

Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



## Original article

## Multiple scavengers respond rapidly to pulsed carrion resources at the land–ocean interface

Thomas A. Schlacher<sup>a,\*</sup>, Simone Strydom<sup>a</sup>, Rod M. Connolly<sup>b</sup><sup>a</sup> Faculty of Science, Health & Education, University of the Sunshine Coast, Maroochydore DC, QLD 4558, Australia<sup>b</sup> Australian Rivers Institute – Coast & Estuaries, and School of Environment, Griffith University, Gold Coast Campus, QLD 4222, Australia

## ARTICLE INFO

## Article history:

Received 12 November 2012

Accepted 21 January 2013

Available online

## Keywords:

Carrion  
Scavengers  
Ghost crabs  
Food webs  
Allochthonous inputs

## ABSTRACT

Sandy beaches are the globe's longest interface region between the oceans and the continents, forming highly permeable boundaries across which matter flows readily. Stranded marine carrion supplies a high-quality food source to scavengers, but the role of animal carcasses is generally under-reported in sandy-beach food webs. We examined the response of scavengers to pulsed subsidies in the form of experimental additions of fish carcasses to the dune–beach interface in eastern Australia. Ghost crabs (*Ocypode* spp.) are the dominant invertebrate scavengers in these habitats and they responded strongly and consistently to changed resource availability: densities increased significantly within days of carrion augmentations. Carcasses added experimentally also formed local nuclei for a diversity of vertebrate scavengers that aggregated at food falls; these included large lizards, several species of birds (including raptors), and foxes. Consumption of fish carrion by the vertebrate scavengers was rapid and often complete. There is also evidence for higher-order interactions, where responses of invertebrate scavengers became depressed in plots where vertebrate scavenger activity was intense. Our findings emphasize that carrion can be a pivotal component of beach food webs.

© 2013 Elsevier Masson SAS. All rights reserved.

## 1. Introduction

Sandy beaches of open coasts form one of the globe's largest interface regions between the sea and the land. Their long and highly permeable border with the oceans is crossed by marine matter that drifts ashore with waves, currents and tides, often forming distinct accumulations – strandlines – near the dunes (Barreiro et al., 2011). These strandlines form important structural and functional component of beach ecosystems, including the provision of habitat, food and nutrients (Dugan et al., 2011).

From an ecosystem perspective, marine organic matter deposited on beaches constitutes a critical dietary input for beach consumers – a trophic subsidy (sensu Polis et al., 1997). The importance of such trophic subsidies is predicted to be particularly high for food webs of open-coast beaches for three principal reasons: i) beaches lack attached larger plants and *in situ* primary production on the unvegetated part of the beach is very low; ii) marine matter is transported onshore by physical forces (e.g. wind, waves, currents) with little mechanical impedance, and

iii) imported material often accumulates at the base of the fore-dunes, enhancing its availability as a food resource (Spiller et al., 2010).

Death of animals is ubiquitous and supplies ecosystems with surprisingly large numbers of animal carcasses generated by non-predation events such as disease and malnutrition (DeVault et al., 2003; Beasley et al., 2012). This rich dietary resource is exploited by a diverse, and abundant assemblage of scavengers (Houston, 1979). Feeding on carcasses is also more widespread than traditionally acknowledged, and channels substantial amounts of energy through many food webs (Wilson and Wolkovich, 2011).

Animal carcasses are part of the spectrum of organic matter stranded on beaches and, as in other ecosystems, are predicted to constitute high-quality food sources exploited by scavengers (Wilson and Wolkovich, 2011). Carrion and scavenging are well represented in the literature on sandy shores, spanning a wide taxonomic ambit from gastropods to hyenas (Skinner et al., 1995; Morton and Jones, 2003). Scavenging on beaches has, however, rarely been contextualized in a broader ecological framework (sensu Beasley et al., 2012).

Fluxes of carrion and other matter between abutting ecosystems constitute important functional linkages in many landscapes (Polis et al., 1997; Schlacher and Connolly, 2009). These exchanges also

\* Corresponding author.

E-mail address: [tschlach@usc.edu.au](mailto:tschlach@usc.edu.au) (T.A. Schlacher).

couple production and consumption processes across ecological boundaries, shaping the dynamics and architecture of consumer populations and recipient food webs (Spiller et al., 2010). On sandy shorelines, organic matter of marine provenance is translocated across two ecotones: first, from neritic waters and the surf-zone to the littoral and, secondly, from the littoral to coastal dunes. Movement of material onto the beach is overwhelming by physical vectors, whereas biological vectors are usually more important in translocating marine production to terrestrial consumers; these fluxes are largely asymmetrical, with the upland movement of marine matter being the dominant spatial trajectory (Sanchez-Pinero and Polis, 2000).

