# Conservation gone to the dogs: when canids rule the beach in small coastal reserves.

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## ABSTRACT

On most developed coastlines, dunes backing ocean beaches constitute an urbanised landscape mosaic containing remnant pockets of small conservation areas. Urbanised beaches are also prime sites for domestic dogs, known to be environmentally harmful in many other settings. It is unknown, however, whether small, protected parcels of dune are adequate for biological conservation and whether dogs compromise their functional conservation objectives. Here we examine, for two small (2 km ocean boundary) reserves in Eastern Australia abutting an urban area, whether such small reserves can continue to function as effective conservation instruments on ocean beaches, using scavenger community composition and efficiency to assess ecosystem function. Two non-native species of canids - domestic dogs (*Canis lupus familiaris*) and red foxes (*Vulpes vulpes*) - were ubiquitous and numerous inside conservation areas, to the point of having become the most abundant vertebrate scavengers at the beach-dune interface, outcompeting native scavengers for wave-cast carrion. Dogs and foxes have effectively supplanted raptors, normally abundant on non-urban beaches in the region, and other avian scavengers, as the principal consumers of animal carcasses both inside the declared reserves and at the urban beach. Whilst the ecological threats posed by foxes are widely and intensively addressed in Australia in the form of fox-control programs, dog controls are less common and stringent. Our data emphasize, however, that managing domestic dogs may be required to the same extent in order to maintain key forms and functions in coastal reserves situated close to urban areas.

**Keywords:** sandy shores; conservation; scavengers; invasive species; domestic dogs; apex predators; red foxes; reserves

## 1. Introduction

Conservation planning and practice usually operate based on spatial patterns of features, whilst conserving processes is much more rarely practiced (Klein et al. 2009). Considering processes in conservation is however, important, chiefly because biodiversity features are generated and maintained by processes (Pressey and Bottrill 2009), and because processes connect populations, food webs and habitats across ecosystem boundaries (Schlacher and Connolly 2009).

Arguably, biological transformation of organic matter is one of *the* pivotal processes in most ecosystems. Scavengers that consume animal carcasses are central to this function (Barton et al. 2013; Wilson and Wolkovich 2011), including the processing and translocation of marine necromass on ocean shores (Schlacher et al. 2013b; Schlacher et al. 2013c).

Conservation reserves are the principal tool for protecting and managing biodiversity and ecological processes (Margules and Pressey 2000). Whilst conservation practitioners regularly invest in a diverse portfolio of activities aimed at protecting natural features and functions (e.g. controlling invasive species, fire management, re-vegetation; Wilson et al. 2007), the acquisition, or designation, of land and sea to create reserves remains the chief tool in most conservation programs (Pressey and Bottrill 2009; Pressey et al. 2007). Many of these conservation programs increasingly have to address threats associated with urban expansion (Noriega et al. 2012; Sushinsky et al. 2013).

Ocean beaches are focal points for urban expansion. The attractiveness of beaches is frequently the *raison de etre* for widespread habitat loss and transformation in the coastal fringe, driven by extensive land conversion through housing developments and associated infrastructure (McLachlan et al. 2013; Noriega et al. 2012). Dunes backing beaches represent real estate of immense monetary value and new developments outside traditional coastal cities often centre on attractive ocean beaches (Nordstrom et al. 2011). These large-scale transformations of the coastal landscape, particularly of sandy shorelines, propagate to widespread ecological changes that can have serious ramifications for biodiversity and key ecological processes (Schlacher et al. 2014).

Biodiversity conservation in urban areas and at the urban fringe provides large social and health benefits to residents (Sushinsky et al. 2013). Conservation planning is possible in areas earmarked for urban expansion (Bekessy et al. 2012), but is very rarely practiced on sandy beaches (Harris et al. 2013). Instead, management of sandy shorelines usually seeks to enhance recreational opportunities and to maximise economic values (e.g. housing, tourism, mining; Nordstrom 2000; Schlacher et al. 2007). This emphasis on social and economic issues has shaped many sandy coastlines into mosaics where the expansion of human land uses has limited and constrained conservation areas to small reserves (Lucrezi et al. 2009). It is unrealistic to expect that the dominance of humans, their activities and impacts will diminish in coastal landscapes formed by sandy beaches. It is, however, realistic, and of importance to conservation, to ask whether small remnant reserves on sandy coastlines can function as effective conservation instruments – this is one of the questions addressed in this paper.

Free-ranging domestic animals that encroach on conservation areas can significantly reduce the effective area protected (Wierzbowska et al. 2012), with multiple ecological impacts that compromise conservation efforts attributed to dogs (Hughes and Macdonald 2013; Silva-Rodríguez and Sieving 2012; Weston and Stankowich 2014). Because beaches are prime recreational sites for dog owners and their animals, we also ask whether dogs can significantly alter a key ecological process on marine shorelines inside and outside reserves: consumption and translocation of marine animal carcasses cast ashore.

