Distribution and habitat of Australian Pied Oystercatchers *Haematopus longirostris* along the SE Australian coast

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SUMMARY

Australian Pied Oystercatchers *Haematopus longirostris* and their habitat were surveyed on 72 beaches and 674 km of the SE Australian Coast, from Fraser Island, Queensland to near the New South Wales–Victoria state border and between 2015–2018. A grand total of 41 oystercatcher territories and 232 individual birds (the sum of mean beach counts) were counted. Bird-habitat models for oystercatcher mean count density indicated a positive response to the abundance of the primary prey species *Donax deltoides*, a large 'surf clam' and commonly known as the 'pipi', a negative response to the proportion of beach length urban and a negative S-N trend. Models for oystercatcher territory density indicated a positive response to pipi abundance and a negative response to pedestrian access density. This report upgrades the coastal development, tourism and human recreation disturbance threats for the species and calls for the long term protection of beach-nesting bird habitat.

Keywords: beach nesting bird; bird-habitat model; coastal development; *Donax deltoides*; human recreation disturbance; sandy ocean beach; species distribution model; surf clam

INTRODUCTION

The Australian Pied Oystercatcher *Haematopus longirostris* inhabits estuaries and ocean beaches around the Australian coast, with major populations in the southern states of Tasmania, South Australia and Victoria (reviewed in Taylor *et al.* 2014). The species is non-migratory and many breeding pairs remain on their territories throughout the year. Like other oystercatcher species, the density of Australian Pied Oystercatcher breeding pairs is usually limited by territorial behaviour. The ecology of oystercatchers on ocean beaches is not well known.

Microtidal, high energy ocean beaches (surf beaches) are common along the SE Australian coast (Short 2007). These are narrow, essentially linear habitats with a narrow intertidal zone. Australian Pied Oystercatchers typically nest on the low fore dune (Wellman *et al.* 2000). Beach width and length spatial constraints and territorial behaviour mean that beach-resident oystercatcher populations are smaller than those counted in large estuaries (see Taylor *et al.* 2014) and are dispersed along the coast.

Spatial constraints amplify human recreation disturbance for shorebirds on ocean beaches. Totterman (2019a) measured mean beach widths in the range 31–84 m (from the base of the fore dune to the middle of the low tide swash zone) for 11 beaches on the Far North Coast of the state of New South Wales (NSW). These beach widths are similar to reported flight initiation distances for Australian Pied Oystercatchers of 39–83 m for a human stimulus (reviewed in Weston *et al.* 2012) or 129 m for a human and dog stimulus (Harrison 2009).

People also disperse from beach access points in the along shore direction. Totterman (2019c) reported that beach walking, commonly with dogs, is the most frequent beach recreation activity on the Far North Coast of NSW and the 444 m mean distance walked along shore is one order of magnitude greater than mean flight initiation distances for Australian Pied Oystercatchers.

Commonly known as the 'pipi', *Donax deltoides* is a large 'surf clam' that inhabits the intertidal and shallow subtidal zones on ocean beaches from Fraser Island, in the state of Queensland, to the Murray River, South Australia (Ferguson *et al.* 2018). Pipis are the major prey for Australian Pied Oystercatchers on ocean beaches in NSW (Owner & Rohweder 1997, Harrison 2009, Totterman 2018). Owner & Rohweder (2003) reported that oystercatchers aggregated at beaches with high pipi biomass (high mean pipi count density and large mean pipi length). Totterman (2018) also reported oystercatcher-pipi abundance correlations, however those results refer to a dynamic period of recovery of pipi stocks on a single beach.

Pipis are also exploited by humans for food and as bait for recreational fishing. Owner & Rohweder (2003) and Harrison (2009) raised concerns about the potential negative impacts of commercial fishing on pipi stocks and oystercatcher populations. However, surf clams are fast-growing and short-lived, and weak or zero pipi recruitment can also result in pipi stock declines (Murray-Jones 1999). Management responses to the recent 2003–2009 'pipi crash' (Totterman 2018) that were introduced for the NSW commercial fishery in 2012 are: an annual Dec–Jun temporal closure; spatial closures for certain beaches and zones within certain beaches; a daily trip limit of 40 kg per fisher and a minimum size limit of 45 mm (Gray 2016a; Ferguson *et al.* 2018). Only hand gathering of pipis is allowed in NSW. The NSW commercial fishery is small, with 52 licenses in 2018 (not all of which were necessarily active) and a FY 2015–16 catch of 176 t (Ferguson *et al.* 2018). There is no commercial pipi fishing in Queensland.

Surf clams burrow themselves into the sand and are also mobile, at times emerging and 'riding' the wash up and down the beach face (Ellers 1995). This mobility and varying beach and surf conditions results in surf clam aggregations that vary across small and large spatial and temporal scales including tidal migrations, seasonal and other rhythmic patterns (*e.g.* Totterman 2019a). Patchy and variable pipi abundance could explain the rather long territories for oystercatchers on ocean beaches. The historical maximum density for South Ballina Beach, which formerly supported the largest beach resident oystercatcher population in NSW, is 18 breeding pairs over 18.7 km of available habitat in 2000 (NSW Department of Planning, Industry and Environment (DPIE), unpubl. data), which equals 1.04 km/pair, although territory lengths are not uniform.

Surf clams feed on suspended organic matter in the swash zone by extending their siphons to the sand-water interface. Oystercatchers can locate buried pipis by visual searching for pipi siphons or by tactile searching, probing the sand with their bills (Totterman 2018). Oystercatchers who have located a pipi have little time to make careful prey size assessments and act before the next wave arrives. Accordingly, and unlike many studies for the Eurasian

Oystercatcher *Haematopus ostralegus*, size selection has not been reported for oystercatchers taking surf clams (Owner 1997, Taylor and Taylor 2005, Totterman 2018). Totterman (2018) further suggested no prey size selection among different prey types and noted that small prey also have small biomass and can reasonably be ignored in studies where large clams are frequently taken. The asymptotic oystercatcher feeding rate estimate in Totterman (2018) was 0.26 pipis per min of active foraging time. Like many other shorebird functional responses reviewed in Goss-Custard *et al.* (2006), this asymptote was reached at a low prey density of *c.* 5 pipis/m^2.

The Australian Pied Oystercatcher is currently listed as Endangered in NSW (NSW DPIE 2019a). For the entire global population, conservation threats recognised by Taylor *et al.* (2014) were human recreation disturbance, habitat loss, predators, clam harvesting, kelp harvesting (which is not relevant for more northerly temperate and sub-tropical beaches, where beach-washed kelp is scarce) and global climate change. BirdLife Australia have stated that the greatest conservation threat to beach nesting birds is disturbance from people visiting the beach (Birdlife Australia 2018).

Johnson (2002) advocated for replication of studies ('metareplication') to have confidence in the generality of findings. This study was motivated by concerns that Owner & Rohweder (2003) missed the coastal development and human recreation disturbance threats for oystercatchers on ocean beaches and overstated the importance of pipis. The objective was to sample a larger number of beaches and re-examine oystercatcher-habitat associations for the SE Australian coast.

STUDY AREA AND METHODS

Sampling design

For estimating species-habitat models it is essential to include in the sample sites where the species is more abundant (Albert *et al.* 2010). A simple random sample of beaches would have resulted in many zero oystercatcher counts and little information for modelling abundance. This study purposely selected beaches where pipis and oystercatchers were expected to be more abundant.

The sampling space for this study extends from the Fraser Island, Queensland S to the NSW–Victoria border (Fig. 1). There are few and short beaches around the NSW–Victoria border. Based on the results of Owner (1997), 117 exposed beaches with a SE to E aspect and > 1.5 km long, where pipis could be relatively abundant, were identified for the sampling frame. Beaches were defined by natural breaks (*e.g.* headlands and rivers). Some short beaches were combined if the break did not present a substantial barrier, *e.g.* a short, low rocky interval that could easily be traversed at all tides. Together with the results of Harrison (2009), sampling prioritised longer, less-developed beaches, where oystercatchers could be relatively abundant. Identification of high pipi abundance and high oystercatcher abundance beaches was also guided by information from other studies and reports (Gray 2016a,b, Totterman 2019b, NSW DPIE 2019b).

The oystercatcher breeding season on the Far North Coast of NSW is Aug–Dec and late attempts generally are replacement clutches (Wellman *et al.* 2000). Sampling occurred early in the breeding season (Jul–Oct) when competition for territories and territory occupancy was assumed to be maximum. Sampling started with beaches in the N of the sampling space, progressed down the coast and usually included some more beaches on the return trip N. Sampling in any one season selected non-adjacent beaches to reduce spatial autocorrelation that could result from short-distance movements of birds.

Counts

Beaches were surveyed with a handheld Global Positioning System (GPS) satellite receiver, marking 4–13 (mode 7) regularly spaced along shore waypoints at the high tide drift line to measure beach length and along shore distances for pipi sampling locations and oystercatcher territory mapping.

Oystercatchers were usually counted at low tide. A four-wheel-drive (4WD) vehicle was used on longer beaches, where permitted. Otherwise, and for shorter beaches, a bicycle was used. Some of the shortest beaches, and those with a steep face and soft sand, were walked.

Oystercatchers present in any estuaries, lakes or on sand spits adjacent to a beach were noted but not added to the beach count. Coastal lakes are common along the NSW South Coast, many of these are inhabited by oystercatchers and these birds can be found roosting and sometimes nesting adjacent to the beach. However, these birds forage and spend most of the time in the estuary or lake and are rarely seen on the intertidal zone of the beach. This study strictly counted oystercatchers on beaches and 'beach residents'.

'Adult'-plumage oystercatchers were counted including second immature plumage attained at *c.* one year old, which looks the same without close inspection. One and two year old oystercatchers have relatively dull colours of bill, legs and iris compared to adults (Marchant and Higgins 1993), but not all individuals could be inspected closely (*e.g.* birds at distance, in unfavourable light or flying past). Birds marked with bands or alphanumeric leg flags were noted to assist in the identification of local residents.