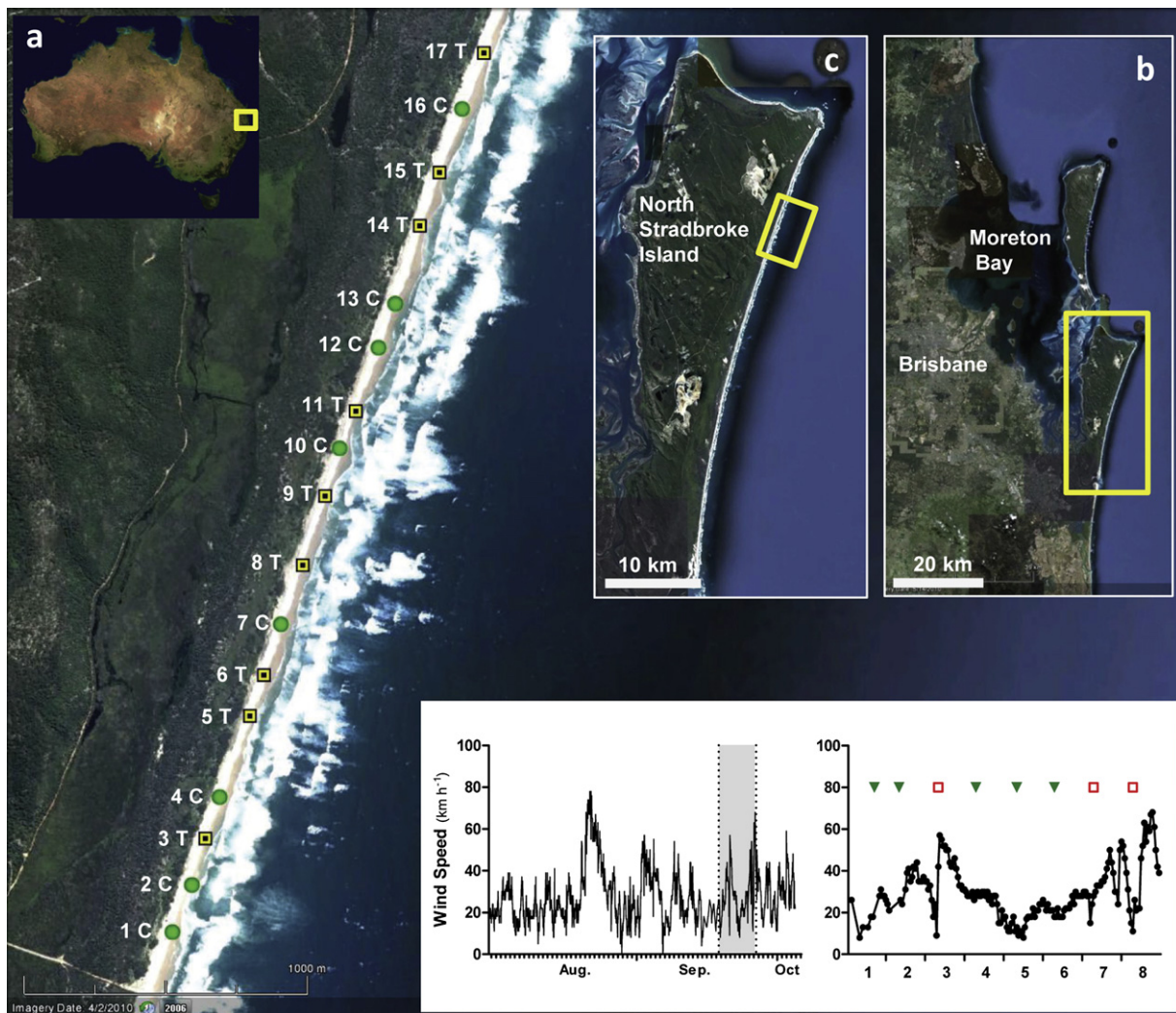
The dependence of sandy-beach food webs on imports of organic matter from the sea, and the increasingly recognized importance of carrion and scavenging in many food webs and across ecotones (Wilson and Wolkovich, 2011) have led to a conceptual understanding of food webs of open-coast beaches as containing species that have evolved to exploit high-quality carrion efficiently. We tested this prediction experimentally by manipulating the availability of a significant carrion source, fish carcasses, and measuring the response of the key scavengers, ghost crabs (*Ocypode* spp.).

## 2. Methods

The site for the experiment was an ocean-exposed sandy shore on North Stradbroke Island, in eastern Australia (Fig. 1). The physical habitat characteristics of the beach are typical of much of the subtropical/warm-temperate coast: intermediate morphodynamic type, waves 1–2 m high, a 50–80 m wide beach-face, and medium-grained sands (Morton, 2008).