## 2. Materials and Methods

### 2.1. Metrics

We used two complementary classes of scavenging metrics to test for reserve effects on sandy beaches in a partly urbanised landscape: i) characteristics of the scavenger guild (i.e., abundance, distribution, diversity and species composition of carrion consumers; identity of species feeding first at carcass), and ii) quantitative measures of carrion consumption efficiency (i.e., time to carcass detection and removal, fraction of carcasses removed; Schlacher et al. in press). The expectations were that the scavenger guild in reserves would comprise more raptors that would consume carrion more quickly and completely. Conversely, urban beaches were expected to support scavengers usually associated with human settlements (e.g. crows, gulls, foxes) that may also differ in how efficient they consume beach-cast carrion (sensu Huijbers et al. 2013).

## 2.2 Study area

The effects of small coastal reserves on beach scavenging were measured in southeast Queensland on the east coast of Australia (Fig. 1). This is one of Australia's fastest-growing regions, where much of the population growth and ongoing urbanisation is concentrated in a narrow coastal strip (Noriega et al. 2012). Development is usually aggregated on dunes landwards of ocean beaches, having led to a situation where most coastal dunes have been converted to housing and infrastructure (Lucrezi et al. 2010). Coastal dunes without houses remain only in the form of a few small landscape fragments interspersed between urban areas; several of these fragments have, however, been assigned formal conservation status in the region. (http://www.nprsr.qld.gov.au/parks/noosa/about.html.)

We studied two conservation areas separated by an urbanised stretch of dunes located on the Sunshine Coast (Fig. 1). These reserves, whilst small in extent, represent the only remaining coastal dune fragments assigned formal conservation status outside of larger national parks in the region. The reserves cover 1.8 and 2.1 km of shoreline and are separated by a 5km stretch of developed beach (Fig. 1). As measures of urbanisation we counted, using Google Earth, the number of dwellings and the number of beach access paths crossing the dunes. The spatial unit for these counts were contiguous 0.5 x 0.5 km quadrats aligned parallel to the shore, with the ocean-facing edge of each quadrat positioned at the dune-beach edge.

## 2.3 Field methods

Carrion consumers were sampled using motion-triggered cameras (ScoutGuard SG560Z-8M with digital passive infrared sensors) baited with two fish carcasses each (sea mullet, *Mugil cephalus*, a species commonly found in the surf-zone of tropical to temperate beaches worldwide). Cameras were placed at the seaward edge of the dunes where marine carrion naturally accumulates. Deployments were made within 2 h of sunrise and retrieved after 24 h following methods detailed in Huijbers et al (2013).

We sampled scavengers every 7 days for 13 consecutive weeks from 03 June to 26 August 2013, yielding a total of 757 valid records of feeding from 164 successful camera deployments. Forty-four camera deployments were compromised, 19 from reserves and 25 from the urban beach. The main reasons for deployment failure were, in descending order frequency: theft, vandalism, removal of fish, malfunction of the camera, and inimical weather factors.

The locations of camera sites along the shore followed a stratified random design. The coastline in each sector was first divided into equal-length segments, followed by random positioning of deployment sites within individual segments (constrained to fall within 200m of the centre of segments to achieve adequate dispersion); mean distances between sites was 551 m (se 141 m, min. 136 m, max. 858 m). Eight sites were located inside reserves and eight sites outside the reserves on the urban beach (Fig. 1).

### 2.4. Data analyses

Multivariate variation in the species composition of the scavenger assemblages was spatially partitioned with Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001), containing the fixed factor *'Reserve'* and the random factor '*Site*' (nested within 'Reserve'). The same design structure was used for spatial contrasts analysed with Generalized Linear Models for the univariate metrics of scavenging (i.e., time to carcass detection, time to removal of carcass, carcasses removed); models for carcass removal (a binary outcome) used logit-link functions (Quinn and Keough 2002).

We modelled times to carcass detection and removal (continuous) and the probability of complete carcass removal (binary; defined as an individual fish carcasses being no longer present on the beach after 24 h) in response to several human and biological factors. Saturated Generalized Linear Models (GLZ) contained two human predictor variables, *'houses'* and *'tracks'* (i.e. beach access paths cut through the dunes, connecting the beach with roads, houses and carparks), and nine biological predictors in the form of presence records for a scavenger species in individual camera deployments i.e. *'fox'* [red fox, *Vulpes vulpes*], *'dog'* [*Canis lupus familiaris*], *'brahminy kite'* [*Haliastur indus*], *'torresian crow'* [*Corvus orru*], *white-bellied sea eagle'* [*Haliaeetus leucogaster*], *'white-faced heron'* [*Egretta novaehollandiae*], *'rat'* [*Rattus* spp.], *'silver gull'* [*Chroicocephalus novaehollandiae*], and *'whistling kite'* [*Haliastur sphenurus*]) Model performance was evaluated using the corrected Akaike Information Criterion (AICc) based on all possible combinations of variables used in model building (Burnham et al. 2011; Symonds and Moussalli 2011). A multi-model inference approach was employed to assess the contributions of individual variables based on their summed Akaike weights (Anderson 2008); summed AICc weights (w+) provide relative probabilities of variable importance, with variables < 0.3 likely to be of minor or no importance (Burnham and Anderson 2002).

# 3. Results

## 3.1. The scavenger guild

Dogs, none of which was a native dingo, and torresian crows were the most abundant beach scavengers, recorded in 100 of 164 camera deployments (61 %, Table 1). Three other scavenger species (brahminy kites, red foxes, silver gulls) occurred at moderate to low frequencies of 12 - 21%, whilst all remaining scavengers (whistling kites, white-faced herons, white-bellied sea eagles, rats, cats) were rare, occurring in 2 to 6 deployments only (Table 1).

