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ORIGINAL ARTICLE

Vehicles *versus* conservation of invertebrates on sandy beaches: mortalities inflicted by off-road vehicles on ghost crabs

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Abstract

Sandy beaches face increasing anthropogenic pressures, with vehicle traffic being ecologically highly harmful. Ghost crabs (Fam. Ocypodidae) are conspicuous on many beaches, and they have been used as a bio-monitoring tool to measure the ecological responses to human disturbance. However, the mechanisms causing declines in crab numbers are unknown, yet conservation must target the actual impact mechanisms. Therefore, we quantified the magnitude and mechanisms of off-road vehicle (ORV) impacts on ghost crabs, addressing three key questions: (i) Does abundance of ghost crabs respond to traffic intensity?; (ii) Can burrows protect crabs from vehicles? and (iii) Can mortalities caused by vehicles contribute to population declines? ORV-impacts were measured on North Stradbroke Island (Australia) for *Ocypode cordimanus* and *Ocypode ceratophthalma*. Crab densities were significantly lower in areas subjected to heavy beach traffic, suggesting direct crushing by vehicles. Burrows only partially protect crabs against cars: all individuals buried shallow (5 cm) are killed by 10 vehicle passes. Mortality declines with depth of burrows, but remains considerable (10–30% killed) at 20 cm and only those crabs buried at least 30 cm are not killed by ORVs: these 'deep-living' crabs represent about half of the population. After crabs emerge at dusk they are killed in large numbers on the beach surface. A single vehicle can crush up to 0.75% of the intertidal population. While conservation measures should primarily regulate night traffic, our results also emphasise that the fossorial life habits of sandy beach animals cannot off-set the impacts caused by ORVs.

Problem

Sandy beaches are the dominant type of shore globally (Bascom 1980). Sandy beaches are the coastal habitat with which most people interact directly, mainly for recreational purposes, and the human use of beaches is becoming more intense (Priskin 2003a). This escalating use of beaches is mainly driven by the rapid growth of coastal populations, coupled with increased availability of leisure time. For example, 85% of Australians live within 50 km from the coast and coastal populations are growing significantly faster than elsewhere (Australian Bureau of Statistics 2004). In economic terms, sandy beaches are amongst the most valuable natural assets, underpinning many coastal developments and related industries (Klein *et al.* 2004).

The intense anthropogenic pressures on the coastal strip frequently have negative environmental consequences for sandy beaches (Finkl & Krupa 2003). Impacts range from the widespread destruction of dunes for housing and infrastructure construction, changes to groundwater and sediment supply, shore armouring, to the harvesting of beach biota (Brown & McLachlan 2002; Schlacher *et al.* 2006). Ecological impacts caused by recreational activities are also emerging as significant issues. Trampling by pedestrians has large detrimental effects on dune vegetation (Liddle 1991) and may also damage invertebrates on the foreshore (Moffett *et al.* 1998).

The recreational activity that causes most environmental harm is driving of off-road vehicles (ORVs) on sandy beaches (Godfrey & Godfrey 1980). Beach driving is common in many countries around the world, including Australia, New Zealand, South Africa and the USA. In South-East Queensland (Australia), a number of beaches are subject to high volumes of ORV traffic, including Fraser Island, Noosa North Shore and North Stradbroke Island (Moss & McPhee 2006). People drive on beaches to reach preferred camping and fishing spots, access remote areas, launch boats, or simply for a change of scenery (Priskin 2003b). Environmental impacts caused by ORVs are numerous. ORVs change the physical properties and stability of dunes and beaches (Anders & Leatherman 1987; Kutiel *et al.* 1999; Priskin 2003b; Schlacher & Thompson in press-a), and they disturb, injure, or kill the vegetation and fauna (Godfrey & Godfrey 1980; van der Merwe & van der Merwe 1991; Watson *et al.* 1996).

Crabs of the genus *Ocypode* (Fam. Ocypodidae), commonly known as Ghost Crabs, are widespread and conspicuous inhabitants of tropical and sub-tropical sandy beaches worldwide (Jones 1972; Quijon *et al.* 2001). They are the top invertebrate predator living on beaches, are highly mobile, and they construct distinctive burrows (Barrass 1963). Ghost crabs are mainly active at night, spending much of the day inside their burrows (Hughes 1966).

Changes in ghost crab abundance have been employed as a bio-indicator for human disturbance on sandy beaches. Lower ghost crab numbers have been reported in areas affected by human trampling (Steiner & Leatherman 1981; Christoffers 1986; Neves & Bemvenuti 2006), ORVs (Wolcott & Wolcott 1984; Blankensteyn 2006; Moss & McPhee 2006), shore armouring (Barros 2001), as well as beach nourishment and bulldozing (Peterson *et al.* 2000). A recurring pattern is significant reductions in ghost crab abundance with increasing levels of human disturbance on beaches.

Despite a growing body of evidence that ghost crabs are negatively affected by human disturbance on sandy beaches, the actual mechanisms that cause the observed reductions in population size are usually not known. Presently, the use of ghost crabs as bio-indicators rests largely on spatial contrasts in burrow counts between areas that differ in the frequency or intensity of human impact (Barros 2001). Yet, in order to develop management measures aimed at protecting or restoring the ecological health of sandy beaches, identification of the mechanisms of impact is essential. Any management intervention will have to specifically regulate the processes that cause the impacts on the biota.

Decreases in ghost crab numbers on beaches subjected to ORV traffic can be caused by a range of impact mechanisms including: (i) direct crushing of individuals by cars (Wolcott & Wolcott 1984), (ii) changes to the habitat suitability, for example when cars loosen the sand which impedes burrow construction (Christoffers 1986), (iii) interference with reproduction and recruitment (Steiner & Leatherman 1981), (iv) reductions in food supplies through ORV-caused crushing of prey items (Wolcott 1978) and (v) light pollution (Bird *et al.* 2004). Direct crushing of ghost crabs has been assessed (Wolcott & Wolcott 1984), indicating that ghost crabs are largely protected from cars when inside their burrows during the day, but are being killed in large numbers when active on the beach surface at night.

On North Stradbroke Island where the present study was conducted, ghost crab numbers were found to be significantly reduced on beaches open to ORVs (Moss & McPhee 2006). Moss & McPhee (2006) suggest that this spatial pattern was because of direct mortality of crabs caused by vehicles driving on the beach at night, but this proposed impact mechanism remains untested.

Given that impacts of ORVs on the biota of sandy beaches are an environmental issue that has significant ecological as well as socio-economic implications (James 2000), beach management and conservation need to develop strategies that address this activity based on sound scientific evidence (Schlacher *et al.* 2006). To this end, the identification of the mechanisms of change is critical in order to efficiently focus any management interventions and conservation measures. Consequently, the chief objective of the present study was to assess the magnitude and mechanisms of direct impacts of ORVs on ghost crabs. Specifically, it aimed to: (i) determine whether the size of ghost crab populations responds to changes in the volumes of beach traffic, (ii) test whether burrows protect crabs from the direct physical impacts of vehicles and (iii) quantify mortality rates inflicted on surface-active ghost crabs by night traffic.