Carrion supply was manipulated and the numerical response of scavengers measured in 17 experimental plots that were dispersed over a 3.2 km long stretch of beach (Fig. 1); distance between plots was randomized within a range of 150–250 m. The type of treatment (i.e. carrion addition or control without carrion addition) was randomly allocated to plots, with the constraint that not more than two of the same type could abut (Fig. 1). Plots measured 3 m (across-shore) × 10 m (along-shore), with the upper edge of the plots aligned with the base of the dunes.

On Day 1 of the experiment, before any manipulation of carrion, sediment samples (three cores per plot) were taken from each experimental plot and the angle of the beach-face measured following standard beach survey methods (see Schlacher et al., 2008). Key habitat metrics were highly similar between treatment and



**Fig. 1.** Location of the experiment in eastern Australia (a) on the ocean-exposed beach of North Stradbroke Island (b, c). Main panel shows spatial arrangement of treatment (squares) and control plots (circles). Size of plots not to scale, being 3 m × 10 m. Insert shows wind speeds recorded in the preceding weeks (left panel) and during the experiment. Green arrows: successful burrow counts of ghost crabs; red squares: data discarded on days with strong winds that obliterated burrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

control plots: there was no significant difference in mean slope values between treatments (ANOVA,  $P = 0.39$ , Control:  $3.8 \pm 0.8^\circ$ ; Treatment:  $2.9 \pm 0.7^\circ$ ), in mean grain size ( $P = 0.92$ ; Control:  $280 \pm 5 \mu\text{m}$ ; Treatment:  $279 \pm 5 \mu\text{m}$ ), or in other sediment statistics (sorting:  $P = 0.42$ , skewness:  $P = 0.19$ , kurtosis:  $P = 0.35$ ). We therefore consider it highly improbable that outcomes of the experiment were confounded by systematic habitat differences between experimental plots.

The experiment was conducted during the austral summer, from 19 to 26 Sep. 2011. Carrion was added approximately 2 h before sunset to the nine treatment plots on day 1, 2, 4 and 5 of the experiment. Carrion was flathead mullet, *Mugil cephalus*, caught locally in the surf zone by a commercial fisher. The fish weighted 499 g on average, and had a mean length of 36 cm. Three fish, each cut into three pieces, were added to a treatment plot. Thus, total carrion augmentation over the course of the experiment was 324 pieces of mullet (9 plots  $\times$  4 days  $\times$  3 fish  $\times$  3 pieces). Every morning (within 2 h of sunrise), the following measurements were made: i) number and opening diameter of ghost crab burrows (see below), ii) number of fish pieces remaining, and iii) presence of vertebrate scavengers (foxes, birds) or their tracks.

The primary ecological response to carrion augmentation that we measured was the density of ghost crabs. Crab density was quantified via counts of burrow openings on the beach surface, which has become the standard method for abundance estimates in this group of organisms (Schlacher et al., 2011; Noriega et al., 2012). Two species of ghost crabs, *Ocyropsis ceratophthalma* and *Ocyropsis cordimana* occur on the beach, but their burrow openings cannot be distinguished with confidence. We therefore report all burrow counts at the genus level. Strong winds (i.e.  $>40 \text{ km h}^{-1}$ ) on days 3, 7 and 8 obliterated burrow openings and hence these data were excluded from numerical analysis.

Total variation in the density of ghost crab burrows was partitioned with a general linear model (GLM) that contained two terms: 1.) 'Treatment' (carrion addition vs. control; fixed), and 2) 'Day' (day of the experiment when burrow counts were made; fixed) (Underwood, 1997).

### 3. Results

#### 3.1. Invertebrate scavengers

Ghost crab scavengers responded rapidly and strongly to enhanced carrion supply on the beach (Fig. 2; GLM: Day  $\times$  Treatment  $F_{(4,75)} = 7.80$ ,  $P < 0.001$ ). On day 4, densities of ghost crabs had increased, on average by 45% and were significantly higher in carrion-treatments than in controls (Fig. 2;  $P = 0.034$ ). Densities of the invertebrate scavengers continued to increase thereafter, being 75% higher on day 5 ( $\Delta_{\text{treatment/control}} = 1.75 \pm 0.19$ ), and more than double on day 6 ( $\Delta_{\text{treatment/control}} = 2.13 \pm 0.27$ ). Conversely, in controls without experimental food augmentations, crab densities changed comparatively little or declined over the course of the experiment (Fig. 2).

#### 3.2. Vertebrate scavengers

In addition to ghost crabs, a number of vertebrate scavengers consumed fish carrion in the experimental plots (Table 1, Fig. 3). We directly observed, or recorded prints of, several species of raptors (whistling kite, *Haliastur sphenurus*; Brahminy kite, *Haliastur indus*; white-bellied sea eagle; *Haliaeetus leucogaster*), Australian pied oystercatchers (*Haematopus longirostris*) and silver gulls (*Chroicocephalus novaehollandiae*). Tracks and prints of red foxes (*Vulpes vulpes*) were common, occurring in most plots on most days (Table 1).