Territory mapping (spot mapping) was applied and each beach was counted a minimum of three times on non-consecutive days. Beaches with higher oystercatcher densities (birds/km) also tend to have higher territory densities and warrant extra counts. Territory mapping effort was increased to a minimum of five counts for beaches with > 0.5 birds/km, based on breeding season densities for oystercatcher breeding beaches on the Far North Coast of NSW of 0.3–1.9 adults/km in Owner & Rohweder (2003) and 0.5–1.9 adults/km in Harrison (2009). Supplementary counts were also made opportunistically for some beaches where pipi sampling continued beyond the oystercatcher counting period. Three to five counts was considered sufficient for a low-cost estimate of territories because oystercatchers on the beach are conspicuous and easy to find, territories are one-dimensional and the observer was experienced with spot-mapping oystercatcher territories on beaches (Totterman 2018).

Oystercatcher territories were identified as adult 'pairs' that were present on the same stretch of beach on at least two of three or three of five counts. These territory estimates are short-term results using standardised methods and not all pairs that occupy a stretch of beach may go on to breed. Counts of breeding pairs are costly, requiring frequent visits throughout the breeding season. Territories are compared with independent counts of breeding pairs in the Results.

Pipi abundance

A new 'feet digging' method (Totterman 2019b) was used to efficiently sample pipis and enable precise beach-scale estimates of pipi abundance and mean pipi length. The method was developed from a recreational fishing technique that involves twisting one's feet into the thixotropic sand to dislodge buried clams which are then recovered by hand. Several plots are sampled across the swash zone in one five-min sampling unit and the process is replicated at several locations along the beach. Totterman (2019b) reported that mean feet digging pipi counts were proportional to mean transect linear pipi densities (r = 0.98) and that pipi length-frequency distributions from feet digging agreed with those from quadrat sampling except that feet digging was not effective for pipis < 16 mm. New pipi recruits are not always present and can be ignored because biomass increases exponentially with shell length (Murray-Jones 1999) and larger clams contribute more to oystercatcher diets (Totterman 2018).

Variance increases strongly with the mean pipi count (Totterman 2019b). A constant precision stopping rule was applied for pipi sampling: stop sampling when SE ≤ 2 pipis/5 min. This stopping rule efficiently allocates effort to prevent oversampling of low pipi abundance beaches and undersampling of high abundance beaches. A first pass sampled pipis at 20 along shore locations, regularly spaced along a beach from a random starting distance and cycling through the tidal stages high, ebb, low and flow (*i.e.* with five locations sampled for each tide stage). If SE > 2 pipis/5 min, then further sampling passes, consisting of multiples of 20 along shore locations, were performed until the SE stopping rule was satisfied or a maximum sample size of 100 was reached. For three long, high pipi abundance beaches (Teewah, Bennetts and Stockton), the beach could be divided into low and high pipi abundance strata based on the first pass(es) and informal observations. Stratified sampling was then applied to more efficiently approach the SE stopping rule.

Pipi lengths were measured with a calliper to the nearest mm (maximum shell length). All pipis were measured in the first sampling pass of 20 locations. If pipi abundance was low and only one pass and 20 locations were sampled then mean pipi length was based on < 100 measurements. Otherwise, and if < 100 pipis were sampled in the first pass, pipis were also measured for each subsequent pass until at least 100 pipis were measured. After that, pipis were only counted because measuring large numbers of pipis is time consuming and a sample size of 100 gives a precise mean pipi length.

Human recreation and other habitat variables

Counts of people, dogs, 4WDs, motorcycles, bicycles, horses and, on Fraser Island, aircraft directly measure human recreation activity and were counted simultaneous with oystercatcher counts. Dogs included dingos (naturalised dogs) that were present in low densities on Fraser Island and in the Myall Lakes region, NSW. Counts of humans and dogs excluded those in 4WDs and in the surf. Motorcycle, bicycle, horse and aircraft counts were small, with grand totals of 3, 32, 42 and 4 respectively, and are not considered further.

Coastal development variables and indirect measures of human recreation that were recorded were: urban length, length of public beach driving zones, whether or not beach driving permits were required, length of dog exercise zones, length of beach adjoining any terrestrial protected areas (National Parks and Nature Reserves), counts of pedestrian and (where 4WDs were permitted) 4WD beach access tracks and counts of beach front and near beach camping grounds and caravan parks. Access tracks include public and private, formal and informal tracks. Tracks had to be frequently used and lead somewhere to be counted (*e.g.* temporary dune driving tracks were not counted). 4WD tracks were also used by pedestrians on many beaches but were not added to that count. Permits are not applicable for the majority of beaches sampled (*i.e.* where driving is not permitted) and this variable is not considered further.

Human population density was obtained from the 1 × 1 km resolution Australian Population Grid 2011 (Australian Bureau of Statistics 2011). The intersection of a line defined by GPS survey waypoints with the Australian Population Grid 2011 identifies beach front grid cells and the sum of these cells equals the beach front human population.

Beach morphodynamic state (Short 2007) was observed during average surf conditions (*i.e.* not during erosive periods associated with storms and large swells) and one handful of intertidal sand was sampled at each GPS waypoint. Sand grain size was classified on the Wentworth scale by visual comparison to graded samples on a sand gauge. Any shell fragments present were ignored. Beach morphodynamic state and sand grain size within beaches were summarised as modal values.

Statistical analysis

Counts, zone lengths and human population are ‘extensive variables’ and scale with beach length. Extensive variables were converted to linear densities (*e.g.* birds/km) and proportions (*e.g.* urban proportion) by dividing by beach lengths (Owner & Rohweder 2003). ‘Intensive variables’, *e.g.* mean pipi abundance and mean pipi length, do not scale with beach length.

There were two response variables in the dataset: oystercatcher mean total count/density and oystercatcher territory count/density. The dataset included 23 predictor variables (Table 2), several of which were less informative than or correlated with other predictors. Multiple regression cannot identify which predictors are associated with the response when there is collinearity (Graham 2003). Data exploration was the major part of the statistical analysis, with the goal to detect patterns in the data and simplify and reduce collinearity in the dataset

(Zuur *et al.* 2010). This involved three steps: 1) spatial patterns (bubble maps, correlograms); 2) bivariate associations and interactions between predictors (scatter plots, box-and-whisker plots), and; 3) collinearity (for continuous predictors).

A simple method for visualising collinearity among continuous predictor variables is a cluster analysis using correlation coefficients. Clusters were identified by cutting the dendrogram at Spearman $r^2 = 0.49$ (equivalent to $|r| < 0.7$). Collinear variables within an identified cluster were combined if this could be done using simple arithmetic (*e.g.* the sum of two collinear count variables) else the variable with the strongest correlation with the response variable was selected (Dormann *et al.* 2013).

Multiple regression was used for modelling oystercatcher counts because this method allows for simple and interpretable inference and the sample size was unbalanced and effectively small, with high oystercatcher densities on only a few beaches. Repeated-measures 'mixed-models' were not necessary because replicate oystercatcher counts from each beach were fairly precise, the number of replicate counts was as small as three and estimating the variance among these repeated counts was of no interest (Murtaugh 2007).

Generalised linear models (GLMs) with a log link were fitted to integer oystercatcher mean counts (rounded to zero decimal places) and oystercatcher territory counts. The negative binomial error distribution was assumed when there was over dispersion in Poisson model residuals. Beach length was included as an offset term was included in GLMs to effectively model density, where:

$$\log\left(\frac{count}{length}\right) = \cdots$$

is equivalent to:

$$\log(count) = 1 \times \log(length) + \cdots$$

and the fixed coefficient of one for log(*length*) indicates that it is an offset.

With a log link, the GLM is a multiplicative model:

$$count = length \times e^{\beta_0} \times e^{\beta_1 x_1} \times e^{\beta_2 x_2} \ldots$$

where the x_i are the predictor variables and β_i are estimated coefficients. The above formula predicts oystercatcher density (count/length) as some constant value (e^{β_0}) multiplied by each predictor term. The exponential function implies monotonic, non-linear effects which is an advantage if there are such non-linear associations in the data or a disadvantage if there are linear or other patterns. However, an additive, ordinary linear model for density would have involved transforming the response variable to approximately satisfy statistical assumptions and then would also have been non-linear and with a difficult mean-variance relationship. Zuur *et al.* (2010) recommended to work with the original data where possible and not to apply transforms.

The GLM distributional assumption was checked by plotting Dunn-Smyth randomised quantile residuals (Dunn & Smyth 1996) versus fitted values, versus individual predictors, square-root absolute residuals versus fitted values and normal-probability plots. Four realisations of the randomised residuals were plotted.

Multiple regression analysis focussed on two groups of models: 1) a pipi abundance model (Owner & Rohweder 2003), and; 2) models based on all predictors. The pipi abundance model formed the basis for extended models in the third group. Models were compared using small sample Akaike's Information Criterion (AICc). AIC takes the model log-likelihood and adds a penalty term for the number of predictor variables to help avoid overfitting. AICc adds a further penalty when the sample size is small relative to the number of fitted parameters (Burnham *et al.* 2011).

Models were compared against the minimum AICc model: ΔAICc < 2 indicates strong support; ΔAICc = 2–7 indicates some support; ΔAICc = 7 to 14 indicates relatively little support and ΔAICc > 14 indicates no support (Burnham *et al.* 2011). Minimum *AIC* models were identified using an exhaustive search of all subsets of models. The resulting ΔAICc < 2 set included models with similar predictors and the model with the fewest variables was selected. Exhaustive searching for minimum AICc models avoids unreliable stepwise variable selection methods. Nonetheless, for the reduced collinearity dataset, the estimated model coefficients and standard errors for the 'full' models (with all predictors) were found to be reliable for variable selection.