Material and Methods

Study sites

North Stradbroke Island is a barrier island located on the eastern side of Moreton Bay (Fig. 1). Because of the island's proximity to the major urban centre of Brisbane, it is a prime holiday destination used for a variety of recreational pursuits, including four-wheel driving on beaches, beach fishing and beach camping. Sandy beaches dominate the island's eastern side, and most of these beaches are open to ORVs (Carter 2005; Schlacher &

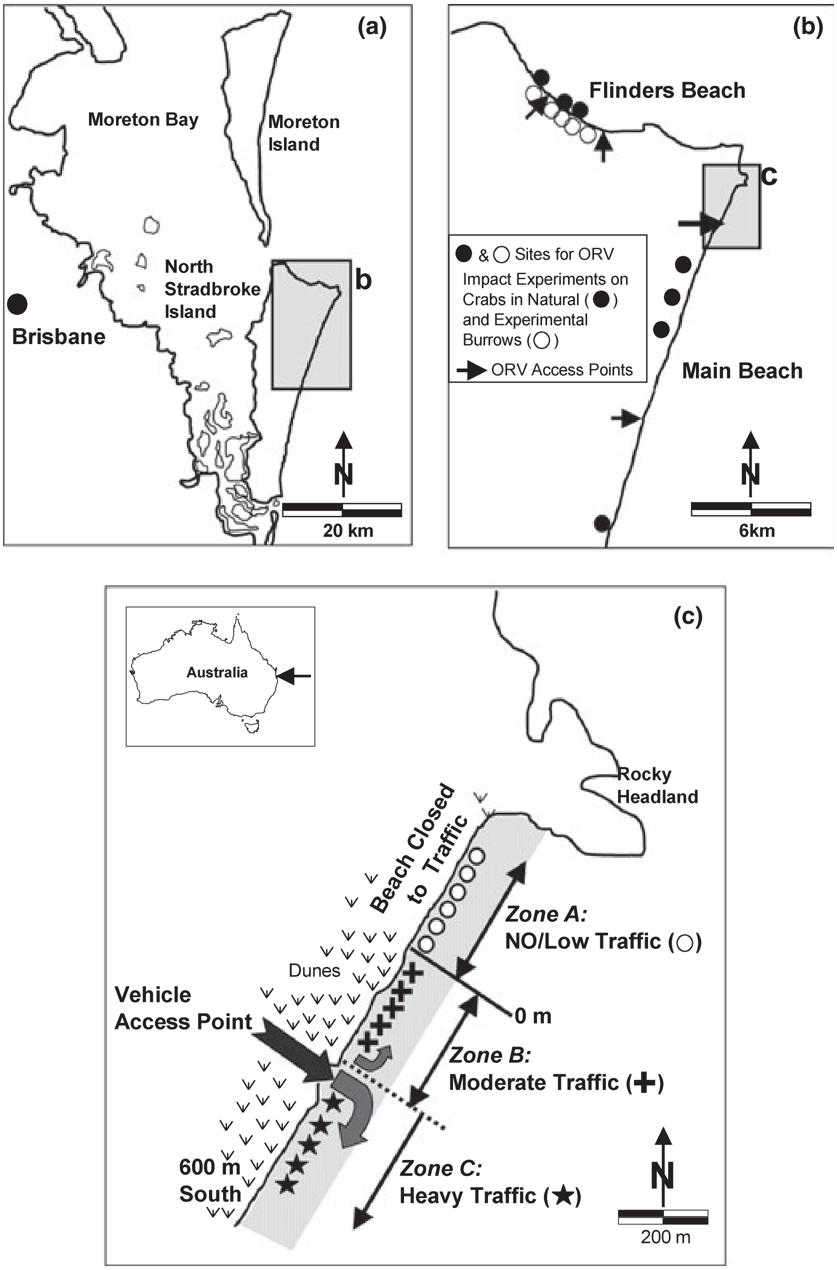

Fig. 1. Location of study sites on North Stradbroke Island, Australia (a). Sites where the experiments were conducted to determine mortality of crabs inside their natural burrows are shown by solid symbols, while simulated burrows that primarily tested the effect of depth on mortality caused by off-road vehicles are shown by open symbols (b). Panel (c) depicts the area on Main Beach where the response of crab density to traffic volumes was measured and where experiments on vehicle crushing of surface-active crabs at night took place.

Thompson in press-a). ORV traffic causes substantial changes to the physical environment of these beaches (Schlacher & Thompson in press-a). Large proportions (54–61%) of the beach face are covered by tyre tracks during peak periods, and the beach can become deeply rutted up to a depth of 28 cm, particularly in the area between the drift line and the foredune (Schlacher & Thompson in press-a).

Field work to determine the response of crab density to traffic volumes and the mortality rates of ghost crabs caused by vehicles was carried out on Main Beach and Flinders Beach (Fig. 1). Main beach is exposed to the predominant south-easterly swell. It is 50–70 m wide at low tide, with a mean sand grain size of 0.27–0.34 mm and a slope of 2.14°–2.70°. Flinders Beach is more sheltered, 50–80 m wide, with sands of 0.26–0.35 mm and a slope of 1.55°–2.83°. Both beaches are of the intermediate morphodynamic type with Beach Index (BI) values of 2.01–2.34 (Carter 2005; Schlacher & Thompson in press-a).

Beach traffic volumes

Traffic volumes on the island's beaches are considerable (Fig. 2). The local authority installed continuous traffic

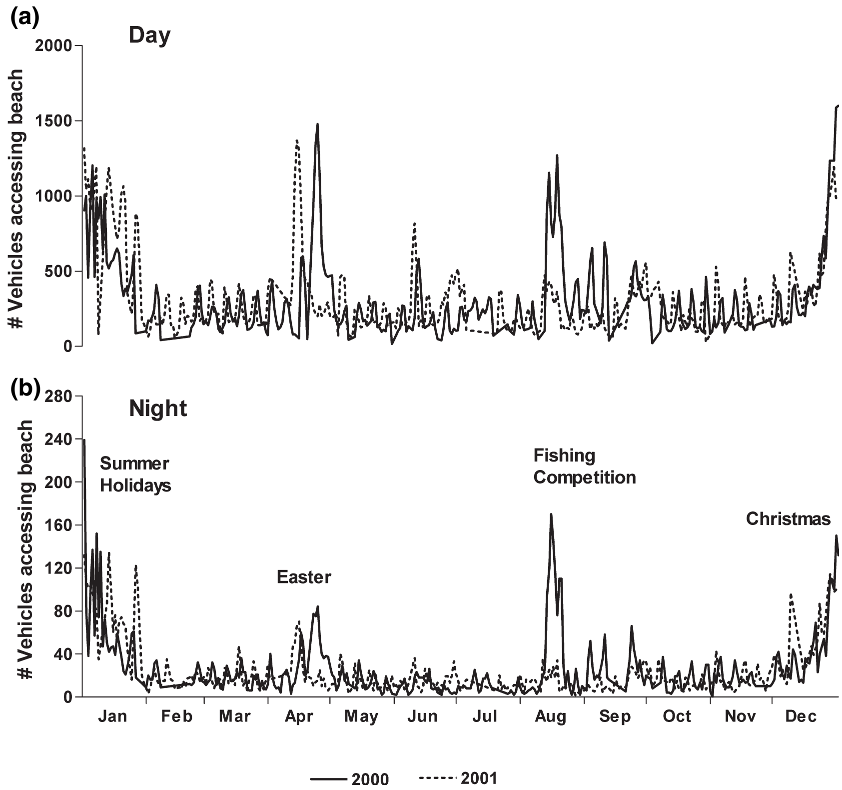

Fig. 2. Daily traffic volumes of off-road vehicles on Flinders Beach, North Stradbroke Island, Australia. Data source is automatic traffic counters that recorded vehicles accessing the beach at hourly intervals, with traffic occurring between 07:00 and 19:00 hours classified as day traffic (a) and cars entering the beach between 19:00 and 07:00 hours as night traffic (b).

recorders that counted all vehicles entering Flinders beach at daily intervals from 1 April 1999 to 4 January 2003. These counts were made available to us and analysed for this study. The average number of vehicles entering Flinders Beach per day is 352, equating to 128,845 cars driving on the beach annually. Daily traffic volumes can reach up to 3168 vehicles during peak periods. ORV traffic occurs on the beaches throughout the year, peaking during holidays and fishing competitions (Fig. 2). Daily traffic volumes roughly double during weekends (mean: 449 cars day^{-1}, range: 79–2934) compared with weekdays (mean: 272 cars day^{-1}, range: 16–2392). Beach traffic is highest on weekends during peak periods (mean: 687 cars day^{-1}, range: 126–2934).