The structure of the scavenger assemblage was very similar (Bray-Curtis similarity = 71 %) between beach sectors inside and outside of the small coastal reserves (Table 1; Fig. 2). We detected only a weak (ANOSIM, R = 0.09; PERMANOVA, P = 0.09) separation of scavenger guild composition between beaches fronting conservation areas and beaches fronting urban areas: both harboured a closely-matched suite of carrion consumers at comparable frequencies (Table 1, Fig. 2).

Remarkably, domestic dogs occurred, on average, at the same frequency inside the reserves as they did outside (Fig. 3). Birds of prey were generally rare and there was no distinct pattern suggesting significantly higher frequencies of any raptor species inside the reserves.

Somewhat paradoxically, in the southern coastal reserve, dogs were recorded at extraordinary high frequency, scavenging on fish carcasses in up to 92% of samples, the highest incidence of scavenging of any one species recorded throughout the study area (Figs. 1, 3 & 4).

Dogs outperformed all other native scavengers in detecting fish carcasses. Dogs were the first scavenger species to feed on fish carcasses on the beach more often than any other species. Out of 164 successful experimental camera deployments, dogs fed first on the carrion 69 times (42%), followed by torresian crows (n = 58), then brahminy kites (n = 14); all other species detected fish carrion in fewer than seven cases. In terms of the frequency of first encounters per site, dogs most often arrived - as the first scavenger species - at the carrion in nine out of 16 sites (56%), and were second at the carcass in a further four sites. At every site, dogs were amongst the top three species that most often detected a carcass first.

Mainly because dogs dominated carrion detection throughout the study area, we detected only a weak spatial separation of assemblages based on the composition of species feeding first at carcasses inside and outside of reserves (ANOSIM, R = 0.12; PERMANOVA, P = 0.10). A higher proportion of carcasses was detected by dogs inside the reserves (48%) than in urban areas (35%), perhaps because most owners unleash their dogs on the beach inside the reserves. Brahminy kites accounted for 14% of first carcass detections in urban areas, but for only 3% inside reserves; all other species showed comparable, and generally low, carrion detection frequencies irrespective of location (Table 1).

## 3.2 Scavenging metrics

Scavengers arrived at carcasses slightly quicker inside the reserves (3.12 ± 0.43 h) than outside (3.75 ± 0.61 h), but means did not differ significantly (GLM, P = 0.58). Time to removal of carcasses was highly variable. Although scavengers took, on average, two hours longer to remove carcasses from urban beaches than from beaches bordering conservation reserves, means of removal times did not differ significantly between reserves and urban beaches (reserves: 7.76 ± 0.61 h, urban: 9.99 ± 0.93 h; GLM, P = 0.23).

Of the 328 fish carcasses that we had experimentally deployed, 308 (94%) were completely scavenged (i.e., removed from the beach) within 24 hours. All but five fish, of 174 deployed inside reserves, were removed by scavengers, yielding a 97% scavenging efficiency. By comparison, on urban beaches, overall scavenging efficiency was lower at 90% (139 of 154 fish removed). Thus, although carcass removal rates were high in both sectors, the probability of a fish being completely scavenged was significantly (logistic GLZ, $P = 0.014$) higher inside reserves (95CI of pred. removal prob.: 0.93 - 0.99) than on the urban beach (95CI of pred. removal prob.: 0.84 - 0.94, Fig. 4).

### 3.3. Factors shaping scavenging attributes

Scavengers arrived quickest at carcasses in the southern reserve and in the centre of the urban beach. Conversely, carcass detection times were longer at the edges of the urban beach and in the northern conservation area (Fig. 4). Time to contact was best predicted by the presence of crows, dogs and brahminy kites - species that generally detected carrion rapidly after experimental placement. Foxes took markedly longer to detect carrion, most likely a consequence of their nocturnal foraging behaviour (Table 2). The density of houses and tracks were weak predictors of detection time (Table 2).

All fish were removed by scavengers from the beach at the southern and northern edges of the study area, whereas scavenging efficiency was lower (~80%) at a number of urban sites (Fig. 4). Housing density was the most important predictor of the probability that an entire carcass became scavenged (i.e., removed within 24 h from the beach), with fewer carcasses removed from beach sites that were backed by more houses (Table 2). Foxes, which were captured on cameras more often in the southern conservation reserve – where carcass removal was 100% at three out of four sites inside that reserve - had a positive effect on removal rates, whereas dogs had the opposite effect (Table 2).

For those carcasses detected by scavengers, time to complete removal was generally shortest at the edges of the study area (Fig. 4). Foxes, which forage nocturnally, were the most important predictor of carcass removal time; foxes generally arrived at carrion much later, but then they scavenged most of the carcasses not previously detected or completely consumed, by diurnal scavengers. A broad suite of other scavengers (rats, white-bellied sea eagles, dogs, and brahminy kites) also affected removal times of carcasses (Table 2).

