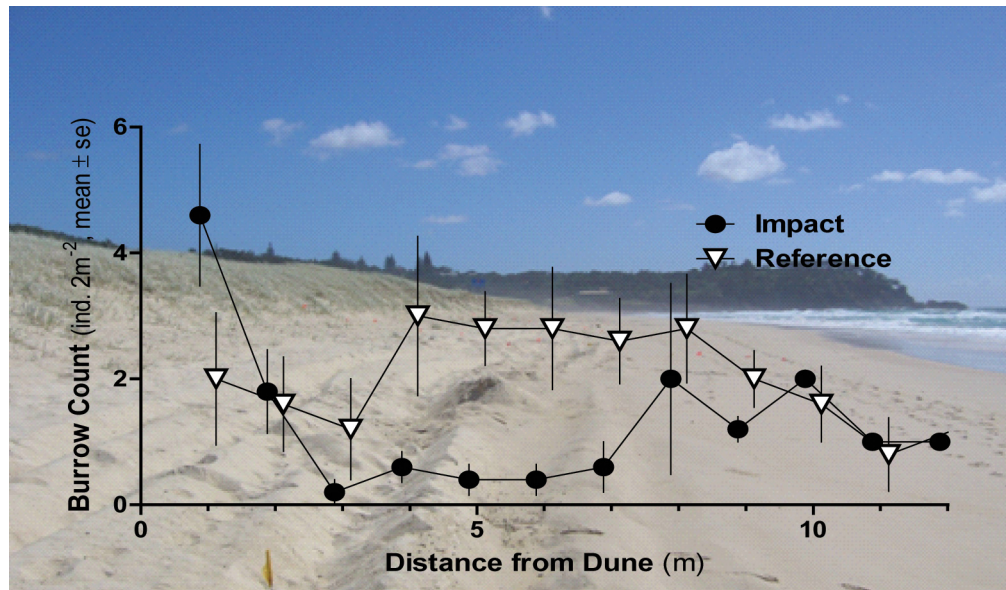
Fig. 4. – Distribution of ghost crab burrows across the shore from the base of the dunes to the lower intertidal, comparing the reference section (no vehicle impacts) and the experimental site (illustrated by tyre tracks in the background image).

ularly re-construct their burrows or repair them. Thus, the shape of crab burrows from impacted beaches is predicted to be simpler and rarely reaches more complex forms (Lucrezi & Schlacher 2010b); the lack of U-shaped burrows in the moderate traffic zone after the vehicle passes supports this interpretation (Table I).

Burrows became deeper and more vertical after the experimental vehicle passes. Also, burrows were substantially longer, deeper, and less inclined in the heavy traffic zone compared to the vehicle exclusion zone. Constructing burrows that reach deeper into the sediment could possibly be interpreted as a behavioural response to lower the risk of being crushed by vehicles. However, burrows only offer limited protection from crushing by vehicles: ghost crab mortality is inversely proportional to burrow depth, but individuals that construct burrows shallower than 25 cm are much less likely to survive vehicle passes (Schlacher et al. 2007b). Our finding of deeper and less-angled burrows appears to be a behavioral response to vehicle traffic, where crabs may react to vibrations from vehicles and shadows that mimic predators. Other behavioural responses to vehicle traffic are compressions in home range while the crabs are active on the beach surface at night (Schlacher & Lucrezi 2010).

On the beach where we conducted the experiment, the number of tyre tracks per linear meter of beach face usually ranges between 2 and 8: more than 50 % of the rutting has been recorded to be deeper than 5 cm and some ruts can be as deep as 28 cm; the total area of beach surface rutted can reach 90 % (Schlacher & Thompson 2008). In the present study, tyre tracks covered the major part of the shore in the moderate and heavy traffic zone, overlapping with the distribution of intertidal species such as ghost crabs. Our impact experiment clearly shows that vehicle

traffic can cause deep rutting of the beach and changes the across-shore distribution of ghost crabs (Fig. 4). Reductions in density are a clear consequence of vehicle traffic (Fig. 4), but additional consequences of distributional shifts at the population level cannot be excluded.

In the preset study, ghost crab burrow densities were lower after the experimental vehicle disturbance (Fig. 3a). The experiment was a typical example of a pulsed impact (Glasby & Underwood 1996, Lake 2000). It must, however, be stressed that traffic on this and other beaches in the region occurs on all days of the year (Schlacher et al. 2008a), and therefore is akin to a press disturbance complemented by pulsed impacts during peak holiday periods (Schlacher et al. 2007b). This combination of continuous vehicle traffic that is exacerbated by pulsed heavy traffic volumes can, theoretically, be expected to lead to sustained and widespread ecological impacts on beaches open to vehicles. In fact, on this beach and others in the region, there is mounting evidence that vehicle traffic is harmful to ghost crabs and other species of invertebrates (Moss & McPhee 2006, Schlacher et al. 2007b, Schlacher & Thompson 2008, Schlacher et al. 2008a, Schlacher et al. 2008b, Thompson & Schlacher 2008, Sheppard et al. 2009, Lucrezi & Schlacher 2010a, Schlacher & Lucrezi 2010, Walker & Schlacher 2010).