About 8% of all beach traffic occurs at night, and this proportion is relatively stable irrespective of weekends or other peak periods. Night traffic shows the same peaks in traffic volumes and can reach up to 247 vehicles per night. Interestingly, during peak periods, there is no large difference between weekdays (2–239 cars day^{-1}) and weekends (2–247 cars day^{-1}), indicating that impacts are likely to be continuous. On average, 28 cars access the beach at night, or 10,220 annually. ORVs drive on the beach almost every night of the year: out of 977 recording days over 4 years at the major access point to Flinders Beach, only 13 nights (1.2%) recorded no night traffic.

Ghost crab abundance in response to traffic volumes

To determine whether densities of intertidal ghost crabs are reduced in areas impacted by beach traffic, counts of active burrow openings were compared between three adjacent sections on the northern end of Main Beach that differ substantially in the volume of vehicle traffic. The northernmost section of Main Beach is closed to all non-essential ORV traffic, except for life-saving and police patrols. This traffic 'no-go' area is clearly marked by a large sign on the beach. The great majority of recreational ORV users obey this exclusion zone and do not travel north into the exclusion zone, except for occasional vehicles that miss the sign at night. The 'No-vehicle' sign was used as the local reference point in this study, and the section to the north of this sign is designated as the 'NO/low impact zone' for the purpose of this study (Fig. 1c).

Most cars enter Main Beach through a large (*c.* 50 m wide) access corridor cut through the dunes approximately 200 m to the south of the exclusion zone (Fig. 1c). The vast majority of traffic entering the beach through this corridor turns south. This section consequently receives the greatest volume of traffic and is designated here as the 'heavy impact zone'. Much fewer vehicles turn north from the access corridor, but some traffic was observed between the access point and the exclusion zone further north. This central section is designated here as the 'moderate impact zone' (Fig. 1c). On those beach sections open to ORVs, vehicle traffic is concentrated on the middle to upper shore above the effluent line (groundwater table outcrop).

Crab densities were assessed from counts of active burrow openings. A burrow was judged active when it either showed signs of recent sediment reworking by the crabs, or fresh tracks were visible emanating from the burrow entrance, or both. Sediment re-working is usually easily discernible as small mounts of pellets deposited near the entrance. Conversely, inactive burrows have usually ill-defined perimeters of the entrance (caused by partial collapse or wind erosion) and show no sign of recent construction activities by crabs or tracks.

In each of the three traffic zones, counts were made at four to seven sites spaced 50 m apart along the beach. At each site, active burrow openings were counted in 10 m wide shore-perpendicular belt transects. Transects were divided into 3 m wide strips, starting at the base of the foredunes and progressing down-shore to the seaward limit of the crab distribution. All active burrow openings were counted in each of these 3 × 10 m plots, and the diameter of each burrow opening was measured to the nearest millimetre. All counts were made on three consecutive days in April 2006 under identical weather conditions of fine, sunny days with very light onshore winds.

Direct impacts of ORVs on ghost crabs: experiments to quantify crushing rates

We ran three types of experiments to quantify direct mortalities inflicted by ORVs on ghost crabs. All experiments were conducted from March to June 2006. In *Experiment 1* and *2* we measured the proportion of crabs crushed inside their burrows during daylight hours at various intensities of traffic and at different depths below the beach surface. In *Experiment 3* we quantified the number of crabs that were crushed on the beach surface by vehicles travelling at night.

Experiment 1: crushing of ghost crabs by ORVs inside natural burrows

We measured the mortality of crabs inside their burrows during the day which is caused by ORVs when they pass over the crabs' burrows in six experimental runs. For each experimental run we first chose a site on the middle to upper beach that showed no obvious signs of recent vehicle passes and which had a reasonable number of active crab burrow openings.

First, a 10–20 m long (depending on burrow density) and 20 cm wide (corresponding to the tyre width of vehicles) plot that ran parallel to the foredunes was marked out. Each crab burrow opening in a plot was numbered and the opening diameter measured. The depth of each burrow was measured by inserting a soft, pliable vine. After burrow dimensions had been recorded, a soft marking ribbon (textile flagging tape) was inserted into each burrow down to the base, using the same soft vine to avoid damage to crabs. A procedural control treatment showed that crabs were not harmed by this procedure. Excess ribbon was left on the sand surface so that burrow openings could again be located after the vehicle had passed over them. After the burrows had been marked, an ORV vehicle, Nissan Patrol with a gross mass of 3080 kg, was driven repeatedly over the plot in a straight line.

Six traffic densities of 5, 10, 15, 20, 25 and 30 vehicle passes over the burrows were tested. This range of experimental impact treatments was chosen to broadly encompass the traffic volumes occurring on the beach (Fig. 2). We calculated the number of times a crab burrow is hit per day by ORVs as follows: (i) vehicles were randomly distributed over the area of the beach between the swash and the base of the foredune which is used by ORVs; this area was on average 54 m wide; (ii) The total 'footprint' of each vehicle is represented as twice its tyre width to account for two tracks made be each car and assuming a typical ORV tyre of 235 mm width. The first tyre track was randomly positioned across the beach face, while the second tyre track was constrained to be 1.3 m further seawards, corresponding to the inner axle width of a typical ORV driven on these beaches; (iii) The footprint of the two tyre tracks of each individual vehicle was then compared against 10 points positioned in a perpendicular line across the beach. These 'intersection points' started at 5 m seawards from the foredune and progressed at 5 m intervals to the swash zone. (iv) If a footprint of a randomly positioned vehicle overlapped with a point it was scored as a 'hit'. Randomisations of vehicle positions were run five times for each of the 10 intersection points, and the average of these 50 intersection 'hits' is taken as the number of vehicle passes over a crab burrow. (v) Finally, the above randomisation steps (i)–(iv) were run for a number of traffic volumes obtained from the automatic traffic counters (Fig. 2) to calculate the number of impacts on crab burrows under different traffic conditions. The maximum recorded traffic volume of 3168 vehicles day^{-1} results in 30 hits on a crab burrow per day, and the grand average volume of 353 vehicles day^{-1} corresponds to four hits per day; these values bracket the applied experimental treatment range of 5–30 vehicle passes.

After the vehicle treatment had been applied, each burrow was carefully excavated by hand, and retrieved crabs were inspected for damage and their carapace width recorded. In most cases mortality was obvious (*e.g.* completely quashed specimens, several or all limbs missing, carapace badly dented, eyestalks broken off, *etc.*). Only in a few cases were the retrieved crabs immobile without showing gross physical damage. These immobile individuals were placed on the sand free to run or burrow: crabs that did not regain mobility after 1 h were judged to be dead.

In each experiment, sand compactness was measured at seven to 10 positions along the vehicle track using a pocket penetrometer before and after the application of the vehicle passes. Triplicate sand cores (10 cm deep) were collected from each plot to determine sand moisture content and granulometry. After the vehicle passes, the depth of the tyre track was recorded at seven to 10 positions along each track. We also recorded the position of each experimental plot relative to the low-water spring tide (LWST) mark and surveyed the beach profile with a theodolite.

Experiment 2: crushing of ghost crabs by ORVs in simulated burrows: effects of depth and traffic intensity

The principal aim of this experiment was to determine whether increased burrow depth can lower crushing of crabs by ORVs; the predictive hypothesis was that fewer crabs would be killed when burrowed deeper as the overlying sediment matrix would offer protection from compaction.