Across all three metrics of scavenging efficiency that we modelled (i.e., detection time, removal rate, removal time), the presence of foxes was the most important predictor. Foxes were included in the best model for every predictor and ranked first (time to removal) and second (detection time and removal rate) based on variable weights (Table 2). Dogs ranked second in terms as predictors of scavenging efficiency (Table 2). Thus, an invasive mammal (red fox) and a domestic mammal (dog) explained a large proportion of scavenging patterns on beaches, whereas houses and tracks (essentially proxies for a location effect with respect to urban and conservation areas) were less influential predictors (Table 2).

# 4. Discussion

## 4.1. Functional reserve performance

Ecosystems globally lose habitat to agriculture, forestry, industry, mining, and expanding human settlements. Conservation areas are often, but not always, effective responses to these threats (Pressey and Bottrill 2009). Significant proximate threats, that continue to transform beaches and coastal dunes worldwide, include extensive habitat conversions by urban development, intensive recreation and tourism, the use of off-road vehicles, and impacts from non-native animals, which can be domestic, invasive, and/or feral (Defeo et al. 2009; Schlacher et al. 2007). Conservation areas are, however, uncommon for beaches or seldom effective where they do exist (Harris et al. 2014; Schlacher et al. 2014; Schlacher et al. 2013a).

Here we present data showing that a core ecological function – removal of wave-cast animal carcasses – has switched from native raptors to non-native mammalian carnivores in a beach and dune reserve invaded by domestic dogs and non-native red foxes. By comparison, on regional beaches where these two mammalian species are much less abundant, a large part of scavenging is done by raptors (Huijbers et al. in press; Huijbers et al. 2013). This functional replacement can theoretically be reversed, as reduction or elimination of both foxes and dogs is well within the practicable bounds of active wildlife management (e.g. baiting, shooting), especially in reserves (Dowling and Weston 1999; Kinnear et al. 2002). Arguably, carcass removal continues inside the coastal reserves, suggesting that net ecological function is maintained despite an abundance of dogs and foxes. Whilst dogs and foxes can indeed be efficient consumers of carrion on beaches, their scavenging activity cannot be considered truly functionally equivalent because of the numerous, often massive, deleterious impacts that both foxes and dogs cause to native wildlife in coastal areas of Australia (Schlacher et al. 2014; Weston et al. 2014b).

## 4.2. Foxes and dogs on beaches: ecological implications

Most fundamentally, the role of reserves is to separate elements of biodiversity and ecological function from the processes that threaten their existence in the wild (Sarkar et al.

2006). The presence of foxes and the large numbers of domestic dogs that we recorded within reserves run, however, counter to conservation objectives.

The red fox is a non-native carnivore in Australia, being a formidable exotic species, widespread and abundant across the continent (Letnic et al. 2012). The red fox was introduced in the 1850s and only became established in the 1870s, well after the colonies ceased to be penal settlements. Indeed, it was introduced for the recreational benefit of the squattocracy – a class whose association with the penal colonies was by that stage quite distant.

Red foxes are generalist predators, consuming, often as cursorial hunters, a broad spectrum of prey items (Mitchell and Banks 2005). Foxes make extensive use of sandy beaches in Australia (Meek and Saunders 2000), and in coastal populations the catholic diet of foxes encompasses carrion that is scavenged from the strandline (Huijbers et al. 2013). Foxes have supplanted similar-sized endemic carnivores in many regions of Australia and now constitute a serious threat to biodiversity, including extirpation of many native vertebrates (McKenzie et al. 2007). Thus, 'fox control' is a widespread management practice in Australia and eradication programs that use a variety of methods (e.g. leg-hold trapping, baiting, hunting, spotlighting, den searches) are carried out by several levels of government (Rout et al. 2013). The local government authority also attempts to control fox populations (both inside and outside the reserve), but our data show that foxes continue to be present throughout the study area, including regular observations of scavenging activity inside reserves (Fig. 1).

In Australia there is a dog for every six people (Hughes and Macdonald 2013). Dogs have numerous destructive impacts on wildlife (reviewed by Hughes and Macdonald 2013; Weston and Stankowich 2014; Young et al. 2011). On the particular beach sites studied here, dogs have effectively supplanted wild scavengers, particularly raptors, which are the principal diurnal scavengers on other, less urbanised, beaches in the region. Impacts on native wildlife are likely to be in the form of competition for food (i.e., removal of marine carrion washed up naturally on beaches by dogs).

While our results were unexpected, dogs have previously been implicated as scavengers Castle et al. (2013) providing some rather dramatic, and unexpected, supporting evidence that domestic dogs can be scavengers of dead fish on beaches. Castle et al. (2013) report that red tides along the Texas coasts caused the death of numerous fish that washed ashore on the beaches, and following this carrion pulse, several coyotes and dogs died or had to be euthanized. The likely cause of the canids' deaths was poisoning by presumptive ingestion of toxic dead fish (Castle et al. 2013).

Animals exposed to carnivores react to predation risks by altering distributions, behaviours or temporal use patterns of landscape elements and resources (Kloppers et al. 2005). It is plausible that dogs also have non-lethal impacts on birds on beaches, possibly via fear-mediated effects. Silva-Rodriguez and Sieving (2012) show that dogs, via predation and non-lethal harassment, shape the landscape-scale distribution of endangered prey species. Thus, when dogs are present on beaches, birds may perceive a 'landscape of fear' (Brown et al. 1999; Laundré et al. 2001), possibly contributing to the low scavenging rates by birds recorded in this setting.