Burrow opening diameter is a good proxy for body size in ghost crabs (Lucrezi et al. 2009b) and it varied according to differences in traffic intensity. Ghost crab burrow size has previously been recorded not to differ significantly between areas varying in vehicle traffic (Maccarone & Mathews 2007). Conversely, vehicle traffic might affect the survival of larger crabs: in areas where traffic is chronic, the life expectancy of ghost crabs may be reduced and small ghost crabs may not mature (Steiner and Leather-

man 1981). In our experiment, mean burrow size dropped at the impact site (Fig. 3b), suggesting higher mortality or emigration of larger crabs following vehicle disturbance.

Impacts caused by four-wheel driving on sandy beaches present a complex and formidable challenge for environmental managers (Bird 1996). Part of this challenge arises from the multiple, often conflicting, demands that span environmental, social, economic, and cultural dimensions (Celliers *et al*. 2004). Physical impacts to beaches and dunes are readily seen as a form of environmental degradation (Priskin 2003b), whereas ecological effects may be less obvious to the public (Schlacher *et al*. 2006, Schlacher *et al*. 2007a). Experimental data from this study not only add to a growing body of evidence highlighting deleterious ecological effects associated with recreational vehicle use, but clearly demonstrate that environmental harm is a direct consequence of vehicle traffic on beaches and dunes. This brings into focus the need to implement visitor management strategies that meet conservation targets without dismissing the social, cultural and economic dimensions of vehicle-based recreation.

REFERENCES

Barrass R 1963. The burrows of *Ocypode ceratophthalmus* (Pallas) (Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island, Mocambique. *J Anim Ecol* 32: 73-85.

Bird ECF, 1996. Beach management. John Wiley, Chichester, New York.

Celliers L, Moffett T, James NC, Mann BQ 2004. A strategic assessment of recreational use areas for off-road vehicles in the coastal zone of KwaZulu-Natal, South Africa. *Ocean Coast Manage* 47: 123-140.

Chakrabarti A 1981. Burrow patterns of *Ocypode ceratophthalma* (Pallas) and their environmental significance. *J Paleont* 55: 431-441.

Chan BKK, Chan KKY, Leung PCM 2006. Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiol*. 560: 43-49

Christoffers EW 1986. Ecology of the ghost crab *Ocypode quadrata* (Fabricius) on Assateague Island, Maryland and the impacts of various human uses of the beach on their distribution and abundance. PhD thesis, Michigan State University, Ann Harbor, Michigan, USA.

Foster-Smith J, Birchenough AC, Evans SM, Prince J 2007. Human impacts on Cable Beach, Broome (Western Australia). *Coast Manage* 35: 181-194.

Glasby TM, Underwood AJ 1996. Sampling to differentiate between pulse and press perturbations. *Environ Monit Assess* 42: 241-252.

Hobbs CH, Landry CB, Perry JE 2008. Assessing anthropogenic and natural impacts on Ghost Crabs (*Ocypode quadrata*) at Cape Hatteras National Seashore, North Carolina. *J Coast Res* 24: 1450-1458.

Hosier PE 1980. Recreational off-road vehicle impacts in coastal North Carolina. *Carol Plan* 6: 34-40.

Hurlbert SH 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54: 187-211.

Lake PS 2000. Disturbance, patchiness, and diversity in streams. *J N Am Benthol Soc* 19: 573-592.

Lucrezi S, Schlacher TA, Robinson W 2009a. Human disturbance as a cause of bias in ecological indicators for sandy beaches: Experimental evidence for the effects of human trampling on ghost crabs (*Ocypode* spp.). *Ecol Ind* 9: 913-921.

Lucrezi S, Schlacher TA, Walker SJ 2009b. Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach. *Environ Monit Assess* 152: 413-424.

Lucrezi S, Schlacher TA 2010a. Impacts of off-road vehicles (ORVs) on burrow architecture of Ghost Crabs (Genus *Ocypode*) on sandy beaches. *Environ Manag* online first: DOI 10.1007/s00267-010-9491-5e.

Lucrezi S, Schlacher TA 2010b. Impacts of off-road vehicles (ORVs) on burrow architecture of Ghost Crabs (Genus *Ocypode*) on sandy beaches. *Environ Manag* 45: 1352–1362.