The general experimental procedure was similar to *Experiment 1* (*e.g.* selection of undisturbed plots, recording of sediment parameters, marking of burrow openings with flagging tapes, inspection of damage to crabs after vehicle passes, *etc.*). The differences were that (i) crabs were first captured from natural burrows and (ii) these crabs were introduced into experimental burrows of various depth (5, 10, 15, 20 and 30 cm). The crabs used in these experiments were carefully excavated from their natural burrows within 50 m of the experimental plot and used within 30 min of capture. The crabs were collected from the upper shore in a section extending from the drift line to the foredunes. Of these, 49% were *Ocypode ceratophthalma* and 51% *Ocypode cordimanus*.

The experimental burrows were made by removing sediment plugs to the desired depth with a corer of 5 cm diameter. A single crab was placed at the bottom of each burrow and loosely covered with sand. Crabs were randomly allocated to treatments and all individuals used in a single experimental run were introduced to the burrows within 10 min of each other. After all crabs had been introduced to the burrows, the vehicle treatments were applied by repeatedly driving over the experimental burrows in a straight line.

Two traffic intensities of 10 and 40 vehicle passes were tested. The mean weekend traffic volume during peak times is 745 vehicles day^{-1}, corresponding to seven vehicle hits on a single crab burrow, and the maximum daily traffic volume of 3168 vehicles results in 30 hits day^{-1}. These calculations do assume a fully random distribution of cars over the beach face, but some drivers tend to follow other cars or use existing tracks. To account for such 'overlapping and cumulative' traffic patterns, we adjusted our experimental treatment intensities by *c.* +33% over the calculated number of hits under the above traffic scenarios.

Ten experimental individuals were used per traffic × depth combination. To check for any possible handling errors that might have injured crabs in the absence of vehicle impacts, we conducted six procedural controls per experimental run. In these control treatments crabs were introduced to burrows of the same depth as in the actual treatments and retrieved after 10–30 min without the application of vehicle passes; these procedural controls were run at the same time as the vehicle treatments and in the same location about 1 m from the experimental vehicle tracks.

Experiment 3: ghost crabs killed by night traffic while surface-active

To quantify the number of crabs killed by night traffic, an ORV was driven along the same section of beach where population censuses were made during the day (Fig. 1c). The vehicle was driven to the start of the designated beach section where a pass was to be completed, the engine was stopped, and the headlights turned off for 10 min. Each impact experiment was carried out with the vehicle travelling for several hundred metres along the beach at *c.* 30–50 km h^{-1} with the headlights switched on. Two to three persons followed behind the car with flashlights to record all crab corpses lying crushed in the tyre tracks. We recorded the longshore position of each carcass, its size, sex and species, except when specimens had been too badly mutilated by the vehicle.

These experiments were attempted on 10 nights. Surface activity of crabs was found to vary considerably, with crabs being active outside their burrows on six out of the 10 nights. We visually scored approximate crab activity by counting the number of individuals that were visible in the *c.* 10 m wide beam of flashlights that observers carried while walking swiftly in a straight line across the beach from the dunes towards the swash. Activity was estimated as 'low' (a few individuals sparsely distributed), 'medium' (several individuals observed in each transect) and 'high' (>10 crabs observed per transect) on two nights each. No crabs were observed on the beach surface on the other four nights.

Table 1. Physical variables of sites where burrow counts of ghost crabs were conducted in each traffic area.

zone	site*	beach slope (1/100)	sand moisture (%), mean ± SD	grain size (∅, μm), mean ± SD
Heavy traffic area	600 S	10.0	1.6 ± 0.48	298 ± 7.3
	550 S	9.4	2.0 ± 0.58	311 ± 25.5
	500 S	9.9	1.9 ± 0.67	294 ± 3.9
	450 S	12.6	5.0 ± 1.88	319 ± 20.8
	400 S	12.8	2.5 ± 0.35	295 ± 15.4
	350 S	10.3	3.8 ± 2.38	331 ± 7.6
	300 S	11.9	2.4 ± 0.54	315 ± 19.9
Moderate traffic area	200 S	12.8	2.2 ± 0.34	320 ± 12.4
	150 S	11.6	2.1 ± 0.40	312 ± 7.9
	100 S	12.4	2.5 ± 0.28	316 ± 18.9
	50 S	12.0	2.9 ± 0.53	321 ± 8.0
NO/low traffic area	0	10.2	3.0 ± 0.49	295 ± 4.6
	50 N	9.9	2.4 ± 0.20	277 ± 27.3
	100 N	12.5	2.4 ± 0.40	337 ± 1.3
	150 N	10.9	2.3 ± 0.29	319 ± 16.5
	200 N	11.2	3.0 ± 0.25	308 ± 5.0
	250 N	8.7	2.5 ± 0.43	332 ± 6.3
	300 N	6.9	2.8 ± 0.26	334 ± 6.6

*Relative to the local reference point which is the 'NO vehicle access sign' (see Fig. 1c).

Table 2. Density of ghost crab burrow openings in areas receiving different amounts of beach vehicle traffic.

distance seawards from foredune	NO/low traffic (7 Sites), mean ± SD	moderate traffic (4 Sites), mean ± SD	heavy traffic (7 Sites), mean ± SD
0–3 m	132.6 ± 45.15	134.0 ± 36.80	85.7 ± 60.88
3–6 m	55.4 ± 26.30	38.3 ± 24.54	19.1 ± 19.49
6–9 m	20.3 ± 11.86	18.5 ± 19.97	6.4 ± 7.41
9–12 m	9.3 ± 9.72	7.5 ± 5.80	3.4 ± 4.61
12–15 m	1.6 ± 1.72	1.3 ± 1.89	0.4 ± 1.13
15–18 m	0.7 ± 1.50	0.3 ± 0.50	0.0 ± 0.00
Entire beach-face	219.9 ± 84.97	199.8 ± 64.49	115.1 ± 87.03

Tabulated values are the number of active burrow openings per 30 m^2 counted in 10 × 3 m plots continuously distributed from the base of the foredune to the lowest down-shore position at which crabs were found.

Results

Ghost crab abundance in relation to traffic intensity

Habitat variables

Physical habitat variables did not differ significantly between beach sections subjected to different volumes of traffic (Table 1). Sand moisture was highly similar between traffic sections (ANOVA, $F_{(2,51)} = 0.41$, $P = 0.66$), as was sediment grain size (ANOVA, $F_{(2,51)} = 1.87$, $P = 0.16$), and slope of the intertidal zone (ANOVA, $F_{(2,15)} = 2.73$, $P = 0.10$). Thus, spatial variation in habitat characteristics is highly unlikely to be the main cause of any differences in ghost crab densities.

Crab abundance and distribution

The density of ghost crab burrows was significantly higher in the two sections that received only very low or moderate amounts of ORV traffic (Table 2; two-way ANOVA, effect traffic intensity: $F_{(2,90)} = 15.68$, $P \le 0.001$). By contrast, ghost crab burrow numbers were reduced by 42–48% in the section south of the access point that received high volumes of beach traffic (Table 2); this effect was consistent across all levels of the beach (*i.e.* ANOVA interaction term – traffic × level: $F_{(10.90)} = 0.75$, $P = 0.68$).

Most beach traffic is concentrated below the drift line, and the distribution of ghost crab burrows across the beach face differed between traffic sections. A significantly (ANOVA, $F_{(2,15)} = 4.97$, $P = 0.02$) smaller percentage of the population was found living below the drift line in the area of heavy traffic (2.2 ± 1.07%) compared with the NO/low (7.2 ± 1.69%) and moderate traffic section (6.27 ± 2.14%). At four out of seven sites surveyed in the heavy traffic area, no active burrow openings were encountered below the drift line, which was located 9 m seawards of the dunes. By contrast, all sites in both the moderate and low traffic area had 2–13% of the intertidal population of crabs located below the drift line.