Beyond the scavenger system, effects of dogs in beach and dune ecosystems are likely to be more numerous and severe than consumption of carrion resources, particularly in terms of the impacts of dogs on nesting birds and turtles (Baudains and Lloyd 2007; Burger and Gochfeld 2013; Weston and Elgar 2005). These putative effects remain to be quantified for the reserve in question.

### 4.3. Dog management on beaches

Managing dogs on beaches is a complex and often highly politically issue (Miller et al. 2014; Williams et al. 2009). Fundamentally, because people hold diverse and opposing views about dogs in the environment, managing dogs is often about managing people, their expectations, behaviours, and attitudes (Holmberg 2013). Most coastal managers have to address competing issues, and managing dogs on beaches can therefore be considered not to be fundamentally different from managing beaches and dunes for other types of uses (Dugan et al. 2010; Schlacher et al. 2006). However, major differences are that the presence of dogs is often incompatible with conservation objectives (Weston and Stankowich 2014;

Young et al. 2011), and that environmental impacts attributable to dogs are more severe than those resulting from other recreational activities, except the highly destructive consequences of driving off-road vehicles (Schlacher et al. 2013d; Weston et al. 2014b).

Zoning of beaches for different forms of dog use (e.g. off-leash, on-leash always, on-leash temporary) is widely practiced, but compliance with leasing regulations is often low and dog zoning is rarely done for conservation objectives. Dogs can be a public health issue (e.g. risk of infections and bites; Kennedy and Collignon 2008). Zoning tries to reduce this risk by excluding dogs from popular swimming areas or regulating for them to be leashed there at all times. Dogs are allowed off the leash on the fringes or outside of recreation nodes; this practice concentrates dogs in parks and nature reserves where conflicts with wildlife become amplified (cf. Fig. 1). This type of zoning partly explains the prevalence of dogs reported by us inside the reserves bordering urban beaches: dogs spill over into conservation areas in large numbers as a result of being banned in urban nodes, and because dog walkers seek more 'natural' environs for their canine's leisure activities where they can let their dogs run free (see also (Maguire et al. 2013). Thus, current practices in urban planning may have paradoxical outcomes for wildlife, concentrating dogs in conservation areas. This situation – dogs being quasi ubiquitous in public green spaces and becoming concentrated in reserves – is not uncommon elsewhere (Weston et al. 2014a). It calls for land-use planning decisions to more clearly articulate the precise objectives of green spaces (e.g. dog recreation, wildlife conservation, non-dog recreation), and to avoid mixing of use types that are inherently incompatible (e.g. free-ranging dog exercise areas versus bird habitats).

If we accept that dogs can in certain situations create a landscape of fear (plausible but not demonstrated at our study site), dogs may have unusual applications in wildlife management. For example, dogs could be used to control the distribution of wildlife species conflicting with human interests (e.g., displacing or changing the behaviour of herbivores in agricultural areas or forestry plantations; Cromsigt et al. 2013; Miller et al. 2001). This thought-provoking logic for morphing dogs into a management tool to intentionally displace animals applies - in reverse - in a conservation context: dogs should, logically, be displaced from nature reserves to avoid the displacement of native wildlife from reserves.

## 5. Conclusions

Reserves – designed to separate wildlife from human pressures – are a pivotal instrument in biological conservation (Huijbers et al. 2014). We asked the general question whether small reserves established for sandy beaches and coastal dunes can maintain ecological function, where function was defined as the removal of wave-cast marine animal carcasses from the shore by vertebrate scavengers. Carcass consumption was rapid and near-complete both inside and outside reserves. However, this ecological function was fulfilled by invasive red foxes and domestic dogs who dominated the scavenger guilds, a situation quite distinct from raptor-dominated scavenging in larger reserves backed by less urbanised areas in the region. Because dogs and red foxes severely impact native wildlife in Australia, biological efficiency in terms of carcass removal does not constitute ecological equivalency because it comes at a high environmental cost. Thus, controlling dogs and foxes in coastal reserves and elsewhere is critical to maintain ecosystem function. Dog management in particular, calls for fresh approaches that better address multiple expectations of society whilst recognising the incompatibility of coastal wildlife and canids.

## 6. Acknowledgements

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**Table 1**

Comparison (based on SIMPER analysis) between urban beaches and reserves for A - species detected first at carcasses, and B - all species detected as interacting with carcasses during a 24 hour deployment period of baited camera traps. Bold values denote higher frequency of occurrence in either the reserves or urban sites.