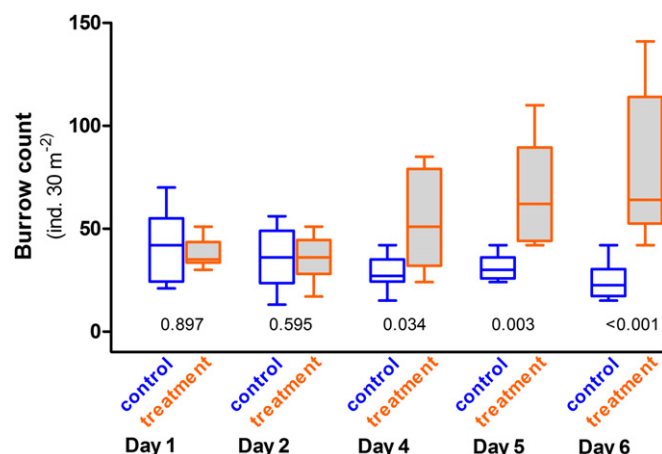


Fig. 2. Effect of pulsed carrion additions on the density of ghost crabs in plots at the base of dunes. Carrion (mullet, *Mugil cephalus*) was added to treatment plots on days 1, 2, 4 and 5. P values refer to pairwise comparisons (using SNK test) following a significant Time  $\times$  Treatment interaction term in the GLM.

These vertebrate scavengers had a major impact on carrion during the experiment: all of the 324 pieces of fish added over the course of the experiment were consumed, and 80% of carrion items placed at sunset had been removed by the next day. These high carrion consumption rates are most probably the result of scavenging by vertebrates for the following reasons: i) we directly observed avian scavengers feeding on carrion in treatment plots, occasionally lifting entire fish off the beach (Fig. 3), ii) fish were too large for ghost crabs to consume them entirely in a single night, and iii) tracks of red foxes converged on carrion pieces and there were clear signs that they had handled the fish carcasses.

#### 3.3. Cascading effects

Vertebrate scavengers modified the numerical response of ghost crab scavengers to enhanced carrion availability (Fig. 4). In experimental plots where raptors, foxes or oystercatchers had been recorded, the abundance of ghost crabs still increased, but by about 20% less than in plots without vertebrates. Higher removal rates of carrion by vertebrate scavengers significantly depressed the aggregative responses of ghost crabs to fish carcasses (Fig. 4).