Burrow openings were significantly smaller in areas with beach traffic compared with the reference area from which recreational ORVs are banned (Table 3). Because burrow diameter is a function of crab size ($r = +0.67^{***}$), spatial differences in burrow dimensions indicate shifts in population size structure. Few large crabs were found in the area most heavily impacted by ORVs, and the population was shifted towards a larger proportion of juveniles. This reduction of burrow opening size was most pronounced on the upper shore close to the foredune (Fig. 3, Table 3).

Crushing of crabs by ORVs inside their burrows

Natural burrow conditions: effects of varying traffic intensity

A total of 97 burrows were examined in the experiments that measured mortality caused by ORVs while the crabs were inside their natural, unmanipulated burrows. Of these, 34% (33 burrows) were occupied by crabs. The mean burrow diameter per experimental site ranged from 10.4 to 26.6 mm and mean burrow depth varied from 20 to 40 cm. Compactness of the sand was not measurably affected by low intensity traffic of five vehicles passes, but most traffic intensities above 10 vehicle passes softened the sediment (Table 4). Cars completely collapsed the top

Table 3. Diameter of ghost crab burrow openings (∅, mm) in three sections of the beach receiving different amounts of vehicle traffic at varying distances downshore from the base of the foredunes.

distance seawards from foredune	traffic volume	mean ± SD	n	ANOVA	SNK *post hoc* test
0–3 m	NO/low	17.9 ± 10.18	928	F = 51.70	a
	Moderate	14.5 ± 8.02	438	df = 2, 1943	b
	Heavy	13.7 ± 7.27	580	P = <0.001	b
3–6 m	NO/low	17.7 ± 9.35	388	F = 22.84	a
	Moderate	13.8 ± 7.65	171	df = 2, 690	b
	Heavy	14.3 ± 8.94	134	P = <0.001	b
6–9 m	NO/low	16.1 ± 6.85	142	F = 7.56	a
	Moderate	14.3 ± 6.59	84	df = 2, 268	b
	Heavy	12.8 ± 5.50	45	P = <0.001	b
9–12 m	NO/low	15.1 ± 4.90	65	F = 0.85	a
	Moderate	14.3 ± 6.39	32	df = 2, 119	a
	Heavy	16.2 ± 8.46	25	P = 0.430	a
12–15 m	NO/low	13.7 ± 5.22	11	F = 0.13	a
	Moderate	12.8 ± 4.07	6	df = 2, 17	a
	Heavy	14.0 ± 2.65	3	P = 0.883	a
15–18 m	NO/low	15.0 ± 4.06	5	F = 0.47	a
	Moderate	12.5 ± 3.54	2	df = 1.15	a
	Heavy	—	0	P = 0.522	
entire beach face	NO/low	17.5 ± 9.52	1539	F = 78.80	a
	Moderate	14.3 ± 7.68	733	df = 2, 3056	b
	Heavy	13.8 ± 7.52	787	P = <0.001	b

5–15 cm of all crab burrows, and caused rutting to a depth of 44 mm after 20 overpasses in relatively compact sand, and 100 mm after 30 overpasses in softer sand.

Three crabs out of a total of 28 retrieved (11%) were crushed by vehicles in these experiments: a single crab was killed at a depth of 23 cm after 15 passes, and 20 vehicle passes killed two crabs at depths of 11 and 23 cm. No crab mortalities were recorded at higher intensities of traffic (*i.e.* 25 and 30 passes), but crabs were buried deeper (39 cm) in these experimental plots. In general, smaller crabs buried shallower into the sediment (correlation between crab size and burrow depth: $r = +0.47$, $P \leq 0.01$).

Crab mortality caused by ORVs at different depths in experimental burrows

Changes in sediment compactness after the application of vehicle treatments were variable depending on local conditions (*e.g.* sediment moisture, position on shore) of the experimental plots, but cars generally loosened the sand matrix (Table 5).

Off-road vehicles killed all ghost crabs if they were buried shallow (5 cm) into the sediment (Fig. 4a). Severe mortality of shallow-living crabs was recorded in both the 10 and 40 vehicle pass treatments (Fig. 4a). Indeed, burial depth appears to be the key factor in determining mortality rates of ghost crabs caused by vehicles. We did not find a significant (F-test to compare non-linear regression models between treatments: $F_{(2,11)} = 1.091$, $P_{(2)} = 0.37$ and Aikake Information Criterion Ratio = 11.91) difference in mortality rates between 10 and 40 vehicles passes; rather, mortality declined exponentially with increasing depth at both traffic intensities (Fig. 4a). Crabs that were buried 30 cm in the sand were generally not killed save for a single individual (Fig. 4a). Of the 210 crabs used in the experiments, 32% of *Ocypode ceratophthalma* and 50% of *Ocypode cordimanus* were killed, indicating that both species are susceptible crushing by vehicles whilst inside their burrows during the day.

Nocturnal vehicle impacts on ghost crabs

In four experimental runs where a vehicle travelled at night along the beach, we found that a considerable number of crabs was crushed. A single vehicle pass killed 13–26 crabs over a relatively short distance of 200–300 m (Fig. 5); this mortality equates to 0.12–0.75% of the intertidal population. However, during several nights when we attempted to conduct experiments no ghost crabs were active on the beach surface. Hence, nocturnal beach traffic would not kill ghost crabs compared with nights when crab activity is high. Of the 78 crabs crushed at night in the four experimental runs, 77% were *Ocypode ceratophthalma* and 23% were *Ocypode cordimanus*.

Discussion

Off-road vehicles causing reductions of ghost crabs populations

Vehicles can inflict considerable mortality on ghost crabs on sandy beaches (Figs 4 and 5). It has previously been suggested – but not measured – that the main mechanism causing the observed lower population size of ghost crabs on beaches open to ORVs on North Stradbroke Island is direct kills of crabs by cars at night (Moss & McPhee 2006). Indeed, crushing of surface-active crabs by vehicles at night appears to be a plausible explanation for the lower number found in the heavy vehicle impact zone (Table 2). Our results from the night impact experiments are broadly similar to Wolcott & Wolcott (1984), who observed up to 19 kills per 100 m on the foreshore and up to 1 kill per 100 m on the backshore. Another similarity is that in both studies crabs were not active during some nights.