Maccarone AD, Mathews PL 2007. Effect of human disturbance on the abundance and spatial distribution of the Atlantic ghost crab (*Ocypode quadrata*) (Fabricius 1798) on a Texas beach. *Texas J Sci* 59: 51-60.

Moss D, McPhee DP 2006. The impacts of recreational four-wheel driving on the abundance of the ghost crab (*Ocypode cordimanus*) on a subtropical sandy beach in SE Queensland. *Coast Manage* 34: 133-140.

Priskin J 2003a. Physical impacts of four-wheel drive related tourism and recreation in a semi-arid, natural environment. *Ocean Coast Manage* 46: 127-155.

Priskin J 2003b. Tourist perceptions of degradation caused by coastal nature-based recreation. *Environ Manage* 32: 189-204.

Schlacher TA, Schoeman DS, Lastra M, Jones A, Dugan J, Scapini F, McLachlan A 2006. Neglected ecosystems bear the brunt of change. *Ethol Ecol Evol* 18: 349-351.

Schlacher TA, Dugan J, Schoeman DS, Lastra M, Jones A, Scapini F, McLachlan A, Defeo O 2007a. Sandy beaches at the brink. *Div Distr* 13: 556-560.

Schlacher TA, Thompson LMC 2007. Exposure of fauna to off-road vehicle (ORV) traffic on sandy beaches. *Coast Manage* 35: 567-583.

Schlacher TA, Thompson LMC, Price S 2007b. Vehicles versus conservation of invertebrates on sandy beaches: quantifying direct mortalities inflicted by off-road vehicles (ORVs) on ghost crabs. *Mar Ecol Evol Persp* 28: 354-367.

Schlacher TA, Morrison JM 2008. Beach disturbance caused by off-road vehicles (ORVs) on sandy shores: relationship with traffic volumes and a new method to quantify impacts using image-based data acquisition and analysis. *Mar Poll Bull* 56: 1646-1649.

Schlacher TA, Richardson D, McLean I 2008a. Impacts of off-road vehicles (ORVs) on macrobenthic assemblages on sandy beaches. *Environ Manage* 41: 878-892.

Schlacher TA, Thompson LMC 2008. Physical impacts caused by off-road vehicles (ORVs) to sandy beaches: spatial quantification of car tracks on an Australian barrier island. *J Coast Res* 224: 234-242.

Schlacher TA, Thompson LMC, Walker SJ 2008b. Mortalities caused by off-road vehicles (ORVs) to a key member of sandy beach assemblages, the surf clam *Donax deltoides*. *Hydrobiol* 610: 345-350.

Schlacher TA, Lucrezi S 2010. Compression of home ranges in ghost crabs on sandy beaches impacted by vehicle traffic. *Mar Biol* 157: 2467-2474.

Schober UM, Christy JH 1993. Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda: Ocypodidae): a possible role in courtship *Mar Biol* 116: 53-60.

Sheppard N, Pitt KA, Schlacher TA 2009. Sub-lethal effects of off-road vehicles (ORVs) on surf clams on sandy beaches. *J Exp Mar Biol Ecol* 380: 113-118.

Silberman J, Andereck KL 2006. Economic value of off-highway vehicle recreation. *J Leis Res* 38: 208-223.

Steiner AJ, Leatherman SP 1981. Recreational impacts on the distribution of Ghost Crabs (*Ocypode quadrata*). *Biol Cons* 20: 111-122.

Thompson LMC, Schlacher TA 2008. Physical damage to coastal foredunes and ecological impacts caused by vehicle tracks associated with beach camping on sandy shores: a case study from Fraser Island, Australia. *J Coast Cons* 12: 67-82.

Underwood AJ 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Vannini M 1980. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 27. Burrows and digging behaviour in *Ocypode* and other crabs (Crustacea, Brachyura). *Monit Zool Ital* Suppl XIII: 12-44.

Walker S, Schlacher TA in press. Impact of a pulse human disturbance experiment on macrofaunal assemblages on an Australian sandy beach. *J Coast Res* in press, accepted 06 Feb 2010.

Williams JA, Ward VL, Underhill LG 2004. Waders respond quickly and positively to the banning of off-road vehicles from beaches in South Africa. *Wader Study Group Bull* 104: 79-81.

Wolcott TG 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fab.) on an ocean beach: scavengers or predators? *J Exp Mar Biol Ecol* 31: 67-82.

Wolcott TG, Wolcott DL 1984. Impact of off-road vehicles on macroinvertebrates of a Mid-Atlantic beach. *Biol Cons* 29: 217-240.

Zar JH 1996. Biostatistical Analysis. Prentice Hall, Upper Saddle River.