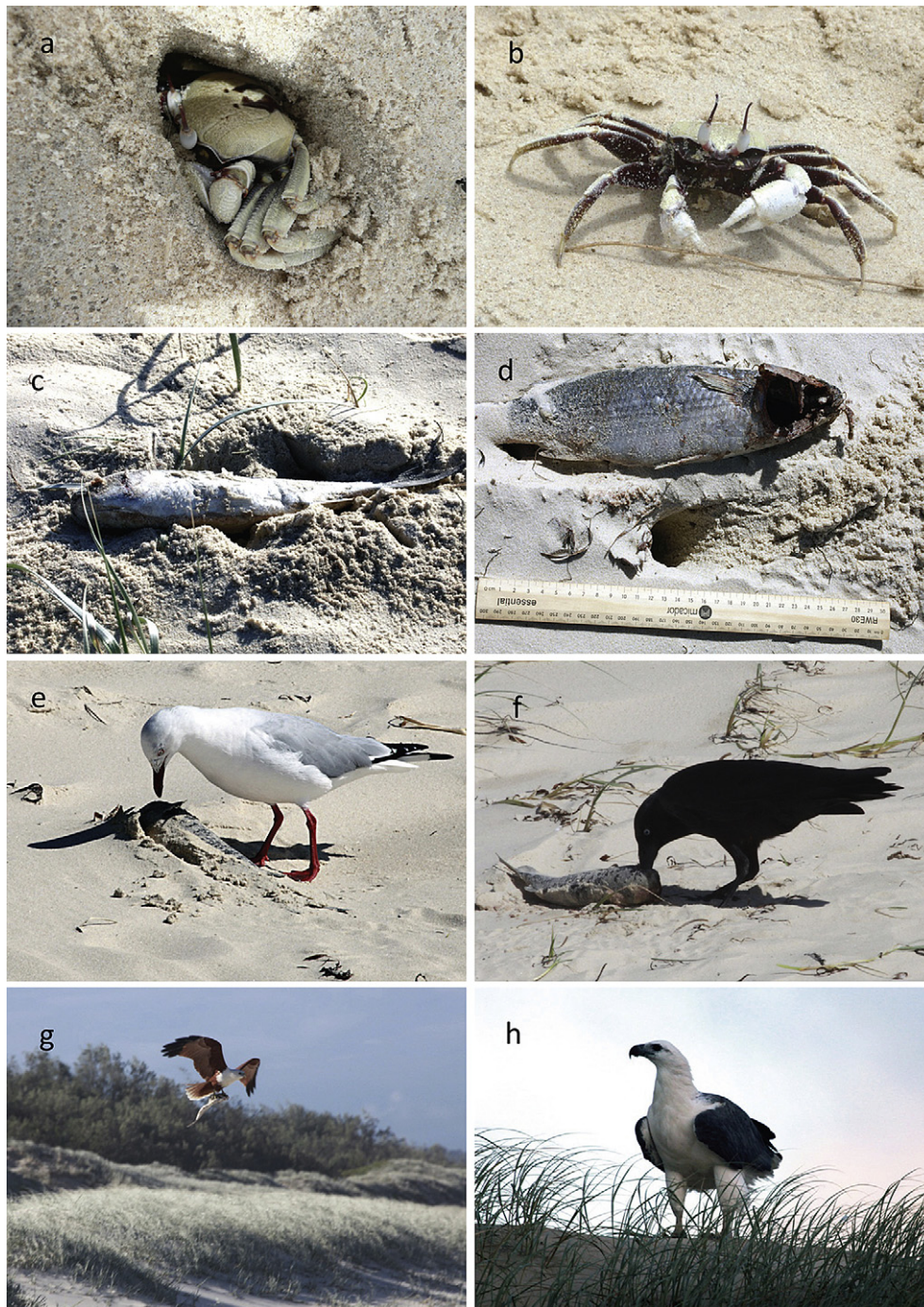
### 4. Discussion

Our experimental augmentation of carrion supply demonstrated bottom-up control of consumers. Scavengers are a commonly reported component of the beach fauna, encompassing a wide diversity of taxa and a broad spectrum of carrion types (Table 2) (Morton and Britton, 1991; McKillup and McKillup, 1994,

Table 1

Occurrence of vertebrate scavengers in the experimental plots, based on either direct observations or tracks/prints left in the sand. Tabulated values are the number of plots (max  $n = 9$ ) with a positive record.

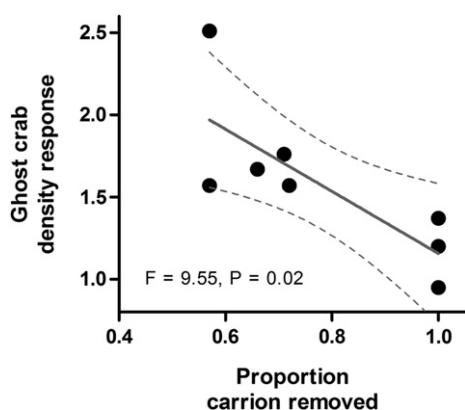
Vertebrate scavenger	Day 2	Day 4	Day 5	Day 6	Experiment
Red fox	6	5	6	6	8 (89%)
Australian pied oystercatchers	1	2	6	6	8 (89%)
Silver gulls	1	2	4	4	6 (67%)
Raptors (Brahminy kite, whistling kite, white-bellied sea eagle) & crows	2	0	5	4	9 (100%)



**Fig. 3.** Ghost crabs and avian scavengers at the beach–dune interface region observed during the study. a) ghost crab (*Ocypode ceratophthalma*) emerging from a burrow and b) active on the beach surface; c) example of intense burrowing activity of crabs around and under a freshly deposited fish carcass; d) example of a burrow opening of a ghost crab next to a fish carcass showing freshly excavated sediment; e) Silver gull (*Chroicocephalus novaehollandiae*) and f) Torresian crow (*Corvus orru*) feeding on fish carrion; g) Brahminy kite (*Haliastur indus*) lifting a fish carcass from an experimental plot; h) white-bellied sea eagle (*Haliaeetus leucogaster*) perched on the primary dune above an experimental plot to which fish carcasses had been added. All photos T. A. Schlacher.

1995; Morton and Britton, 2002, 2003; Morton and Jones, 2003; Morton, 2008). Yet important functional ecological aspects of scavenging remain to be quantified in beach systems, across four broad thematic areas: i) population and community-wide effects of altered carrion resources, ii) the spatial structure of carrion-based food webs on sedimentary shorelines, iii) properties of resource pulses and their influence on scavenger dynamics, and iv) interactions between scavengers.

Our experiment showed a clear aggregative response of scavengers to carrion, significantly changing local densities of consumers to create spatial concentrations of intense feeding along the shore. Although the duration of the experiment did not allow us to measure numerical responses in the populations, these are not implausible for the scavengers examined. Enhanced food resources have been shown to have population-wide consequences for consumers on shorelines, positively affecting reproductive output and



**Fig. 4.** Numerical response of invertebrate scavengers (ghost crabs) as a function of the proportion of carrion removed by vertebrate scavengers. The metric of scavenger response is the change in burrow counts recorded in individual plots after experimental additions of fish carcasses.