Burrows offer only partial protection from crushing by cars. Crab mortality inside burrows is strongly dependent on burrow depth, with individuals that construct burrows shallower than 25 cm being killed by ORVs (Fig. 4). Our data on impact rates of buried crabs contrast to some

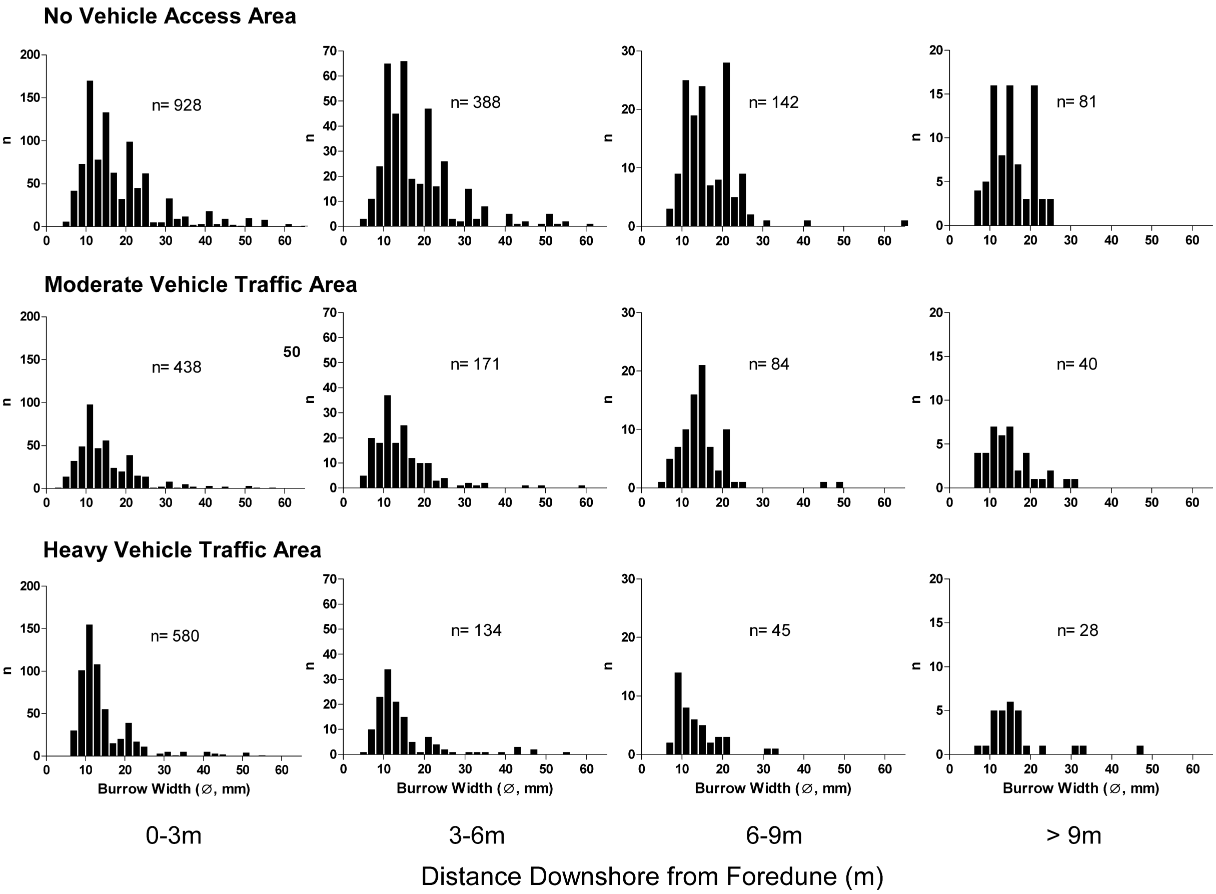

Fig. 3. Comparison of the size frequency of ghost crab burrow openings (∅, mm) amongst three beach sections subjected to different volumes of traffic.

Table 4. Changes in sediment compactness following application of vehicle overpasses to experimental plots that contained unmanipulated ghost crab burrows (n = 12 for moisture and sediment granulometry samples).

vehicle passes	sand moisture (%)	grain size (mean, μm)	n	compactness before (kgf cm^{-2}), mean ± SD	compactness after (kgf cm^{-2}), mean ± SD	Δ: after – before	t	$P_{(2)}$
5	2.4	260	9	0.7 ± 0.18	0.7 ± 0.06	0	0	1.00
10	2.8	210	9	2.4 ± 0.32	1.1 ± 0.09	–1.2	11.73	<0.001
15	3.2	225	15	1.3 ± 0.30	1.0 ± 0.50	–0.3	1.99	0.058
20	2.0	215	12	2.4 ± 0.36	1.2 ± 0.16	–1.2	10.55	<0.001
25	1.9	303	15	0.7 ± 0.33	0.4 ± 0.12	–0.3	3.31	0.004
30	2.1	217	9	0.9 ± 0.24	0.6 ± 0.05	–0.3	3.67	0.006

extend with those of Wolcott & Wolcott (1984). They observed no crab mortalities during the day even in the shallowest (5 cm) of their experimental burrows. This discrepancy may be due to differences in sediment properties (*e.g.* compactness, moisture content) or the weight of the ORV vehicle used in the experiments. In our experiments, almost all crabs were protected from ORV impacts in burrows deeper than 25 cm, and 72% of the burrows examined were deeper than this. Conversely, roughly one-third of crabs are vulnerable to direct crushing by ORVs inside their burrows during the day (Fig. 4). Thus, ORVs impact ghost crabs both during the day when crabs are generally inside their burrows and at night when they emerge onto the beach surface.

We observed that around the full moon ghost crabs stayed inside their burrows at night. Whether this was a

Table 5. Changes in sediment compactness following the application of vehicle treatments to simulated burrows in which crab mortality caused by off-road vehicles was measured.

vehicle passes	depth (cm)	sand moisture (%)	grain size (μm)	n	compactness (kgf cm^{-2}) before, mean ± SD	compactness (kgf cm^{-2}) after, mean ± SD	Δ: after – before	t	$P_{(2)}$
10	5	3.0	231	10	2.9 ± 1.64	1.8 ± 0.66	−1.1	1.97	0.070
10	5	2.6	271	10	2.3 ± 0.67	1.7 ± 0.51	−0.6	2.25	0.038
10	10	3.7	283	15	2.3 ± 0.46	0.7 ± 0.33	−1.6	10.95	<0.001
10	10	4.0	243	15	1.5 ± 0.63	0.9 ± 0.15	−0.6	3.59	0.003
10	20	2.6	231	10	2.9 ± 1.64	1.8 ± 0.66	−1.1	1.97	0.075
10	30	4.0	271	15	1.5 ± 0.63	0.9 ± 0.15	−0.6	3.56	0.003
10	30	3.0	243	10	2.3 ± 0.67	1.7 ± 0.51	−0.6	2.25	0.039
40	5	3.3	231	15	0.2 ± 0.12	0.3 ± 0.15	+0.1	2.02	0.054
40	10	4.1	246	15	3.2 ± 1.19	1.5 ± 0.38	−1.7	5.27	<0.001
40	10	2.8	203	10	2.3 ± 0.29	1.4 ± 0.46	−0.9	5.23	<0.001
40	15	2.5	185	10	1.1 ± 0.30	1.2 ± 0.64	+0.1	0.45	0.662
40	20	3.3	231	15	0.2 ± 0.12	0.3 ± 0.15	+0.1	2.02	0.054
40	20	2.5	185	10	1.1 ± 0.30	1.2 ± 0.64	+0.1	0.45	0.662
40	30	4.1	246	15	3.2 ± 1.19	1.5 ± 0.38	−1.7	5.27	<0.001
40	30	2.8	203	10	2.3 ± 0.29	1.4 ± 0.46	−0.9	5.23	<0.001

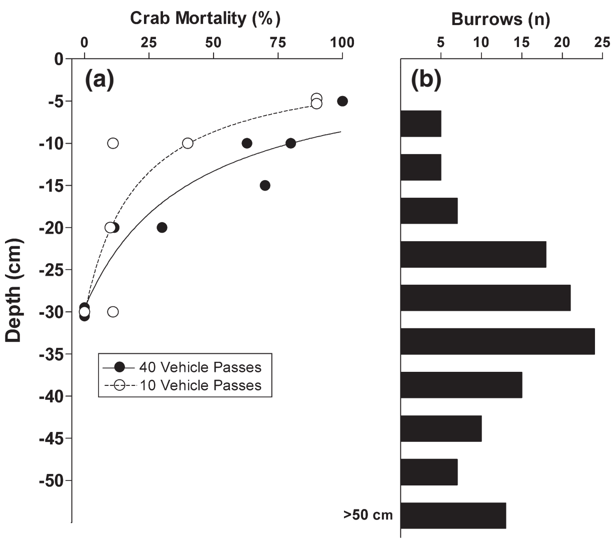

Fig. 4. Mortality of ghost crabs through direct crushing by off-road vehicles (ORVs) at different depth in the sediment at two traffic intensities of 40 (solid symbols) and 10 (open symbols) overpasses by an ORV vehicle (a), compared with the distribution of the crabs' burrow depth (b).

direct response to light intensity, weather conditions, an internal timing mechanism, or simply a random behaviour remains unknown. Avoiding surface activity on moonlit nights is plausible given that ghost crabs are seldom seen on the surface during the day (Hughes 1966), and that they also avoid artificial light (Christoffers 1986). Our observations stress the need to identify external factors that influence surface activity in ghost crabs.

