

Urban stormwater runoff limits distribution of platypus

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Abstract The platypus (*Ornithorhynchus anatinus*), like many other stream-dependent species, is reportedly sensitive to catchment urbanization. However, the primary mechanism limiting its distribution in urban environments has not been identified. We created species distribution models for three platypus demographic classes: adult females (which are exclusively responsible for raising young), adult males (which are more mobile than females), and first-year juveniles. Using live-trapping data collected in Melbourne, Australia, we tested whether distributions of the three demographic classes were better predicted by catchment urban density (total imperviousness), by urban stormwater runoff (catchment attenuated imperviousness), or by stream size (catchment area). Two variants of each predictor variable were developed, one that accounted for platypus mobility, and one that did not. Female distribution was most plausibly predicted by stormwater runoff (accounting for mobility), with a steep decline in reporting rate from 0 to 10% attenuated imperviousness. Male distribution was equally plausibly predicted by stormwater runoff and urban density (both accounting for mobility), with a less steep and more uncertain decline with imperviousness than females. Juvenile distribution was most plausibly predicted by stream size (accounting for mobility), but both stormwater runoff and urban density (accounting for mobility) were nearly equally plausible predictors. The superior performance of models that accounted for mobility underscores the importance of accounting for this in species distribution models of highly mobile species. Platypus populations in urban areas are likely to be affected adversely by urban stormwater runoff conveyed by conventional drainage systems, with adult females more limited by runoff-related impacts than adult males or juveniles. Urban platypus conservation efforts have generally focused on restoring riparian and in-stream habitats on a local scale. This is unlikely to protect platypus from adverse impacts of urban stormwater runoff, which is most effectively managed at the catchment scale.

Key words: imperviousness, mobility, platypus habitat requirement, spatial autocorrelation, species distribution model.

INTRODUCTION

Human land use in river catchments is a strong determinant of in-stream ecological structure and function (Allan 2004). This is particularly so in urban catchments, in which upland urban surfaces usually have efficient hydraulic connections with streams through constructed stormwater drainage networks (Walsh *et al.* 2005b). Distributions of species with limited short-term mobility such as benthic invertebrates and many fish species are well predicted by measures of catchment land cover, particularly when land cover is weighted by its hydrologic influence on each reach (e.g. Van Sickle & Johnson 2008; Walsh & Kunapo 2009; Sheldon *et al.* 2012). However, for highly mobile fauna, potentially using different reaches for different purposes, such as the platypus (*Ornithorhynchus anatinus*), the interactions of unidirectional hydrolo-

gic flows and multidirectional short-term movements can complicate the prediction of species distributions. Distribution modelling of such fauna may be improved by an approach that accounts for both the nature of rivers as catchment integrators, and faunal use of rivers as corridors (Puth & Wilson 2001).

The platypus is an iconic species of monotreme that occupies a wide variety of lentic and lotic freshwater habitats along the eastern and south-eastern coasts of Australia (Grant 1992). However, its distribution has become fragmented and numbers have declined since European settlement as a result of habitat change and other anthropogenic factors (Grant & Temple-Smith 1998; Serena & Williams 2010). For example, platypus inhabited water bodies within 5 km of Melbourne, Victoria, as recently as the 1950s (Faithfull 1987). However, with subsequent rapid urbanization resulting in a human population of about four million, they are now rarely observed within 15 km of the city centre (Serena & Pettigrove 2005).

The commonly observed loss of disturbance-sensitive species from urban streams is associated with conventional urban stormwater systems. Stormwater

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drainage leads to altered hydrologic regimes, poor water quality, and altered channel form (Walsh *et al.* 2005b). However, other symptoms of urbanization, such as the loss of riparian forest are also likely to contribute to the loss of species (Walsh *et al.* 2005b). For long-lived mobile species such as platypus, factors such as increased visitation by humans, or proximity to streams that are less affected by human land use, could also play a part.

Using total catchment imperviousness (TI, proportion of the catchment covered in impervious surfaces) as a measure of urban density, Serena and Pettigrove (2005) concluded that platypus in streams of the Melbourne region were sensitive to urbanization. They posited that an important driving mechanism was poor sediment and water quality, either through direct toxicity or by reduction in the platypus' benthic invertebrate food source. However, the use of TI as the primary descriptor of urbanization precludes inference as to which of the many elements of urban land use might be the ultimate cause of in-stream degradation (Walsh *et al.* 2005b). Such knowledge is required to target management actions to conserve platypus populations in urban landscapes.