**Table 2**  
Examples of published records of carrion and scavengers on beaches.

Scavenger	Carrion type	Location	Reference
<b>Invertebrates</b>			
Whelks ( <i>Bullia rhodostoma</i> , <i>B. digitalis</i> )	Cnidarians	Eastern Cape, South Africa	(Brown, 1961, 1971, 1982)
<i>Nassarius festivus</i>	Fish carrion	Hong Kong	(Morton and Yuen, 2000)
<b>Isopods, Polychaetes, Beetles</b>	Various drift carrion	California, USA	(Dugan et al., 2003)
Ghost crabs ( <i>Ocypode</i> spp.)	Fish and invertebrates	Eastern Australia, global	This study; (Cott, 1929; Wolcott, 1978)
<b>Reptiles</b>			
Cottonmouth snake ( <i>Agkistrodon piscivorus conanti</i> )	Various dead fish	Gulf Coast Islands, USA	(Lillywhite and McCleary, 2008; Lillywhite et al., 2008)
<b>Birds</b>			
White-Bellied Sea eagle ( <i>Haliaeetus Leucogaster</i> )	Various mammals, other birds, fish, crabs	Coastal areas, Australia	(Smith, 1985)
Whistling kite ( <i>Haliastur sphenurus</i> )	Various terrestrial and marine animals (rodents, reptiles, fish)	Coastal areas, Australia	(Gosper, 1983)
Brahminy kite ( <i>Haliastur indus</i> )	Fish, crabs & other marine carrion	Coastal areas, Australia	(Smith, 1992; Lutter et al., 2006)
<b>Mammals</b>			
Coyote ( <i>Canis latrans</i> )	Seals, birds, sea turtles, fish, marine arthropods	California, USA	(Rose and Polis, 1998)
Tasmanian devil ( <i>Sarcophilus harrisii</i> )	N/A	Tasmania, Australia	(Moore, 2002)
Brown hyena ( <i>Parahyaena brunnea</i> )	Seals	Skeleton Coast, Namibia	(Skinner et al., 1995; Kuhn et al., 2008)
Black-backed jackal ( <i>Canis mesomelas</i> )	Seals, birds, fish	Skeleton Coast, Namibia	(Avery et al., 1987)
Dingo ( <i>Canis lupus dingo</i> )	Dugong and whale carcasses	Fraser Island, Australia	(Moore, 2002)
Lion ( <i>Panthera leo</i> )	Seals	Skeleton Coast, Namibia	(Bridgeford, 1984)

population sizes in both invertebrate and vertebrate scavengers benefiting from imports of marine matter (Spiller, 1992). Because true numerical responses depend mainly on the generation time of the consumers, these would be predicted to occur within months for ghost crabs, but may take years for raptors. Notwithstanding the time scales required, enhancing local populations of scavenging raptors on shorelines with carrion augmentations offers an opportunity to investigate a potentially novel conservation tool for threatened bird species (along the lines of augmented feeding of hen harriers, a vulnerable raptor in the United Kingdom (Thompson et al., 2009)).

Aggregative responses of scavengers were distinct in the experimental plots. A central goal of ecology is to derive generalizations about processes that are applicable to broader temporal and spatial scales. In this sense, ‘scaling-up’ from small-scale field experiments to larger areas will be important. Carrion addition experiments, like the one conducted here, are highly amenable to examine such scale-dependence of ecological processes. At regional scales, the links between scavenger dynamics and their food supply can be determined by manipulating carrion availability among beaches separated sufficiently to avoid the mixing of consumer populations (i.e. islands or geographically distant beaches). This approach would also lend itself to a still wider scale, encompassing latitudinal gradients and different biogeographic provinces.

Carrion removal in our experiment was rapid and efficient, with most fish carcasses having been completely consumed within a day. This high rate of carrion detection and consumption on beaches rivals, or exceeds, that of other habitats (reviewed by DeVault et al., 2003). It demonstrates that scavengers on beaches are highly adapted to exploit resource bounties in the form of pulsed carrion inputs. More generally, pulsed resources have a major influence on consumer dynamics and food webs across many ecosystems (Yang et al., 2010). Factors that modify ecological responses to pulsed resources include the quality, quantity, duration and predictability of the inputs. Although it seems logical to posit that carrion constitutes an unpredictable resource pulse on sandy shores, patterns of marine carrion inputs to beach food webs are essentially unknown. Standing stocks of carrion in the size range of fish carcasses are usually low on beaches. This does not necessarily reflect low inputs of carcasses, but, alternatively, could result from rapid location and consumption of carcasses by efficient scavengers as shown here.