Ghost crab burrows as indicators of human impacts

Significantly fewer burrow openings occurred in areas affected by vehicles (Fig. 3, Table 2). This result is consistent with other studies documenting lower ghost crab numbers in areas affected by human trampling (Steiner & Leatherman 1981; Christoffers 1986; Neves & Bemvenuti 2006), ORVs (Wolcott & Wolcott 1984; Blankensteyn 2006; Moss & McPhee 2006), shore armouring (Barros 2001), as well as beach nourishment and bulldozing (Peterson *et al.* 2000). Only Steiner & Leatherman (1981) reported higher crab abundance from beach areas used by pedestrians; they suggest that crabs were more abundant in these areas because they benefited from food scraps left behind by humans.

The significantly lower number of crab burrow openings found in the beach section used heavily by ORVs found in this study (Fig. 3, Table 2) is broadly similar to previous work by Moss & McPhee (2006) on North Stradbroke Island. A point of difference is the smaller spatial scale over which we made these contrasts. Our data suggest that spatial contrasts of ghost crab burrow counts can be used as a biological indicator of human disturbance on sandy beaches at smaller spatial scales (10s to 100s of metres) than previously done (Barros 2001; Moss & McPhee 2006).

Estimates of ghost crab abundance are usually obtained from counts of burrow openings (Barros 2001). There are, however, several potential sources of error associated with this technique. Crabs plug their burrows to escape the heat of the day (Barrass 1963). Also, wind and human disturbance (trampling, cars) obscure and collapse burrow

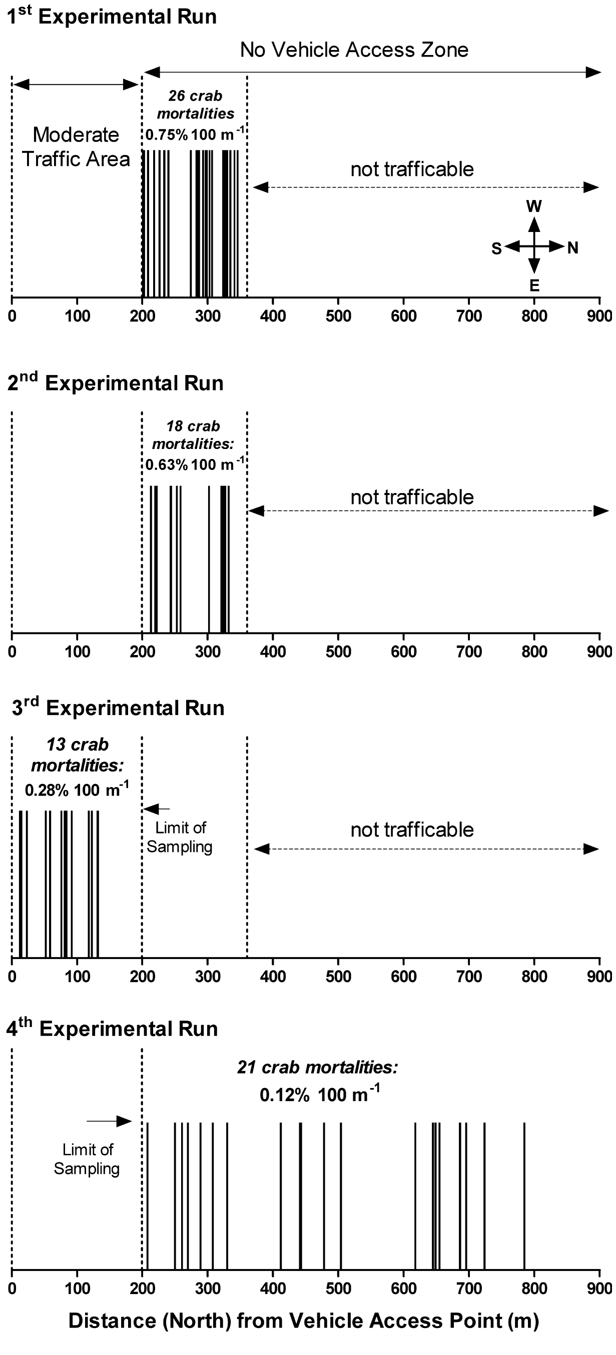

Fig. 5. Ghost crab mortalities caused by night traffic. Each bar represents a single individual found crushed in the tyre tracks after as single vehicle pass. Percentage values refer to the fraction of the intertidal population killed by a single vehicle pass.

openings. Ghost crabs can move several hundred meters alongshore at night and construct a new burrow before sunrise (Wolcott 1978); old, unoccupied, burrows that are out of the tide's reach could remain intact and positively bias population estimates. By contrast, ghost crabs may renovate existing burrows (Barrass 1963; Hill & Hunter 1973). Ghost crabs generally do not emerge during cold weather when they plug their burrows for thermal insulation (Barrass 1963; Hill & Hunter 1973). Equally, during rainy weather, the crabs remain inside their burrows which may be plugged closed (Hughes 1966). Finally, Barros (2001) cautions that ghost crabs may change their behaviour (*e.g.* not readily maintaining burrows) in response to human activity, resulting in an apparent reduction in the population.

The location of burrow counts across the shore should spatially match the area over which a human disturbance occurs. Counts in the unvegetated, intertidal part of the beach are most practical, quickest and easiest to execute. Counts in dune areas may be useful if the population migrates in response to storms or cold weather, as was shown for *Ocypode quadrata* (Christoffers 1986). Burrow counts are usually restricted to the un-vegetated part of the beach and generally do not encompass the dunes (*e.g.* Barros 2001). We observed crab holes in the dunes above the storm drift line. In our field setting, the seaward edge of the dunes was a near vertical face up to 2 m high and this is present for most of the year. Thus, there may be little opportunity for movement of crabs from the beach into the dunes, or crabs that move from the dunes onto the beach may not be able to return.

Possible complementary causes of changes in ghost crab numbers

Off-road vehicle traffic overlaps with the distribution of many intertidal macrobenthic species (Schlacher & Thompson in press-b), and can thus reduce the diversity and standing stocks of prey items available to ghost crabs (Schlacher *et al.* in press). Thus, smaller population sizes may also reflect diminished prey availability on beaches impacted by ORVs. Vehicles also significantly modify the sand properties on beaches (Anders & Leatherman 1987), and physically disrupt large areas of the intertidal habitat (Schlacher & Thompson in press-a). Less cohesive sediment after vehicle disturbance (Table 4) may be less suitable for the construction of burrows (Christoffers 1986), or impede the recruitment of the early instars of ghost crabs. Constant disruption of burrows by cars (Schlacher & Thompson in press-a) may also force crabs to continually maintain their burrows during the day, exposing them more frequently to bird and mammal predators (Moore 2002; Carlton & Hodder 2003).