A number of studies have demonstrated that stormwater drainage connection (proportion of impervious surface area connected to stormwater drains) and effective imperviousness (proportion of catchment covered by connected impervious surfaces) are stronger predictors of a range of in-stream ecological indicators than TI (e.g. Taylor *et al.* 2004; Walsh 2004; Walsh *et al.* 2005a). These studies concluded that urban stormwater runoff delivered through conventional drainage systems (Burns *et al.* 2012) is a primary driver of stream degradation in this region.

In this study we develop species distribution models (Guisan *et al.* 2005) to assess if impervious surfaces with direct drainage connection better predict platypus distribution than all impervious surfaces. We quantify effective imperviousness as attenuated imperviousness (AI), in which each impervious surface is weighted by its distance from the nearest downslope stormwater drain or stream (Walsh & Kunapo 2009). AI is thus an estimate of the area of impervious surfaces that are likely to be connected by sealed drainage systems to receiving streams. It indicates a range of hydrologic and water quality changes that in turn drive geomorphic and in-stream ecological changes. The primary hydrologic changes that are likely to affect in-stream changes are an increase in the frequency and magnitude of high flows, which are likely to transport elevated concentrations of pollutants, and a reduction in baseflows (Walsh *et al.* 2012). The resulting changes in composition of invertebrate and plant assemblages and channel morphology are well documented (Walsh *et al.* 2005b; Chin 2006).

If AI is a stronger predictor of platypus distribution than TI, this is evidence that urban stormwater runoff is a likely mechanism influencing platypus distribution in urban environments. Given that platypus are highly mobile animals, we also construct variants of TI and AI that take vagility into account when assigning habitat quality within foraging areas. In doing so, we identify urban stormwater runoff as an important limiting factor of platypus distribution in urban landscapes.

METHODS

Platypus distributional data

Platypus live-trapping data were collected from 400 sites in 50 waterways, spanning a rural to urban land-use gradient in the Melbourne region (Fig. 1). Data were obtained over 13 consecutive field seasons, from early 1995 through to mid-2007. Each live-trapping site was sampled on 1–37 nights (4.6 ± 6.6 , mean \pm SD). One pair of fyke nets was deployed per site to capture animals travelling upstream or downstream; 4–8 sites were typically monitored in each overnight session, spaced at intervals of 1.1 ± 0.3 km (mean \pm SE) (Serena & Pettigrove 2005). Sex and age of captured platypus were identified based on the size and appearance of calcaneal spurs on the hind legs, allowing three demographic classes to be reliably assigned: juvenile (≤ 11 months) and adult or subadult males and females (> 11 months) (Williams *et al.* 2013). Platypus have been documented to survive to an age of 21 years in the wild (Grant 2004) and population turnover rates are correspondingly low. Given the adult/subadult age-class is dominated by sexually mature individuals, it will hereafter be referred to as 'adult'.

Landscape data

Urban land use in the Melbourne region was mapped from 2005 aerial imagery with a 35-cm-resolution infrared band (Melbourne Water Corporation, unpubl. data, 2005). For all stream reaches of the region, catchment area (CA, range = 1–3391 km²) was calculated from a digital elevation model (DEM) conditioned on the drainage and stream network (Walsh & Kunapo 2009; Urrutiaguer *et al.* 2012). Total impervious area was then divided by CA to determine TI (range = 0.02–44.5%). AI (range = 0–29.9%) was calculated by weighting all impervious surfaces by overland-flow distance (calculated from the DEM) from the most downstream point of the surface to the nearest downslope stream or stormwater drain. Surfaces were weighted using the exponential decay function that was the best predictor of macroinvertebrate assemblage composition in the region and dividing by CA (Walsh & Kunapo 2009). In addition, we used CA as a predictor variable to test the hypothesis that platypus distribution was influenced by waterway size, independent of stream condition.

We accounted for platypus mobility within a heterogeneous environment by calculating variants of TI, AI and CA that represented the highest quality habitat located within 4 km downstream of survey sites: minimum TI (TI_{min}, range =