Goodness of fit was examined by plotting fitted oystercatcher densities versus observed densities and calculating the squared Pearson linear correlation statistic (r^2). Additionally, the explained deviance statistic is reported:

$$D^2 = \frac{Null\ deviance - Residual\ deviance}{Null\ deviance}$$

where the null deviance is the deviance of the fitted model with the intercept only and the residual deviance is the deviance that remains unexplained by the model (Guisan & Zimmerman 2000). Predictive performance (*e.g.* cross-validation accuracy) was not evaluated because there were few high density sites for testing.

All GIS and statistical analyses were performed using the software R version 3.5-2 (R Core Team 2018). GIS analyses used the R packages *sp* version 1.3.1 (Pebesma & Bivand 2005), *rgdal* version 1.3-6 (Bivand *et al.* 2018) and *raster* version 3.0-2 (Hijmans 2019). Spatial analyses used the R packages *ncf* version 1.2-6 (Bjørnstad 2018) and *spdep* version 0.8-1 (Bivand & Piras 2015). Clustering of collinear predictors was performed using the R package *Hmisc* version 4.2-0 (Harrell 2019). Negative binomial models were fitted with the *MASS* package in base R (Venables & Ripley 2002). Randomized quantile residuals were computed using the R package *statmod* version 1.4.32 (https://CRAN.R-project.org/package=statmod). Spatial autocorrelation in GLM residuals was checked using the lm.morantest function in *spdep*. This function is not intended for GLMs, however no ready alternative that takes into

account predictor variables was found and the results were useful for relative comparisons between models.

RESULTS

Spatial patterns

72 of 117 beaches (62%) and 674 of *c.* 942 km (72%) from the sampling frame were sampled including all of the longer beaches in NSW (except for Budgewoi on the Central Coast), all of the known pipi beaches and all beach Key Management Sites for the Australian Pied Oystercatcher (NSW DPIE 2019b) (Fig. 1). *Ad hoc* analysis split the coastline into five contiguous regions: SE Queensland (from Fraser Island S to the Queensland-NSW state border); Far North Coast (to Coffs Harbour); Mid-north Coast (to the Hunter River); Central Coast (to Broken Bay), Sydney (to Port Hacking), and; South Coast (to the NSW-Victoria border). Sample sizes were larger for regions where oystercatchers were more abundant: 20 of 28 beaches in the sampling frame from the Far North Coast; 27 of 30 from the Mid-north Coast, and; 18 of 37 from the South Coast. Three of 7 beaches in the sampling frame were sampled from the Central Coast (where only one oystercatcher was counted), zero of four beaches from Sydney and four of 11 beaches from SE Queensland.

A grand total of 41 Australian Pied Oystercatcher territories and 232 individual birds (the sum of mean beach counts) were counted. The majority of oystercatchers counted, 155 individuals (67%), were non-territorial. Counts were fairly precise, with a mean range of 2.1 (*i.e.* ±1 bird). Variance increased with the mean and the maximum range was 18 for a mean count of 66 (*i.e.* ±9 birds). These fairly narrow ranges indicate that there were no substantial movements of birds in to and out of beaches between counts. Territory estimates agreed reasonably well with breeding pair counts from monitored sites (Fig. 2).

A spline correlogram (Bjørnstad & Falck 2001) for oystercatcher mean count density indicated a spatial autocorrelation range of 63 km (95% CI 28–111 km). A radius of 50 km was used for calculating binary spatial weights for spatial statistics. The spatial pattern for oystercatchers was strongly aggregated with a ‘hot spot’ in the Richmond River area of the Far North Coast (Figs. 3a,b). Pipi abundance showed a different spatial pattern, with a hot spot in the Mid-north Coast region (Fig. 3c). Large pipis were available on all beaches and pipi mean length showed a spatial trend, increasing from an average of *c.* 35 mm on the South Coast to an average of *c.* 46 mm on the Far North Coast (Fig. 4).

Bivariate associations

A correlation matrix for all variables is presented in Table 2 and scatterplots for oystercatcher mean count density and territory count density in Figures 5 and 6. There were positive correlations between oystercatcher count density and the proportion of the beach length protected (Spearman $r = 0.47$) and mean pipi count (Spearman $r = 0.38$). There were negative correlations between oystercatcher count density and the proportion of the beach length urban (Spearman $r = -0.53$), human population density (Spearman $r = -0.53$), pedestrian access density (Spearman $r = -0.45$), dog mean count density (Spearman $r = -0.45$), people mean

count density (Spearman $r = -0.40$) and the proportion of the beach length with dogs allowed (Spearman $r = -0.39$). Correlations were weaker than like correlations in Owner & Rohweder (2003), who sampled 11 Far North Coast beaches, N of the Clarence River. This disagreement was largely resolved by recomputing correlations for only Far North Coast beaches in this study (Table 3). The strong oystercatcher-pipi association that was reported by Owner & Rohweder (2003) apparently holds only for the Far North Coast region (Figs. 5h, 6c).

There were 12 beaches sampled where commercial pipi fishing was observed or known from other sources to occur (see Methods) and 60 beaches that were not fished. Mean pipi abundance and length were 5.4 pipis/min and 5.8 mm greater for fished beaches than for those without commercial shellfishing (Figs. 7a, b). Mean oystercatcher count density and territory density were 0.36 birds/km and 0.05 territories/km greater on fished beaches (Figs. 7c, d). These results suggest that both fishers and oystercatchers target beaches with higher pipi biomass. These were not equal probability samples but the sampling design selected beaches where pipis and oystercatchers could be abundant, including all known fished beaches. The sample of fished beaches is assumed to be exhaustive and positive bias is assumed for pipi and oystercatcher abundance means for the non-fished beach sample (which would act to reduce, rather than increase, observed mean differences).

Sixty-two beaches sampled (86%) had transverse bar and rip inner bars and 64 (89%) had medium sand (0.25–0.5 mm). Short (2007) has previously reported that these are the most common conditions for ocean beaches in NSW. With so little variation, these two variables are not considered further.

Collinearity

Hierarchical clustering of continuous predictor variables indicated four groups of collinear variables with Spearman $r^2 \geq 0.49$ (Fig. 8). Nearly all dogs were domestic and so human and dog densities were added together. The proportion of beach length protected (and where dogs are not allowed) was negatively correlated with the proportion with dogs permitted (Spearman $r = -0.70$). These two complementary variables were combined by subtracting the latter from the former (which emphasises protection).

After eliminating two uninformative variables (see the previous section) and acting to reduce collinearity, the set of predictors was reduced from 21 to 17 variables (Table 2). The same predictors were adopted for oystercatcher territory density, where correlations were similar to those for oystercatcher mean count density. Square-root transforms were applied to human population density, people plus dogs mean count density and pedestrian access density to improve model fit (ΔAICc > 2 for univariate oystercatcher mean count density models). The square-root transform was assumed because, unlike the logarithmic transform, application is straightforward for zero values.

Oystercatcher density models

Oystercatcher density models are summarised in Table 5. The selected oystercatcher mean count density minimum AICc model was, for the Far North Coast region:

$$\log(count.B) = \log(length) + 8.83 + 0.17pipis - 3.4prop.urban - 1.4\mathrm{e}^{-03}\,\mathrm{y}$$

and, for other regions:

$$\log(count.B) = \log(length) + 7.55 + 0.048pipis - 3.4prop.urban - 1.4\mathrm{e}^{-03}\,\mathrm{y}$$

This model incorporates a strong, positive pipi effect for the Far North Coast relative to other regions (Fig. 5h) and a negative urban effect. The large intercept occurs because of large UTM y values (note UTM y is in km). This model suggests a negative S-N gradient even though the highest oystercatcher densities were on the Far North Coast. In combination with the other predictors, the negative S–N gradient could be fitting the high pipi abundance, non-urban, low oystercatcher density Teewah and 75 Mile beaches in SE Queensland.

There was some support for the alternate predictors urban proportion (ΔAICc = 4.1), UTM x (ΔAICc = 3.9) and an oystercatcher mean count density model without UTM y (ΔAICc = 6.0). There was no support for the alternate predictor mean people and dogs count density (ΔAICc = 14.3) and the basic pipi abundance model (ΔAICc = 27.7). Fitted densities are compared with observed mean count densities in Fig. 9. The pipi abundance model (r^2 = 0.53, D^2 = 0.32) provides a reasonable fit to higher densities on the Far North Coast. Including urban proportion improves the fit to lower densities (r^2 = 0.55, D^2 = 0.61).

The selected oystercatcher territory density minimum AICc model was, for the Far North Coast region:

$$\log(count.T) = \log(length) - 0.87 + 0.15pipis - 1.86\sqrt{dens.acc.people}$$

and, for other regions:

$$\log(count.T) = \log(length) - 2.34 + 0.040pipis - 1.86\sqrt{dens.acc.people}$$

Compared to the mean count density model above, urban proportion has been replaced by pedestrian access density. There were no collinear alternative predictors for pedestrian access density (Fig. 8) and there was no support for the basic pipi abundance model (ΔAICc = 18.2). Expected zeros closely agreed with observed zeros (Table 5), which indicates that the high frequency of zeros was well described by the systematic component of the models (Warton 2005). Zero-augmented models, while conceptually appealing (Martin *et al.* 2005), were not necessary and the extra parameters increase AICc when these models do not substantially increase log-likelihood. Fitted densities are compared with observed territory densities in Fig. 10. For the selected model (r^2 = 0.46, D^2 = 0.62) there are some false positive results (observed = 0 and fitted > 0) as well as underestimation of intermediate densities.