Foxes are an alien species in Australia and hence regarded as a pest on North Stradbroke Island. On one occasion we observed fox tracks and signs of foxes having excavated crab burrows at night. Predation of ghost crabs by foxes and coyotes has been reported elsewhere

(Christoffers 1986; Rose & Polis 1998). Feral and domestic dogs may also kill ghost crabs at night, and fishermen attract birds such as seagulls and terns which in turn can prey on ghost crabs (T.A. Schlacher, personal observation). However, enhanced predation pressure on ghost crabs could only be a plausible explanation for the observed reduction in ghost crab abundance (Table 2), if it were significantly higher on beach sections open to ORVs. This is unlikely to be the case for the abutting, small areas investigated by us (Fig. 1c). Several human activities such as camping and fishing that attract predators (*e.g.* food scraps, discarded bait, fish guts, *etc.*) require ORVs for access on the island, and thus a connection between ORV use and indirect negative impacts on ghost crabs cannot be excluded.

Ghost crabs are remarkably well adapted to the harsh environmental conditions of sandy beaches, and have successfully exploited the niche of top invertebrate predator on many shores (Barrass 1963; Hughes 1966; Jones 1972). Behavioural plasticity is a key trait of most sandy beach animals (Brown 1996), and ghost crabs appear to respond to the novel evolutionary pressure of human modifications to their habitat. For example, we have observed ghost crabs to scavenge actively for food scraps in camping areas in the dunes, and they can even invade coastal houses (T.A. Schlacher & L. Thompson, personal observation). Whether ORVs influence ghost crab behaviour and life histories has not been quantified to date. It is, however, not unlikely that crabs may show behavioural adaptations to human disturbance such as changed activity rhythms, modifications to their burrow architecture, or heightened escape behaviour. Similarly, shifts in burrow size structure in heavy traffic areas (Fig. 3) indicate age-selective mortality caused by vehicles, and such effects may propagate to influence recruitment and population dynamics and ultimately life-history traits.

Conservation and management implications

Given the high traffic volumes on the beaches studied, particularly during peak periods (Fig. 2), and the substantial mortalities inflicted by ORVs on ghost crabs (Figs 3 and 4), off-road driving on beaches can be regarded as an environmentally harmful activity. In fact, simple modelling of three impact scenarios indicates that ORVs can contribute to population declines of ghost crabs. Under a 'best case scenario' that incorporates the lowest nocturnal mortality rate by a single vehicle recorded by us (0.12%), and which assumes that ghost crabs are surface-active in one out of four nights only, 2311 vehicles travelling on the beach at night would reduce the population to half (Fig. 6). Under a 'worst-case scenario' (*i.e.* highest recorded experimental mortality rate and surface activity of crabs every night), less than 100 cars would kill 50% of the intertidal ghost crab population.

We found that nocturnal surface activity of ghost crabs was variable, with crabs being active outside their burrows on six out of 10 nights only. Thus, the 'worst-case' scenario which assumes emergence every night is likely to represent a maximum impact probability. The 'best case' scenario assumes only a 25% probability of emergence (*i.e.* one out four nights) which is lower than our preliminary data of 60% activity, and consequently may be a conservative estimate.

Traffic volumes on Flinders Beach (10,220 cars annually) are significantly higher than the above figures, roughly fivefold the modelled number of cars causing a 50% reduction in ghost crab numbers under the 'best

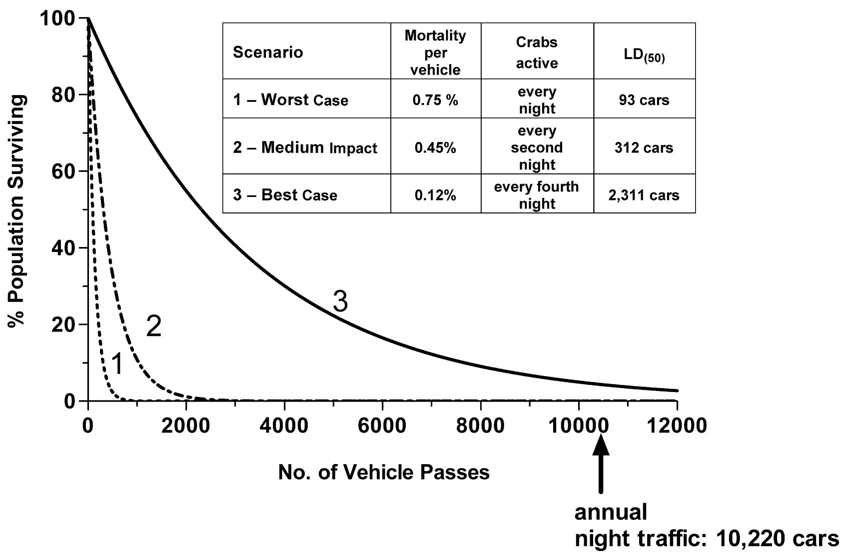

Fig. 6. Modelled declines in ghost crab populations as a result of direct mortalities caused by night-traffic. Scenarios are based on three levels of mortality recorded by us in this study, and different levels of crab activity. $LD_{(50)}$ denotes the numbers of cars predicted to reduce intertidal populations of ghost crabs by half (lethal dose 50).

case'. These figures are first-order guides only, as the model does not take into account recruitment, but equally does not incorporate additional losses through natural mortality and predation, or other human causes such as daytime kills by ORVs. Nevertheless, it does suggest that beach traffic at night can play a role in reducing populations of intertidal ghost crabs under existing levels of use.

Restrictions placed on night traffic would be an effective conservation measure. Although night driving represents only a relatively small fraction (*c.* 8%) of all beach traffic in the present situation, it does occur throughout the year and is a major part of the recreational fishing fraternity. Exclusion of ORV traffic from beaches, or sections of beaches, is an alternative or complementary management option. This has proven highly successful in terms of environmental outcomes in South Africa (Williams *et al.* 2004), but requires careful spatial planning and the use of multiple criteria spanning ecological, economic and social-cultural criteria (Celliers *et al.* 2004).

A number of small pocket beaches on North Stradbroke Island, such as Frenchman's Beach or Home Beach, are physically or legally inaccessible to vehicles. These beaches may act as source populations for the surrounding impacted beaches. Very high ghost crab activity (possibly a spawning event) occurred around New Year on Home Beach (T.A. Schlacher and L. Thompson, personal observation) and the presence of freshly recruited megalopa in March suggests that local *Ocypode* reproduction and recruitment has a seasonal component. Spawning of ghost crabs in South-East Queensland is probably restricted to the summer months since temperatures can drop below the reported *Ocypode* activity threshold (*c.* 16 °C) between May and September. If that is the case, then the summer peaks in beach traffic (Fig. 2) overlap with the spawning period of ghost crabs.

Regulating beach traffic to achieve conservation outcomes is a formidable management challenge (James 2000; Celliers *et al.* 2004). Beach driving is immensely popular amongst fishermen, campers and the general public and thus has social value (Priskin 2003a). Arguably, a sizeable proportion of the local tourism industry on the island is presently based on ORVs accessing the beaches (Carter 2005), but this activity may at the same time deter other user groups from visiting the island. The net balance of economic gains and losses of beach traffic has not been quantified, but economic arguments should be considered in developing encompassing management approaches.

Conclusions

Recreational demands on sandy beaches are escalating worldwide (Schlacher *et al.* 2006; Schlacher *et al.* in press). Driving of recreational ORVs results in measurable declines in ghost crab density on beaches and directly crushes animals. This impact occurs mostly during the night when crabs are active on the beach surface, but burrows offer only partial protection against cars while the crabs are buried during the day. Overall, our data strongly argue that driving of ORVs on sandy beaches is a form of human recreation that has negative ecological consequences that need to be managed within the full spectrum of socio-cultural and economic demands to achieve lasting conservation outcomes for sandy beaches.

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