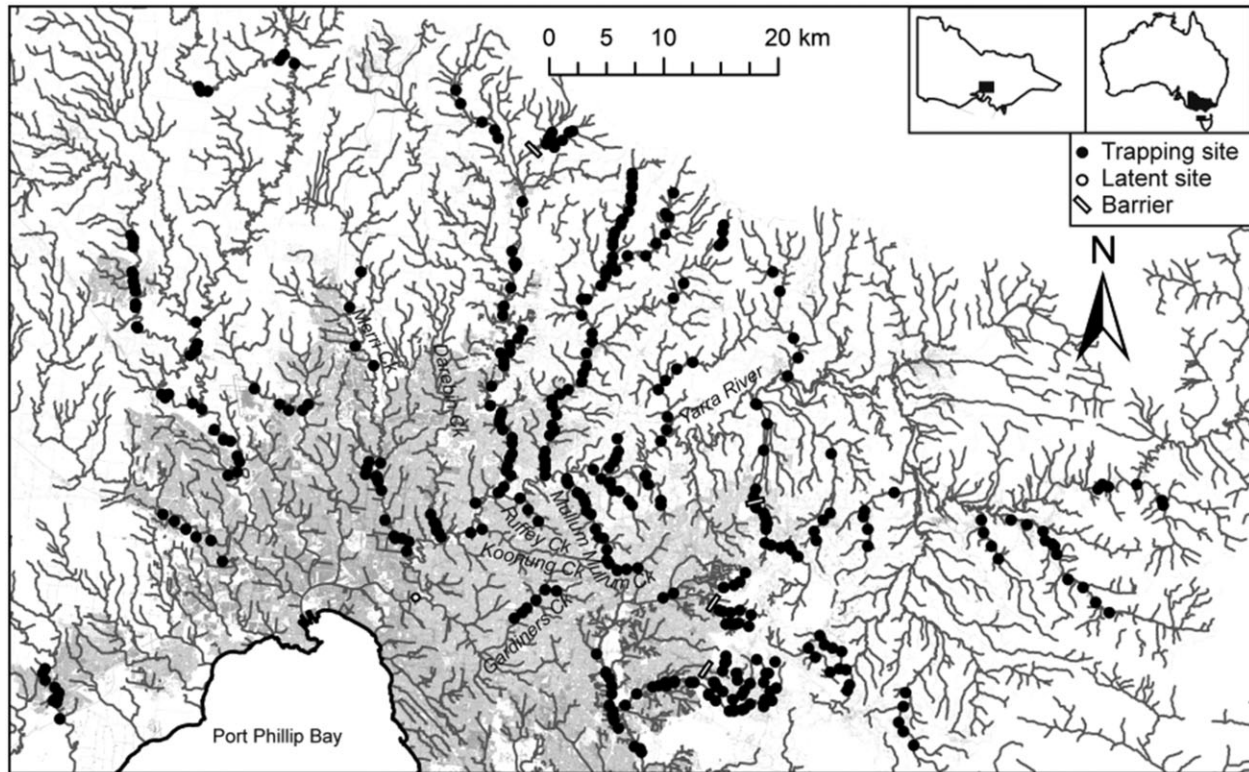


Fig. 1. Locations of platypus trapping sites ($n = 400$) in the Melbourne region, Victoria, Australia. A single latent site in the lower Yarra River and four barriers to platypus movement are also indicated. The light gray shading indicates impervious surfaces of the region.

0.02–39.9%), minimum AI (AI_{\min} , range = 0–29.3%) and maximum CA (CA_{\max} , range = 7–3391 km²). We chose the highest quality habitat based on the assumption that platypus optimize foraging success by seeking out and frequenting the most productive areas available to them. The value of 4 km closely approximates the mean maximum home range length of radio-tagged adult males and females occupying lotic systems in south-eastern Australia (3.9 km: Grant *et al.* 1992; Serena 1994; Gardner & Serena 1995; Gust & Handasyde 1995; Serena *et al.* 1998; 2001). We used the downstream direction to quantify the best available habitat because the amount of potential foraging area per unit length of channel is likely to increase downstream with increasing stream size, and decrease upstream. If minimum values of TI or AI within 4 km were calculated for both directions and the lowest value chosen, values for many reaches of highly urban streams were close to zero because of very small tributaries draining non-urban or reserved sub-catchments that were unlikely to provide foraging area because of their small size. If they were calculated for downstream only, the only reaches for which the minimum imperviousness value differed greatly from the unadjusted value were those that were within 4 km of larger, less urbanized streams.