DISCUSSION

Four predictors for Australian Pied Oystercatcher abundance were selected in this study: pipi abundance had a positive effect, beach front development and beach access density had negative effects and regional/spatial predictors accounted for regional/spatial variability. The first three of these predictors are habitat variables and it is proposed that the fourth results from local and regional population histories.

Some readers would be aghast at the *ad hoc* descriptive modelling (*sensu* Shmueli 2010) and 'data mining' in this study. Some would insist that only intensive ecological studies and theory are reliable for model building (like in Goss-Custard 1996). However, there currently is not the detailed ecological knowledge for oystercatchers on ocean beaches to attempt explanatory modelling. It is also not necessarily true that predictive power can be inferred from explanatory power (Smith 2000). With the usual caveat that 'association is not causation', the models in this study provide a compact summary of oystercatcher-habitat associations and indicate some potentially important variables for conservation management and further research. Predictive performance for low oystercatcher density sites is suggested to be good because negative development and human recreation effects are plausible and the correlations were clear. Predictive performance for high oystercatcher density sites is suggested to be poor because the positive pipi abundance effect varied between regions and the models do not incorporate population dynamics.

The Far North Coast supports the largest numbers of beach resident Australian Pied Oystercatchers in NSW. The NSW Wader Study Group counted 232 oystercatchers on NSW ocean beaches in Oct 1998 with 113 between the Tweed and Clarence Rivers (Owner & Rohweder 2003). Harrison (2009) counted 26 oystercatcher territories on beaches between the Richmond River and Bonville Creek (Sawtell) in 2003 and 27 territories in 2005. There were 122 individual oystercatchers and 27 territories on the Far North Coast (N of Coffs Harbour) counted in this study. Two decades of conservation management for the Australian Pied Oystercatcher in the Richmond River area and *c.* 200 young fledged (NSW DPIE unpubl. data) has apparently not increased the regional population. Taylor *et al.* (2014) noted that high predation rates of eggs and chicks is quite normal for most oystercatcher species and then suggested that Australian Pied Oystercatcher breeding population sizes are not limited by breeding productivity.

The NSW DPIE have estimated that there are < 200 Australian Pied Oystercatcher breeding pairs in NSW (NSW DPIE 2019a), with 88 pairs at 15 Key Management Sites including 24 pairs at four beach sites: South Ballina, Broadwater, Bombing Range and a number of beaches within Yuraygir National Park (NSW DPIE 2019b). Broadwater Beach is contiguous with and was included with South Ballina Beach in this study. These data indicate that *c.* one quarter (24/88 = 0.27) of oystercatcher pairs are beach residents from which it can be estimated that there are < 50 (0.25 × 200) beach resident pairs in NSW. This estimate and NSW Wader Study Group counts (in Owner & Rohweder 2003) agree with 40 territories and 222 individual oystercatchers on NSW ocean beaches from this study. Exhaustive sampling of all NSW beaches would not have substantially increased these counts.

The selected oystercatcher mean count density model achieved a satisfactory fit to observed densities. This model indicated that oystercatchers aggregate at Far North Coast beaches with high pipi abundance and at less urbanised beaches. The oystercatcher-pipi correlations of Owner and Rohweder (2003) were valid only for Far North Coast beaches. For example, there were several long and largely undeveloped Mid-north Coast beaches with high mean pipi counts but only moderate oystercatcher densities. Established pipi fisheries in both of these regions indicate that both have a long history of high pipi abundance and, several years after the 2003–2009 pipi crash, results from this 'snapshot' study are assumed to be representative of typical pipi abundances. The Far North Coast oystercatcher-pipi correlation in this study was defined by only two high oystercatcher density beaches: South Ballina and Bombing Range. In Owner and Rohweder (2003; who combined Ten Mile and Bombing Range beaches) this correlation was defined by only South Ballina. Exceptionally high territory densities for South Ballina and Bombing Range beaches suggest that local population histories are important and that the Far North Coast effect is not a simple predator-prey association. Despite this uncertainty about the oystercatcher-pipi relationship, mean pipi count, together with a region covariate, was useful for the *ad hoc* modelling of oystercatcher density in this study.

No overall negative fishing effects for pipi stocks and oystercatcher abundance were found in this study. Instead, pipi biomass and oystercatcher abundance were higher on commercially fished beaches than on unfished beaches. Together with uncertainty about the oystercatcher-pipi relationship discussed above, it is recommended that the pipi harvesting threat for the Australian Pied Oystercatcher be downgraded. Objectors to this proposal are advised to conduct their own research into pipi stock dynamics and fishing effects.

Urban proportion (or human population density) substantially improved the oystercatcher mean count density model for low density beaches. The proposed explanation is that coastal development and associated human recreation disturbance displaces shorebirds from otherwise suitable habitat (reviewed by Hockin *et al.* 1992). For example, Harrison (2009) noted a gap in the distribution of breeding oystercatchers around the village of Patch's Beach (currently with 19 dwellings) on South Ballina Beach.

Pedestrian access density was selected for the oystercatcher territory density model. The proposed explanation is that higher access density can result in shorter separation distances between access points and shorebird habitat zones, higher intrusion rates into those zones and more frequent disturbance (Dowling & Weston 1999; Totterman 2019c). The maximum oystercatcher territory density in this study was 0.67 pairs/km for Bombing Range Beach, which is 10.5 km long and with zero public access. With the exception of Tallow Beach, where spot mapping indicated one territory at Tallow Creek but where breeding is not known to occur, zero oystercatcher territories were observed in this study when pedestrian access density exceeded 1.3 tracks/km. This result suggests that beach access points should be at least *c*. 800 m distant from oystercatcher breeding habitat.

Beach access density is not only an issue for more urban beaches. Coastal tourism can reduce the breeding range, density and breeding success for shorebirds (reviewed by Pienkowski

1993). For example, Fisher *et al.* (1998) proposed that camping and associated pedestrian traffic on the fore dunes of Fraser Island could negatively impact oystercatchers via disturbance to nesting habitat. Teewah Beach and 75 Mile Beach (Fraser Island) sampled in this study were long, largely undeveloped (both are within Great Sandy National Park) and have high pipi abundance but also extensive beach front camping zones with high densities of pedestrian and 4WD tracks. Spot mapping indicated only one oystercatcher territory (near Wyuna Creek on 75 Mile Beach) for these two beaches with a combined length of 132 km. Oystercatcher counts on 75 Mile Beach appear to have declined since Fisher *et al.* (1998) counted an average of 15 birds between Hook Point and Indian Head. The mean count in this study for the same stretch of beach was three birds. This comparison suggests that vehicle-based recreation conflicts with conservation objectives for Great Sandy National Park.

The unsatisfactory fit to observed densities for the selected oystercatcher territory density model indicates that territorial birds are less responsive to habitat than are non-territorial birds. For example, pipi density at South Ballina declined from $20/m^2$ in 2003 to near zero in 2009 during the recent pipi crash but there remained 23 oystercatchers on the beach (Totterman 2018). However, in the long term, results from this study indicate that territory density decreases towards zero on beaches with higher pedestrian access density. With growing development and human recreation pressures on beaches and shorebirds in SE Australia (Priest, Straw & Weston 2002), it is predicted that beach resident oystercatcher populations will decline slowly as older breeders pass away and are not replaced, *i.e.* recruitment failure despite the surplus of non-territorial birds of breeding age. It is recommended that the coastal development, tourism and human recreation disturbance threats for the Australian Pied Oystercatcher be upgraded.

Current conservation efforts for Australian Pied Oystercatchers on ocean beaches focus on breeding success (Wellman *et al.* 2000) and will fail in the long term unless the beach habitat is protected from urbanisation, tourism and intense human recreation. Recommendations from this study are to focus conservation efforts on existing large beach nesting oystercatcher populations and not *ad hoc* groups of beaches like in current Key Management Sites (a number of Mid-north Coast beaches could also be recognised, in particular Stockton Beach, Fraser & Lindsey 2018), to prohibit new development for these beaches, to prohibit dogs (because dogs amplify human recreation disturbance effects and non-compliance with dog regulations is common, *e.g.* Dowling and Weston 1999) and to restrain tourism. Oystercatcher breeding habitat zones need to be identified and large separation distances between beach access points and these zones implemented (Totterman 2019c). 4WDs enable people to access more remote sections of a beach and should be prohibited. Permits have only encouraged commercialisation of beach driving, *e.g.* the beaches of SE Queensland and Stockton and Nine Mile (Belmont) beaches in NSW.

The recommendations above could best be described as ‘wishful thinking’ because of commercial interests in developing coastal land and social interests in maintaining the *status quo* for access and recreation. Historical habitat loss to coastal development, continued poor planning decisions and weak conservation management show that people have priority over wildlife. Conservationists should increase pressure upon relevant public authorities to act in

the long-term public interest, as they are required to do under relevant environmental and planning legislation, and make the 'tough decisions' to protect the remaining natural coastline.

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Table 1. Table of beaches sampled in this study with oystercatcher counts (beaches are ordered N to S by mid-point latitude). Coded breeding records accompany beach territory counts: *n* number of pairs; habitat (Beach, Estuary, Lake); observation (C = Copulation; N = nest with eggs; Y = dependent young), and; M indicates marked nests. For example, 2BNM translates to 2 Beach Nests Marked. Several of these records were of estuary/lake resident birds and are not recorded as beach territories. Breeding pair counts data are for comparison with territory counts. Data sources are: 1) Harrison 2009 (breeding season 2005); 2) NPWS pers. comm. 2015; 3) NSW DPIE unpubl. data (br. season 2016), and; 4) NSW DPIE unpubl. data (br. season 2018), and; 5) Fraser & Lindsey 2018 (br. seasons 2014–2017; there were only five reliable territories and probably < five breeding pairs). Nest coordinates have been used to assign breeding pairs from the NSW DPIE reports to beaches defined in this study (*i.e.* Broadwater Beach is included with South Ballina Beach and Black Rocks is not included with Ten Mile Beach, to the south, or Bombing Range Beach, to the north). Regions are SE Queensland (SEQ), the Far North Coast of NSW (FNC), Mid-north Coast (MNC), Central Coast (CEC) and South Coast (SOC). Bherwerre Beach is within the Commonwealth Territory of Jervis Bay. Beaches with commercial pipi fishing are indicated (Y).