Ghost crabs aggregated in significantly lower numbers in experimental plots where more intense scavenging activity by birds and foxes had removed more carrion (Fig. 4). This negative relationship between one consumer’s response as a function of another consumer’s use of a common resource strongly suggests asymmetrical biological interactions between invertebrate and vertebrate scavengers. There are several, interrelated mechanisms that are plausible to explain the observed relationship between diminished aggregative responses of ghost crabs in situations when vertebrate scavengers had removed more of the available carrion: 1.) competition for carrion, resulting in lower food availability to ghost crabs due to removal of carcasses by the competitively dominant vertebrate scavengers, 2.) lower foraging activity of ghost crabs when vertebrate scavengers are more abundant or active, due to higher predation risk for crabs – a trait-mediated effect (sensu Werner and Peacor, 2003), and/or 3.) predation by birds and foxes of ghost crabs that had aggregated around fish carcasses. Carrion falls and scavengers can profoundly influence predator–prey dynamics and competition (Cortés-Avizanda et al., 2009). Because ghost crabs are prey for birds on beaches (Schlacher pers. obs.) and vertebrates remove large amounts of carrion, each of the three mechanisms – competition, trait-mediated effects, predation – can operate in this food web. Future experiments that distinguish between multiple biological

interactions and determine their interaction strengths in these food webs will be important to determine the structure and dynamics of scavenging food webs at the beach–dune interface.

### Acknowledgements

A warm “Thank YOU” to Tara Nielsen and Sam Masters for their unfaltering assistance in the field, showing steely resolve before the enemy ‘mullet odour’: you never made a ghost of crabs.