**A – species first detecting a carcass**

| Species | Reserves (proportion of camera deployments) | Urban (proportion of camera deployments) | Diss/SD | Contrib% |
|---|---|---|---|---|
| Dog | **48%** | 35% | 1.13 | 20.36 |
| Brahminy kite | 3% | **14%** | 0.94 | 18.78 |
| Silver gull | **7%** | 1% | 0.98 | 13.99 |
| Whistling kite | 0% | **5%** | 0.98 | 12.35 |
| Fox | **5%** | 4% | 0.95 | 12.14 |
| Torresian crow | **36%** | 35% | 1.28 | 11.23 |
| White-faced heron | 0% | **5%** | 0.53 | 8.32 |
| White-bellied sea eagle | **1%** | 0% | 0.37 | 2.83 |

**B – all species interacting with carcass during deployment**

| Species | Reserves (proportion of samples) | Urban (proportion of samples) | Diss/SD | Contrib% |
|---|---|---|---|---|
| Red fox | **22%** | 21% | 1.30 | 16.75 |
| Brahminy kite | 20% | **23%** | 1.38 | 15.78 |
| Silver gull | **13%** | 12% | 1.27 | 14.80 |
| Whistling kite | 1% | **6%** | 1.21 | 11.79 |
| Dog | **64%** | 57% | 1.55 | 10.39 |
| White-faced heron | 0% | **6%** | 0.73 | 8.42 |
| Rat | **3%** | 0% | 0.76 | 6.67 |
| White-bellied sea eagle | **3%** | 1% | 0.66 | 6.03 |
| Torresian crow | 60% | **62%** | 1.02 | 4.96 |

**Table 2**

Contributions of variables to GLZ models used to predict three metrics of scavenging efficiency: 1) time between carcass placement and the first scavenger species arriving at a carcass ('*Time to Detection*'), 2) the proportion of fish carcasses removed ('*Carcasses removed*') , and 3) the time between carcass deployment and its removal ('*Time to Removal*').

Variable contributions are assessed in a multi-model inference approach using cumulative weights, w+(j). Variables in bold, and marked with *, are included in the best (i.e. lowest AICc) model for a particular metric. Variables are ordered by their mean rank across the three metrics of scavenging.

| | **1 - Time to detection** | | **2 - Carcasses removed** | | **3 - Time to removal** | |
|---|---|---|---|---|---|---|
| Predictor Variable | w+(j) | 'best' model | w+(j) | 'best' model | w+(j) | 'best' model |
| Red fox | **0.99** | * | **0.58** | * | **1.00** | * |
| Dog | **0.94** | * | **0.45** | * | **0.71** | * |
| Brahminy kite | **0.82** | * | **0.47** | * | **0.59** | * |
| Tracks | 0.51 | | 0.34 | | **0.92** | * |
| Torresian crow | **0.99** | * | 0.34 | | 0.37 | |
| Houses | 0.35 | | **0.88** | * | 0.40 | |
| White-bellied sea eagle | 0.41 | | 0.35 | | **0.78** | * |
| White-faced heron | 0.41 | | 0.50 | | 0.30 | |
| Rat | 0.33 | | 0.31 | | **0.99** | * |
| Silver gull | 0.42 | | 0.27 | | 0.44 | |
| Whistling kite | 0.42 | | 0.26 | | 0.26 | |

## Figure Captions

**Fig. 1** Location of the study sites in Eastern Australia, comprising two small coastal conservation reserves (green triangles) to the north and south of an urban beach (red circles). Scavengers were surveyed with camera traps baited with fish at the dune-beach interface to mimic the stranding of marine animal carcasses on the upper part of the sandy shore. Animal symbols (foxes and dogs) represent the frequency at which each of these two carnivores was recorded in repeated camera surveys. The labels 'dog', 'crow' and 'brahminy kite' denote which species was most often the first scavenger to feed at the fish carcasses.

**Fig. 2** Ordination diagrams (PCO – Principal Coordinate Analysis) illustrating variation in species composition of the scavenger assemblages based on a) species that detected carcasses first, and b) the full suite of species feeding at carcasses over the deployment period.

**Fig. 3** Spatial patterns in beach land-use (top) and in the abundance of vertebrate scavengers (b-g) that forage at the interface between the dunes and the sandy shore. Abundance estimates for vertebrate scavengers are derived from repeated camera-trap surveys using experimentally-placed fish carcasses, at eight sites located in two small coastal reserves (green triangles) and eight sites fronting an urban beach (red circles). Bars on the right margin of each panel represent the 95% confidence intervals for abundance estimates inside (green) and outside (red) reserves.

**Fig. 4** Spatial variation in scavenging as measured by three complementary metrics: a) time elapsed before scavengers make contact with a deployed carcass, b) the fraction of carcasses completely scavenged (i.e., removed from the site by a scavenger within 24 hours), and c) time elapsed between carcass deposition and removal.