Beach	Region	Sampled	S–N end	Lat. (°S)	Length (km)	Oystercatcher Mean count	Oystercatcher Territory count	Br. pairs	Fished
75 Mile (Fraser Island)	SEQ	Jul-16	11 km ramp (Hook Pt.) to Indian Head	25.33	84.5	3.3	1		
Teewah (Cooloola)	SEQ	Jul-17	Noosa River to Double Island Point	26.20	51.0	7.0	0		
Coolum	SEQ	Jul-16	Coolum Beach to Noosa Head	26.47	15.4	0.0	0		
Warana	SEQ	Jul-16	Currimundi Lake to Point Cartwright	26.72	9.1	0.0	0		
Kingscliff	FNC	Oct-18	Cudgen Creek to Fingal Head	28.23	7.0	0.7	0		
Bogangar	FNC	Jul-16	Cabarita Beach to Cudgen Creek	28.30	8.6	0.7	0		
Cudgera	FNC	Oct-18	Mooball Creek to Hastings Point	28.38	2.8	0.0	0		
Wooyung	FNC	Jul-16	Brunswick River to Mooball Creek	28.46	16.6	0.7	0		
Tallow	FNC	Oct-17	Cocked Hat Rock to Cape Byron	28.68	7.4	3.7	1		
Seven Mile (Lennox Head)	FNC	Oct-17	Lennox Head to Jews Point	28.77	8.4	4.0	0		
Angels & Sharpes	FNC	Oct-18	Black Head to Whites Head	28.85	2.9	0.0	0		
South Ballina	FNC	Aug-16	Broadwater Headland to Richmond River	28.96	23.0	66.0	11	8[3]	Y
Airforce	FNC	Aug-15	Evans River to 'Coffee rocks'	29.09	5.8	4.8	2 (1BC)	2[3]	
Bombing Range	FNC	Aug-18	Jerusalem Creek to Goanna Headland	29.18	10.5	16.7	7	8[4]	
Ten Mile (Iluka)	FNC	Aug-16	Shark Bay to Black Rocks	29.31	12.5	8.7	1	1[3]	Y
Pippi (Yamba)	FNC	Sep-18	Green Point to Yamba Point	29.45	3.3	0.7	0		
Plumbago & Shelley (L. Arragan)	FNC	Sep-15	Red Cliff to Shelley Beach Head	29.55	4.6	2.7	1 (1BCM)	1[1]	
Sandon	FNC	Sep-17	Sandon River to Brooms Head	29.64	7.0	4.3	2 (2BNM)		
Illaroo	FNC	Aug-16	Illaroo to Sandon Bluffs	29.72	9.0	3.3	0		
Minnie Water Back	FNC	Sep-17	Diggers Camp to Minnie Water	29.79	2.8	0.7	0	0[1]	

Wooli	FNC	Sep-15	Wooli Wooli River to Wilsons Head	29.86	6.7	3.7	2 (1BY)	1[2]	
Station Creek	FNC	Sep-18	Corindi River to Station Creek	29.97	3.9	0.7	0 (1EYM)		
Hearns L. & Woolgoolga Back	FNC	Sep-18	Sandy Beach to Woolgoolga Headland	30.13	3.7	0.0	0		
Moonee	MNC	Sep-17	Moonee Creek to Look At Me Now Hd.	30.19	4.4	0.0	0		
Boambee	MNC	Oct-16	Boambee Creek to Corambirra Point	30.33	5.5	0.3	0	0[1]	
Bonville	MNC	Sep-18	Bundagen Headland to Bonville Creek	30.40	6.6	3.0	1		
North Beach (Mylestom)	MNC	Aug-16	Bellinger River to Bundagen Headland	30.47	8.4	0.7	0		
South Urunga (Hungry Head)	MNC	Sep-18	Wenonah Head to Bellinger River	30.53	4.9	0.7	0		
South Valla	MNC	Sep-15	Nambucca Heads to Deep Creek	30.62	4.8	0.0	0		
Forster (Scotts Head)	MNC	Oct-16	Scotts Head to Nambucca River	30.70	10.8	0.7	0		
Grassy and Middle	MNC	Sep-15	Grassy Head to Scotts Head	30.78	3.4	0.0	0		
South Smoky	MNC	Aug-17	Korogoro Creek to Smoky Cape	30.99	15.9	2.0	1		Y
Killick	MNC	Aug-16	Killick Creek to Hungry Hill	31.14	13.9	5.5	2		Y
Goolawah	MNC	Aug-17	Racecourse Head to Crescent Head	31.22	6.4	0.0	0		Y
North Shore (Port Macquarie)	MNC	Oct-16	Hastings River to Queens Head	31.37	12.6	1.7	0		Y
Lighthouse (Port Macquarie)	MNC	Aug-17	Lake Cathie (open) to Tacking Point	31.51	10.1	1.0	0		Y
Grants (North Haven)	MNC	Aug-16	Camden Haven Inlet to Grants Head	31.62	3.1	0.0	0		
Dunbogan	MNC	Aug-17	Diamond Head to Camden Head	31.68	8.9	1.3	0		Y
Crowdy Bay	MNC	Sep-15	Crowdy Head to Diamond Head	31.78	14.3	5.2	0		
Crowdy Head (Harrington)	MNC	Aug-17	Harrington Inlet to Crowdy Head	31.86	6.7	1.3	0		
Manning Point	MNC	Oct-16	Farquhar Inlet to Harrington Inlet	31.92	10.4	0.0	0		
Old Bar	MNC	Sep-15	Wallabi Point (N) to Farquhar Inlet	31.98	5.4	0.0	0		
Diamond	MNC	Sep-18	Diamond Beach to Wallabi Point (S)	32.03	5.0	0.3	0		
Nine Mile (Tuncurry)	MNC	Aug-16	Wallis Lake to Hallidays Point	32.12	12.0	7.0	0		
Seven Mile (Forster)	MNC	Aug-17	Booti Booti to Cape Hawke	32.28	9.6	8.0	0		Y
Sandbar (Smiths Lake)	MNC	Oct-16	Smiths Lake (Sandbar) to Bald Head	32.39	2.8	3.3	1 (1BN)		
Fiona & Submarine	MNC	Aug-17	Big Gibber Headland to Yagon Headland	32.47	8.9	3.3	2 (1BC)		
Mungo (Myall Lakes)	MNC	Sep-16	Sandy Point to Big Gibber Headland	32.53	15.4	1.7	0		Y
Bennetts (Hawks Nest)	MNC	Sep-17	Yacaaba Head to Dark Point	32.64	14.3	7.7	1 (1BN)		
One Mile (Anna Bay)	MNC	Sep-16	Anna Bay	32.77	2.5	0.0	0		
Stockton	MNC	Oct-15	Hunter River to Birubi Point	32.83	31.9	19.6	3 (1BC)	5[5]	Y

Nine Mile (Belmont)	CEC	Sep-18	Lake Entrance to Redhead Point	33.04	10.2	0.3	0	
Middle Camp (Cath. Hill Bay)	CEC	Sep-18	Catherine Hill Bay	33.15	1.7	0.0	0	
Tuggerah	CEC	Sep-16	Tuggerah Entrance to Pelican Point	33.31	7.6	0.0	0	
Bellambi & Woonona	SOC	Oct-15	Swimming pools to Flat Rock	34.36	2.1	0.0	0	
Perkins (Windang)	SOC	Sep-16	Lake Illawarra to Red Point	34.52	6.6	0.0	0	
Seven Mile (Shoalhaven)	SOC	Oct-15	Shoalhaven Hds. (open) to Crooked River	34.81	12.2	2.0	0	
Comerong Island	SOC	Sep-16	Crookhaven R. to Shoalhaven Hds. (open)	34.88	4.4	0.7	0 (1EN, 1ENM)	
Bherwerre	SOC	Sep-16	Sussex Inlet to Cave Head	35.17	6.8	7.6	2 (2BN)	Y
Cudmirrah	SOC	Sep-17	Cudmirrah to Sussex Inlet	35.19	3.6	0.0	0	
Buckleys & Conjola	SOC	Sep-16	Narrawallee Inlet to Conjola Lake	35.28	4.6	1.3	0 (1ENM, 1LNM)	
Wairo	SOC	Sep-17	Tabourie Creek to Lagoon Head	35.43	4.7	1.7	0	
Durras Lake South	SOC	Sep-16	Durras to Durras Lake (open)	35.65	2.2	0.0	1 (1LNM)	
Bengello (Moruya North)	SOC	Sep-16	Moruya River to Broulee Head	35.88	5.9	0.0	0	
Pedro & Moruya South	SOC	Sep-17	Congo Point to Toragy Point	35.94	4.8	0.0	1 (1ENM)	
Bingie	SOC	Oct-15	Coila Lake (open) to Bingie Bingie Point	36.03	3.8	0.0	0	
Brou Lake	SOC	Oct-15	Lake Mummuga to Jemisons Point	36.14	6.5	5.0	0	
Wallaga	SOC	Sep-16	Wallaga Lake to Tilba Head	36.35	5.1	2.7	0	
Baragoot	SOC	Sep-17	Cuttagee Point to Baragoot Point	36.47	3.1	1.3	0	
Gillards & Middle	SOC	Oct-15	Cowdroys Head to Middle Beach	36.66	3.0	1.0	0 (1LN)	
Merimbula	SOC	Oct-15	Pambula Beach to Merimbula Lake	36.92	5.8	0.7	0	
Wonboyn	SOC	Oct-15	Greenglade to Bay Cliff	37.27	4.1	1.7	0	

Table 2. Table of variables used in the statistical analysis. Extensive variables were converted to densities (*dens.*) and proportions (*prop.*) by dividing by beach length. Final variables are those resulting from data exploration (see Results). Generalised linear models fitted oystercatcher counts (*count.T*, *count.TNF*) with a log link and beach length as an offset. Square-root transforms were applied to a few predictor variables to improve model fit. Regions are SE Queensland (SEQ), the Far North Coast of NSW (FNC), Mid-north Coast (MNC), Central Coast (CEC) and South Coast (SOC).