### References

- Avery, G., Avery, D.M., Braine, S., Loutit, R., 1987. Prey of coastal black-backed jackal *Canis mesomelas* (Mammalia: Canidae) in the Skeleton Coast Park, Namibia. *Journal of Zoology* 213 (1), 81–94.
- Barreiro, F., Gómez, M., Lastra, M., López, J., De la Huz, R., 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. *Marine Ecology Progress Series* 433, 65–74.
- Beasley, J.C., Olson, Z.H., Devault, T.L., 2012. Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos* 121 (7), 1021–1026.
- Bridgford, P.A., 1984. Unusual diet of the lion *Panthera leo* in the Skeleton Coast Park, Namibia. *Madoqua* 14, 187–188.
- Brown, A.C., 1961. Physiological-ecological studies on two sandy-beach gastropoda from South Africa: *Bullia digitalis*; *meuschen* and *Bullia laevissima* (gmelin). *Zoomorphology* 49 (6), 629–657.
- Brown, A.C., 1971. The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 1: introduction. *Transactions of the Royal Society of South Africa* 39 (3), 247–279.
- Brown, A.C., 1982. The biology of sandy-beach whelks of the genus *Bullia* (Nassariidae). In: Barnes, H., Barnes, M. (Eds.), *Oceanography and Marine Biology: an Annual Review*. Aberdeen University Press, pp. 309–361.
- Cortés-Avizanda, A., Selva, N., Carrete, M., Donazar, J.A., 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic and Applied Ecology* 10 (3), 265–272.
- Cott, H., 1929. Observations on the natural history of the racing-crab *Ocypode ceratophthalma* from Beira. *Proceedings of the Zoological Society of London* 1929, 755–765.
- DeVault, T.L., Rhodes Jr., O.E., Shivik, J.A., 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102 (2), 225–234.
- Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science* 58 (Suppl. S), 25–40.
- Dugan, J.E., Hubbard, D.M., Page, H.M., Schimel, J.P., 2011. Marine macrophyte wrack inputs and dissolved nutrients in beach sands. *Estuaries and Coasts*, 1–12.
- Gosper, D.J., 1983. Birds in the Richmond River district, NSW. *Corella* 7, 7–13.
- Houston, D.C., 1979. The adaptation of scavengers. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, pp. 263–286.
- Kuhn, B.F., Wiesel, I., Skinner, J.D., 2008. Diet of brown hyenas (*Parahyaena brunnea*) on the Namibian coast. *Transactions of the Royal Society of South Africa* 63 (2), 150–159.
- Lillywhite, McCleary, 2008. Trophic ecology of insular cottonmouth snakes: review and perspective. *South American Journal of Herpetology* 3, 175–185.
- Lillywhite, H.B., Sheehy, C.M., Zaidan, F., 2008. Pitviper scavenging at the intertidal zone: an evolutionary scenario for invasion of the sea. *BioScience* 58 (10), 947–955.
- Lutter, H., McGrath, M., McGrath, M., Debus, S., 2006. Observations on nesting brahminy kites *Haliastur indus* in Northern New South Wales. *Australian Field Ornithology* 23 (4), 177.
- McKillup, S.C., McKillup, R.V., 1994. The decision to feed by a scavenger in relation to the risks of predation and starvation. *Oecologia* 97 (1), 41–48.
- McKillup, S.C., McKillup, R.V., 1995. The responses of intertidal scavengers to damaged conspecifics in the field. *Marine and Freshwater Behaviour and Physiology* 27 (1), 49–57.
- Moore, P.G., 2002. Mammals in intertidal and maritime ecosystems: interactions, impacts and implications. *Oceanography and Marine Biology* 40, 491–608.
- Morton, B., Britton, J.C., 1991. Resource partitioning strategies of two sympatric scavenging snails on a sandy beach in Western Australia. In: Wells, F.E. (Ed.), *The Marine Flora and Fauna of Albany, Western Australia*. Western Australian Museum, Perth, pp. 579–595.
- Morton, B., Yuen, W.Y., 2000. The feeding behaviour and competition for carrion between two sympatric scavengers on a sandy shore in Hong Kong: the gastropod, *Nassarius festivus* (Powys) and the hermit crab, *Diogenes edwardsii* (De Haan). *Journal of Experimental Marine Biology and Ecology* 246 (1), 1–29.
- Morton, B., Britton, J.C., 2002. Holothurian feeding by *Nassarius dorsatus* on a beach in Western Australia. *Journal of Molluscan Studies* 68 (2), 187–189.
- Morton, B., Jones, D.S., 2003. The dietary preferences of a suite of carrion-scavenging gastropods (Nassariidae, Buccinidae) in princess royal harbour, Albany, Western Australia. *Journal of Molluscan Studies* 69 (2), 151–156.
- Morton, B., Britton, J.C., 2003. The behaviour and feeding ecology of a suite of gastropod scavengers at Watering Cove, Burrup Peninsula, Western Australia. In: Wells, F.E. (Ed.), *The Marine Flora and Fauna of Dampier, Western Australia*. The Western Australian Museum, Perth, pp. 147–172.
- Morton, B., 2008. Biology of the swash-riding Moon Snail *Polinices incei* (Gastropoda: Naticidae) preying on the Pipi, *Donax deltooides* (Bivalvia: Donacidae), on the wave-exposed sandy beaches of North Stradbroke Island, Queensland, Australia. *Memoirs of the Queensland Museum – Nature* 54, 303–322.
- Noriga, R., Schlacher, T.A., Smeuninx, B., 2012. Reductions in ghost crab populations reflect urbanization of beaches and dunes. *Journal of Coastal Research* 28 (1), 123–131.
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28, 289–316.
- Rose, M.D., Polis, G.A., 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79 (3), 998–1007.
- Sanchez-Pinero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81 (11), 3117–3132.
- Schlacher, T.A., Richardson, D., McLean, I., 2008. Impacts of off-road vehicles (ORVs) on macrobenthic assemblages on sandy beaches. *Environmental Management* 41, 878–892.
- Schlacher, T.A., Connolly, R.M., 2009. Land-ocean coupling of carbon and nitrogen fluxes on sandy beaches. *Ecosystems* 12 (2), 311–321.
- Schlacher, T.A., de Jager, R., Nielsen, T., 2011. Vegetation and ghost crabs in coastal dunes as indicators of putative stressors from tourism. *Ecological Indicators* 11, 284–294.
- Skinner, J.D., Van Aarde, R.J., Goss, R.A., 1995. Space and resource use by brown hyenas (*Hyaena brunnea*) in the Namib Desert. *Journal of Zoology* 237, 123–131.
- Smith, G.C., 1985. An analysis of prey remnants from Osprey (*Pandion haliaetus*) and White-Bellied sea eagle (*Haliaeetus leucogaster*) feeding roosts. *Emu* 85, 198.
- Smith, J.L.D., 1992. The Feeding Ecology of Brahminy Kites, *Haliastur indus* from South-east Queensland. BSc(Hons) thesis. University of Queensland, Brisbane, Australia.
- Spiller, D.A., 1992. Numerical response to prey abundance by *Zygiella x-notata* (Araneae, Araneidae). *Journal of Arachnology* 20 (3), 179–188.
- Spiller, D.A., Piovio-Scott, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W., Iwata, T., 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology* 91 (5), 1424–1434.
- Thompson, P.S., Amar, A., Hoccom, D.G., Knott, J., Wilson, J.D., 2009. Resolving the conflict between driven-grouse shooting and conservation of hen harriers. *Journal of Applied Ecology* 46 (5), 950–954.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge Univ. Press, Cambridge, U.K., 504 pp.
- Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84 (5), 1083–1100.
- Wilson, E.E., Wolkovich, E.M., 2011. Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26 (3), 129–135.
- Wolcott, T.G., 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fab.) on an ocean beach: scavengers or predators? *Journal of Experimental Marine Biology and Ecology* 31, 67–82.
- Yang, L.H., E.K.F. Byrnes, J., Bastow, J.L., Wright, A.N., Spence, K.O., 2010. A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs by the Ecological Society of America* 80 (1), 125–151.