Figure 1

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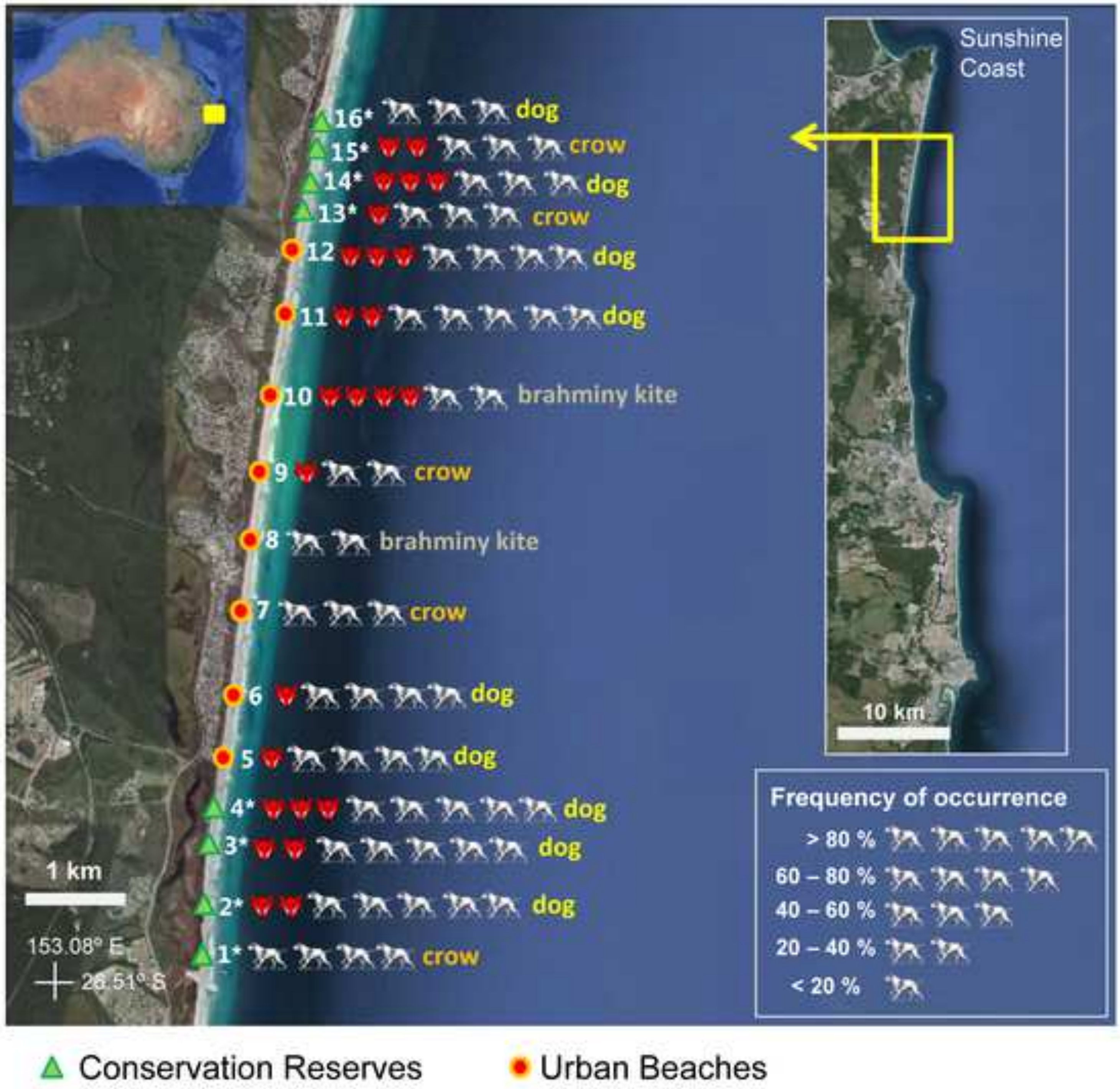

Figure 2
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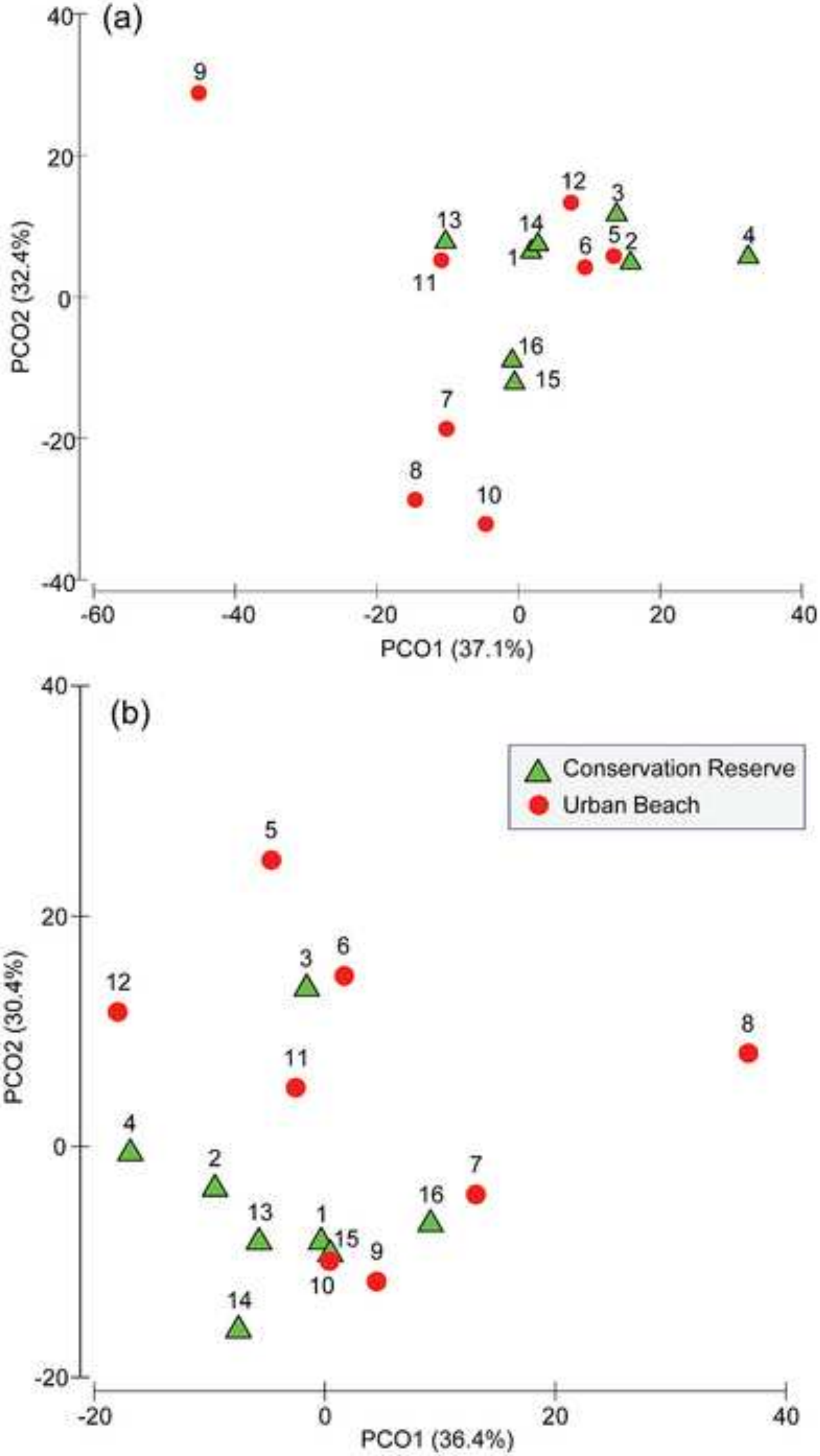