Measured variables			**Final variables**	
Description	**Name**	**Scale**	**Name**	**Transform**
Oyc. terr. count	*count.T*	length	*count/dens.T*	
Oyc. mean count	*count.B*	length	*count/dens.B*	round(*count.B*, *0*)
Beach length	*length*		*length*	
Urban length	*length.urban*	length	*prop.urban*	
4WD length	*length.4WD*	length	*prop.4WD*	
Dogs length	*length.dogs*	length		
Dogs off-leash length	*length.offleash*	length	*prop.offleash*	
Protected area length	*length.protect*	length	*protect*	(*prop.protect – prop.dogs*)
Pedestrian access	*access.people*	length	*dens.acc.people*	√(*dens.access.people*)
4WD access	*access.4WD*	length	*dens.acc.4WD*	
Camping & c'van parks	*count.camps*	length	*dens.camps*	
People mean count	*count.people*	length	*dens.people.dogs*	√(*dens.people* + *dens.dogs*)
Dogs mean count	*count.dogs*	length		
4WDs mean count	*count.4WDs*	length	*dens.4WDs*	
Human pop. (1 km^2)	*pop1*	length	*dens.pop1*	√(*dens.pop1*)
Pipi mean count	*pipis*		*pipis*	
Pipi mean length	*pipis.length*		*pipis.length*	
UTM x-coordinate	*x*		*x*	*x*/1000
UTM y-coordinate	*y*		*y*	*y*/1000
Mode morph. state	*beach*			
Mode sand grain size	*band*			
Commercial fishing	*fished* (Y/N)		*fished*	
Region	*region* (SEQ/FNC/MNC /CEC/SOC)		*region2* (FNC/Others)	

Table 3. Spearman rank-based correlation matrix for all continuous predictor variables (Table 2). Correlations have been rounded to one decimal place and weak correlations (absolute value < 0.3) are not presented.

	dens.B	length	prop.urban	prop.4WD	prop.dogs	prop.offleash	prop.protect	dens.access.people	dens.access.4WD	dens.camps	dens.people	dens.dogs	dens.4WD	dens.pop1	pipis	pipis.length	x	y
dens.T	0.6						0.4	−0.4								0.3		
dens.B			−0.5		−0.4		0.5	−0.5			−0.4	−0.5		−0.5	0.4			
length				0.5				−0.4	0.3				0.3		0.5	0.3		0.3
prop.urban					0.4	0.4	−0.6	0.6			0.8	0.8		0.8				
prop.4WD								−0.4	0.9				0.8		0.3	0.3		0.3
prop.dogs						0.5	−0.7	0.4			0.4	0.5		0.5				
prop.offleash							−0.6					0.4		0.3				
prop.protect								−0.6			−0.6	−0.7		−0.5				
dens.access.people									−0.3		0.7	0.5		0.6				
dens.access.4WD													0.8		0.3			
dens.camps																		
dens.people												0.8		0.7				
dens.dogs														0.7				
dens.4WD															0.3			
dens.pop1																		
pipis																		
pipis.length																	0.5	0.5
x																		1.0

Table 4. Comparison of Pearson correlation results for oystercatcher mean count density in Owner (1997; for birds/km), Owner & Rohweder (2003; for birds/km^2) and results from this study (for birds/km). Far North Coast (FNC) beaches are those between Coffs Harbour and the NSW-Queensland border.

Oystercatcher density ~	**Owner (1997)**	**Owner & Rohweder (2003)**	**This study – all beaches**	**This study – NSW FNC**
	r	***r***	***r***	***r***
Pipi abundance	0.78	0.83	0.26	0.76
Mean pipi length	0.70	0.66	0.22	0.44
Beach length	0.55	0.64	0.09	0.72
4WD count density	0.39	0.24	−0.02	0.04
Human count density	−0.17	−0.03	−0.15	−0.23

Table 5. Summary of oystercatcher abundance models with small-sample Akaike's Information Criterion (AICc), explained deviance (D^2) and squared Pearson linear correlation coefficient between observed and fitted values (r^2). Intercept only models predict mean density for all beaches. An asterix (*) denotes an interaction between pipi abundance and *region2* (Far North Coast/other). Size refers to the negative binomial overdispersion parameter (zero indicates a Poisson error distribution). *K* equals the number of parameters in the model. Expected zeros can be compared with observed zeros of 25 for total oystercatcher counts and 55 for territory counts. Expected zeros is calculated from the assumed count distribution and is not the same as fitted zeros (formulae in Zeileis *et al.* 2008). Moran's *I* measures spatial autocorrelation in the residuals.

Predictor variables	**Size**	***K***	**ΔAICc**	D^2	r^2	**Expected zeros**	**Moran's *I***
Mean total count models							
pipis*region2, prop.urban, y	0.2	7	0.0	0.61	0.55	25.4	0.03
pipis*region2, prop.urban, x	0.3	7	3.9	0.58	0.56	26.6	0.01
pipis*region2, dens.pop1, y	0.3	7	4.1	0.58	0.53	24.9	0.03
pipis*region2, prop.urban	0.4	6	6.0	0.54	0.56	27.6	0.08
pipis*region2, dens.people.dogs, y	0.3	7	14.3	0.51	0.54	23.5	0.00
pipis*region2	0.5	5	27.7	0.32	0.53	25.2	0.09
Intercept only	1.2	2	46.7		0.01	25.9	0.30
Territory count models							
pipis*region2, √(dens.acc.people)	0	5	0.0	0.62	0.46	55.1	0.00
pipis*region2	0.9	5	18.2	0.33	0.27	54.4	0.09
Intercept only	3.1	2	27.3		0.00	54.8	0.22

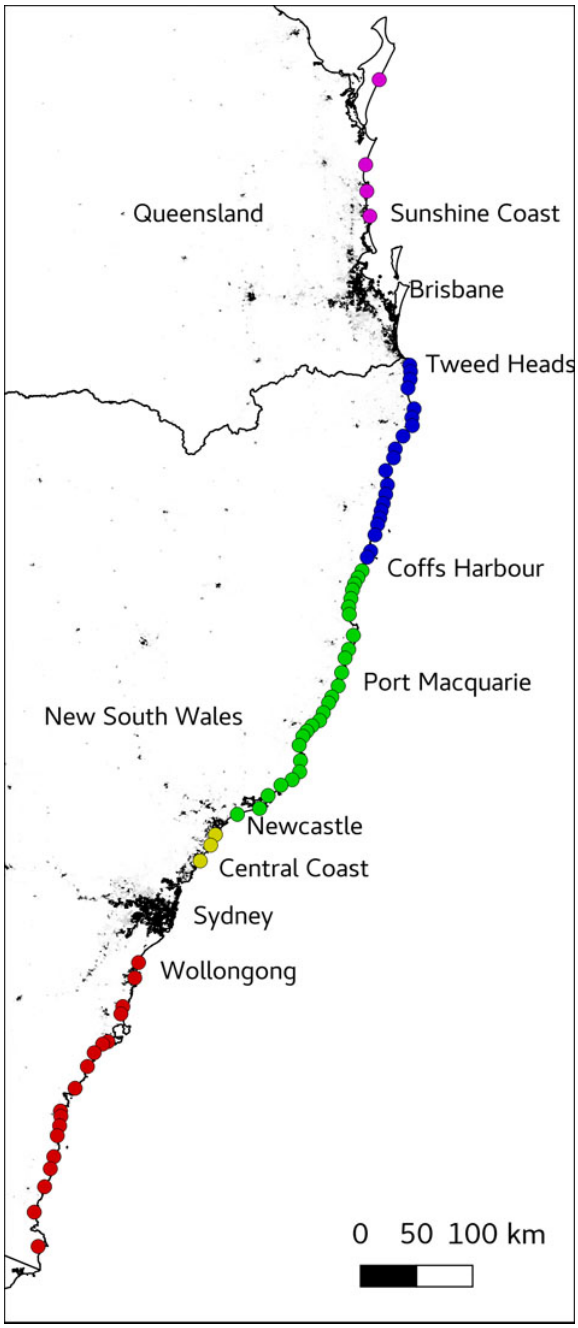

Fig. 1. Map of the SE Australian coast showing the location of beaches (circles plotted at beach centres) sampled in this study (Table 1). Colour-fill identifies regions: SE Queensland (magenta), Far North Coast (blue), Mid-north Coast (green), Central Coast (yellow) and South Coast (red). The background image shows human population densities (scale 0–1000 persons/km^2) from the Australian Population Grid 2011 (Australian Bureau of Statistics 2011). Text annotations identify states and larger coastal cities, towns and populated regions.

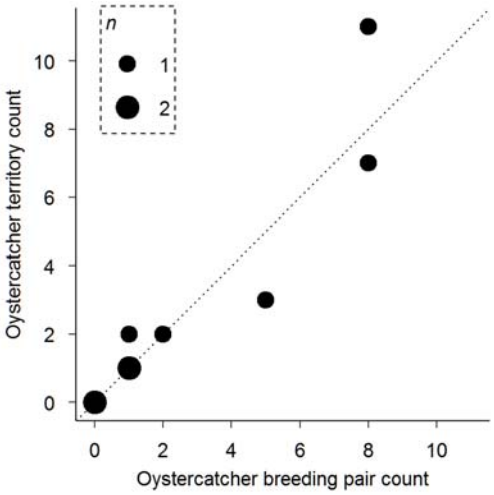

Fig. 2. Oystercatcher territory estimates from territory mapping versus breeding pairs (data and references in Table 1). Point areas are proportional to the number of observations at each location as shown in the legend. A statistical comparison is not useful because the sample size (nine beaches) is small and there is insufficient power to detect small deviations from the 1:1 line of agreement (dotted line).

