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
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 separating 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 dimensions and crab density: In each of the three traffic zones, burrow casts were made in a 100 m long and 2 m wide strip, running 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™) 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 laboratory, each cast was photographed and the following measurements 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 surface), angle of inclination, and weight (proxy for volume); diameter measurements were made at the widest and narrowest
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).
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 emanating 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 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.

<table>
<thead>
<tr>
<th>Burrow Shape</th>
<th>Heavy Traffic</th>
<th>Moderate Traffic</th>
<th>No Traffic</th>
<th>Heavy Traffic</th>
<th>Moderate Traffic</th>
<th>No Traffic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y</td>
<td>15 (44%)</td>
<td>22 (65%)</td>
<td>26 (76%)</td>
<td>5 (29%)</td>
<td>21 (75%)</td>
<td>10 (48%)</td>
</tr>
<tr>
<td>I</td>
<td>18 (53%)</td>
<td>7 (21%)</td>
<td>0 (0%)</td>
<td>9 (53%)</td>
<td>4 (14%)</td>
<td>5 (24%)</td>
</tr>
<tr>
<td>U</td>
<td>0 (0%)</td>
<td>1 (3%)</td>
<td>1 (3%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>1 (5%)</td>
</tr>
<tr>
<td>J</td>
<td>1 (3%)</td>
<td>4 (12%)</td>
<td>7 (21%)</td>
<td>2 (12%)</td>
<td>1 (4%)</td>
<td>3 (14%)</td>
</tr>
<tr>
<td>M</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>1 (6%)</td>
<td>0 (0%)</td>
<td>2 (10%)</td>
</tr>
<tr>
<td>S</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
<td>2 (7%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>34</strong></td>
<td><strong>34</strong></td>
<td><strong>34</strong></td>
<td><strong>17</strong></td>
<td><strong>28</strong></td>
<td><strong>21</strong></td>
</tr>
</tbody>
</table>

### 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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Df</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Traffic Zone</td>
<td>2</td>
<td>3098.3</td>
<td>3.96*</td>
<td>6242.8</td>
<td>3.81*</td>
<td>0.01</td>
<td>0.01</td>
<td>3.63</td>
<td>3.84*</td>
<td>9.95</td>
<td>3.56*</td>
</tr>
<tr>
<td>Time</td>
<td>1</td>
<td>786.7</td>
<td>1.01</td>
<td>2083.2</td>
<td>1.27</td>
<td>0.08</td>
<td>0.87</td>
<td>0.72</td>
<td>0.76</td>
<td>28.20</td>
<td>10.09*</td>
</tr>
<tr>
<td>Zone x Time</td>
<td>2</td>
<td>2258.2</td>
<td>2.88</td>
<td>3539.4</td>
<td>2.16</td>
<td>0.13</td>
<td>1.39</td>
<td>2.43</td>
<td>2.58</td>
<td>25.16</td>
<td>9.00***</td>
</tr>
<tr>
<td>Error</td>
<td>162</td>
<td>782.7</td>
<td>1.01</td>
<td>1639.8</td>
<td>0.94</td>
<td>0.94</td>
<td>1.46</td>
<td>2.79</td>
<td>1.71</td>
<td>2.79</td>
<td>1.71</td>
</tr>
</tbody>
</table>

### 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).

<table>
<thead>
<tr>
<th>Vehicle use zone</th>
<th>Time</th>
<th>Vertical height (c)</th>
<th>Length (cm)</th>
<th>Diameter (cm)</th>
<th>Weight (g)</th>
<th>Angle of inclination (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>SE</td>
<td>x</td>
<td>SE</td>
<td>x</td>
<td>SE</td>
</tr>
<tr>
<td>Heavy Traffic</td>
<td>1</td>
<td>34</td>
<td>39.35</td>
<td>5.85</td>
<td>57.72</td>
<td>8.76</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>17</td>
<td>25.47</td>
<td>5.74</td>
<td>33.94</td>
<td>7.48</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>34</td>
<td>42.07</td>
<td>4.35</td>
<td>62.97</td>
<td>7.00</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>28</td>
<td>52.11</td>
<td>4.68</td>
<td>72.03</td>
<td>5.55</td>
</tr>
<tr>
<td>Moderate Traffic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>34</td>
<td>41.60</td>
<td>5.32</td>
<td>59.26</td>
<td>6.75</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>21</td>
<td>31.99</td>
<td>4.86</td>
<td>52.09</td>
<td>9.13</td>
</tr>
</tbody>
</table>

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.

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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-

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.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Traffic Zone</td>
<td>1</td>
<td>1.488</td>
<td>1.488</td>
<td>7.79</td>
<td>0.0315</td>
</tr>
<tr>
<td>Time</td>
<td>1</td>
<td>0.172</td>
<td>0.171</td>
<td>0.90</td>
<td>0.3796</td>
</tr>
<tr>
<td>Time x Zone</td>
<td>1</td>
<td>1.744</td>
<td>1.744</td>
<td>9.13</td>
<td>0.0233</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>1.146</td>
<td>0.190</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 present 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.

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