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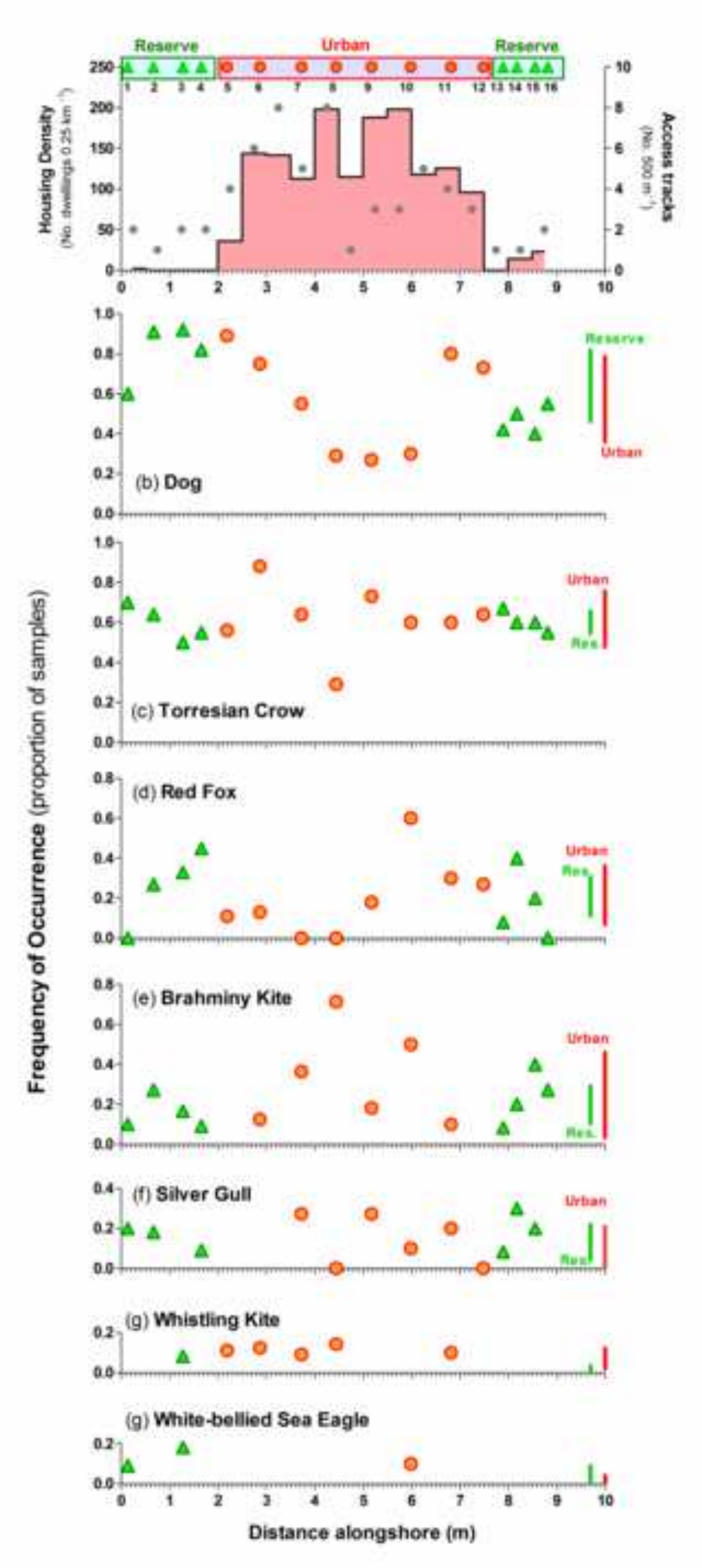

Figure 4
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