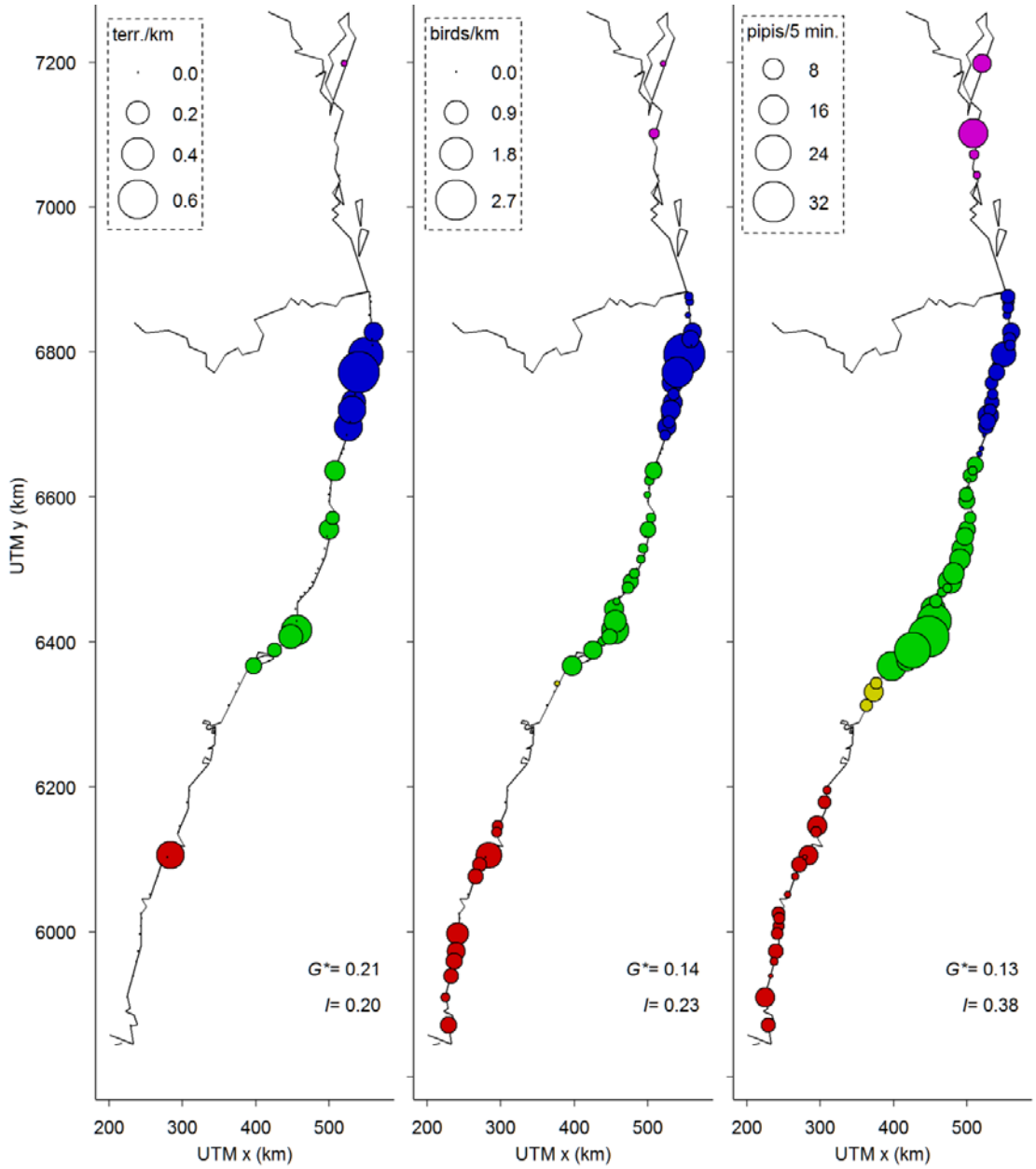

Fig. 3. Bubble maps showing spatial patterns for oystercatcher territory density (a), oystercatcher mean count density (b) and mean pipi count (c) along the SE Australian coast (Fig. 1). Circles are proportional to abundance and colour identifies regions: SE Queensland (magenta), Far North Coast (blue), Mid-north Coast (green), Central Coast (yellow) and South Coast (red). Getis-Ord *G** and Moran's *I* statistics measure spatial concentration and similarity (autocorrelation) respectively and all *P*-values were < 0.001.

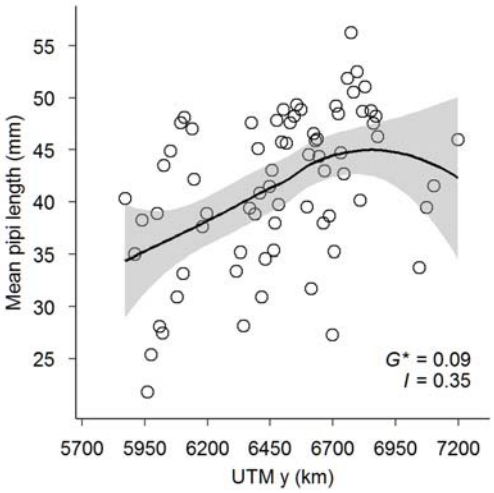

Fig. 4. Scatterplot showing the spatial trend in mean pipi length with a smooth curve fitted by local polynomial regression (the grey envelope indicates a 95% *CI*). Getis-Ord *G** and Moran's *I* statistics measure spatial concentration and similarity (autocorrelation) respectively and all *P*-values were < 0.001.

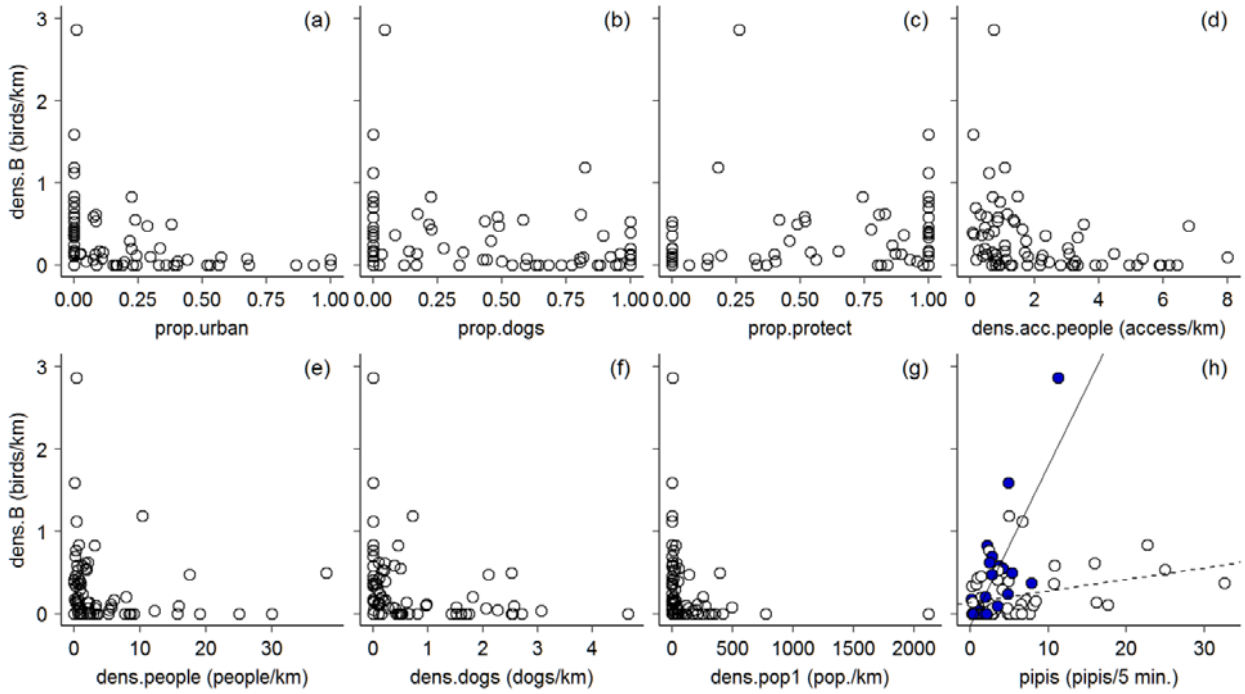

Fig. 5. Oystercatcher mean count density versus proportion of beach length urban (a), proportion of beach length with dogs allowed (b), proportion of beach length adjoining a terrestrial protected area (c), pedestrian access density (d), people mean count density (e), dogs mean count density (f), beach front human population density (g) and pipi abundance (h). All Spearman rank correlations for these scatterplots are ≥ 0.3 (Table 3). In (h), Far North Coast beaches (Coffs Harbour to NSW-Queensland border) are plotted as blue-filled circles and other regions are plotted as white-filled circles. Oystercatcher-pipi lines were fitted by ordinary linear regression with *region2* (Far North Coast/other) as a covariate.

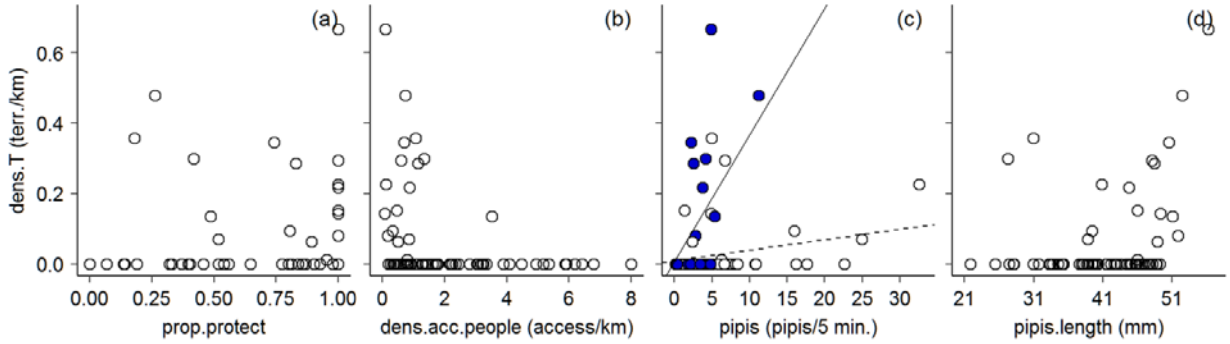

Fig. 6. Oystercatcher territory density versus proportion of beach length adjoining a terrestrial protected area (a), pedestrian access density (b), pipi abundance (c) and mean pipi length (d). All correlations for these scatterplots are ≥ 0.3 (Table 3) except for territories-pipis (Spearman r = 0.28). In (c), Far North Coast beaches (Coffs Harbour to NSW-Queensland border) are plotted as blue-filled circles and other regions are plotted as white-filled circles. Territory-pipi lines were fitted by ordinary linear regression with *region2* (Far North Coast/other) as a covariate.

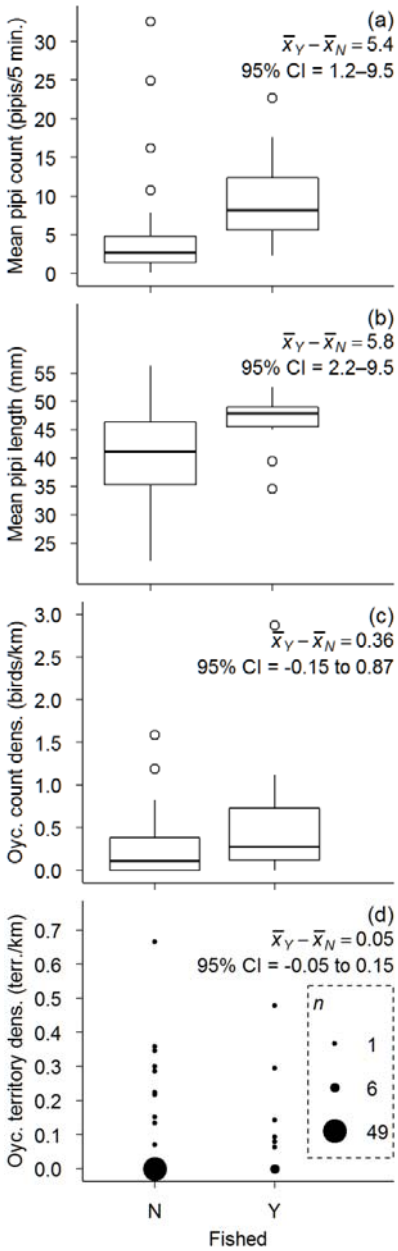

Fig. 7. Box-and-whisker plots for pipi abundance (a), pipi length (b), oystercatcher mean count density (c) and a scatterplot for oystercatcher territory density (d), all comparing beaches with (n_Y = 12) and without (n_N = 60) commercial fishing for pipis. Boxes show the first quartile, median and third quartile, whiskers extend to a maximum of 1.5 times the interquartile range and data outside the whiskers are plotted as individual points (white-filled circles). Box-and-whisker plots were not used in (d) because of the many zeros and zero interquartile ranges. Point areas in (d) are proportional to the number of observations at each location and exactly match those in the legend. Mean difference CIs were computed using unequal variance *t*-tests with the Welch approximate degrees of freedom.

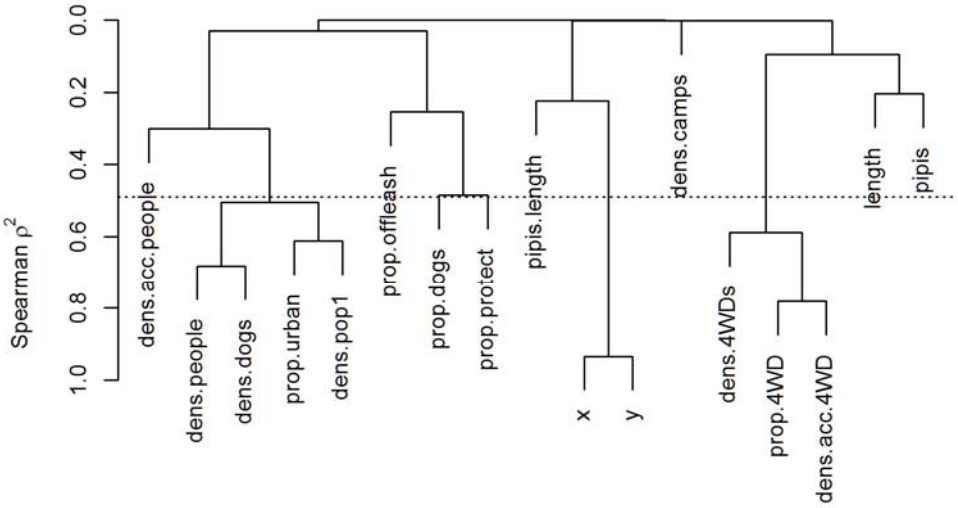

Fig. 8. Hierarchical clustering of continuous predictor variables using squared Spearman correlation coefficients. Variables are described in Table 1. The horizontal line cuts the dendrogram at Spearman $r^2 = 0.49$ and indicates four clusters of collinear variables below the line: 1) *dens.people*, *dens.dogs*, *prop.urban*, *dens.pop1*; 2) *prop.dogs*, *prop.protect*; 3) *x*, *y*, and; 4) *dens.4WDs*, *prop.4WD*, *dens.acc.4WD*. The correlation between *prop.dogs* and *prop.protect* was Spearman $r = -0.696$ and close enough to the $r = -0.7$ cut-off.

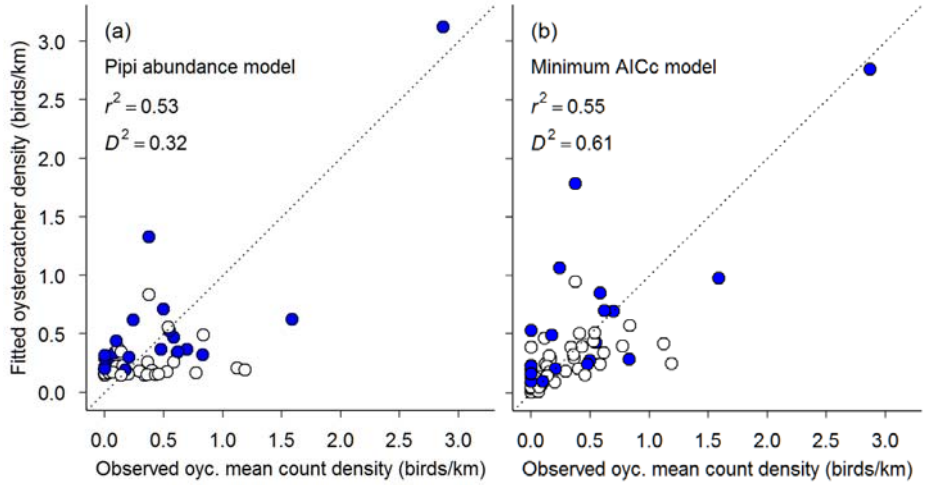

Fig. 9. Fitted versus observed oystercatcher mean count density for the pipi abundance model (a) and the selected model including urban proportion and UTM y (b). Far North Coast beaches (Coffs Harbour to NSW-Queensland border) are plotted as blue-filled circles and other regions are plotted as white-filled circles.

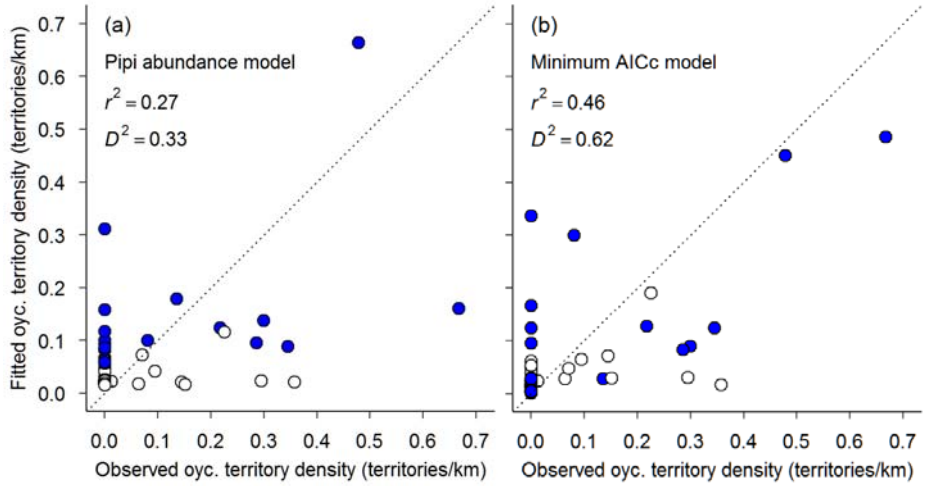

Fig. 10. Fitted versus observed oystercatcher territory density for the pipi abundance model (a) and the selected model including pedestrian access density (b). Far North Coast beaches (Coffs Harbour to NSW-Queensland border) are plotted as blue-filled circles and other regions are plotted as white-filled circles.