Statistical model

We constructed a spatially explicit logistic regression model in a Bayesian framework to predict the platypus reporting

rate (i.e. the probability a platypus is present and detected) at a site contingent upon each one of the predictor variables. We accounted for the potential bias in parameter estimation that would be caused by assuming perfect detectability in a survey method (Tyre *et al.* 2003) by using site-level reporting rate (number of detections per number of samples over the entire sampling period) instead of presence and absence data. We thus modelled platypus reporting rate d as a binomially distributed variable with mean, θ and a sample size of n (Eqn 1). The (logit-transformed) reporting rate at site i was initially conceived as a linear function of the predictor variable x (Eqn 2), where β is the estimated parameter governing the size of the effect and α is the intercept:

$$d_i \sim \text{Bin}(\theta_i, n_i) \quad (1)$$

$$\text{logit}(\theta_i) = \alpha + \beta x_i \quad (2)$$

The model was then further developed to account for spatial autocorrelation in the occurrence data. If spatial autocorrelation is not taken into account when modelling species–habitat relationships, estimates of probability of occurrence can be biased (Beale *et al.* 2010; Miller 2012). We accounted for autocorrelation by including a dependency on the neighbourhood reporting rate u in the estimation of reporting rate (Eqn 3; modified from Wintle & Bardsos 2006). The size of the spatial autocorrelation effect is estimated by the parameter ρ :

$$\text{logit}(\theta_i) = \alpha + \beta x_i + \rho u_i \quad (3)$$

We defined the neighbourhood of a survey site as all immediately upstream sites (modified from Webb & King 2009). Most sites had only one upstream neighbour, but those immediately downstream of confluences could have two or more neighbours. We calculated upstream reporting rate as the average reporting rate d of the n neighbouring sites (Eqn 4). We incorporated the expectation that spatial autocorrelation decreases with increasing distance between neighbouring sites by weighting the upstream reporting rate by the negative exponent of stream distance m between site i and upstream site j :

$$u_i = \frac{\sum_{j \in n_i} d_j e^{-m_j}}{n_i} \quad (4)$$

By incorporating spatial autocorrelation in this way it was possible to explicitly account for the spatial structure of the survey site network. For instance, definitive barriers to routine platypus movements, such as dam spillways and significant lengths of underground piped reaches, were incorporated by isolating these sites from the next-downstream sites in the quantification of spatial autocorrelation (Fig. 1). It was also possible to spatially associate sites that were not linked by a downstream survey site. This was achieved for the lowest tributaries of the Yarra River (Koonung, Darebin, Merri and Gardiners Creeks; Fig. 1) by including a latent site in the spatial network below the confluence of Gardiners Creek. This site was hypothetically sampled once, the result of which was unknown and fitted in the model (Congdon 2006). The requirement that a site have an upstream neighbour in order to quantify spatial autocorrelation, means that terminal sites in the most upstream waterways of the network, and sites immediately downstream of movement barriers, were used only to condition the model, and their data were not directly used to quantify effects of urbanization (Congdon 2006).

The use of a binomial distribution for modelling reporting rate data does not allow for the incorporation of temporal autocorrelation among sampling events in the estimation of reporting rates at individual sites. However, using a model structure that could include such effects (e.g. modelling each survey as a Bernoulli-distributed event with temporal autocorrelation among repeat surveys and a site random effect to account for sites that have higher/lower than expected reporting rates) would lead to the effective exclusion of data from all sites that were only surveyed once (i.e. the first survey at a site is used to condition the model – equivalent to the process for assessing for spatial autocorrelation), some 45% of the sites. Moreover, we visually assessed temporal autocorrelation within sites for which good repeat survey data were available (10 or more surveys), and found no indication of autocorrelation at these sites. Accordingly, we felt the binomial-based model was appropriate for our data set.

Model analysis and implementation

Adult females, adult males and juveniles were considered separately to allow for different responses to urbanization, and variation in spatial autocorrelation that may result from behavioural or other relevant biological differences among sex and age-classes (Guisan *et al.* 2005). Six competing reporting rate models were run for each demographic class,

that is, one for each predictor variable (TI, AI, CA, TI_{\min} , AI_{\min} or CA_{\max}). Model parameters had minimally informative normal priors with a mean of 0 and a variance of 1×10^6 and were estimated using three independent Markov chains. Each chain was run for 150 000 iterations with the first 50 000 discarded as a burn-in, resulting in 300 000 samples used for parameter estimation. Convergence of the Markov Chains was confirmed using the Brooks–Gelman–Rubin diagnostic (Brooks & Gelman 1998). Models were run using OpenBUGS version 3.2.1 (Lunn *et al.* 2009).

We compared models within demographic classes using two methods. First, the Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002), with the lowest DIC value indicating the ‘best’ model among a set of plausible alternatives. Models with a difference in DIC (Δ DIC) ≤ 2 are considered equally plausible, Δ DIC of 4–6 indicates that the model with the lower DIC is moderately superior, whereas Δ DIC > 10 indicates that the model with the lower DIC is strongly preferred (Burnham & Anderson 2002). Second, we conducted a posterior predictive test (Gelman *et al.* 2004) comparing predicted reporting rates with observed reporting rates. We calculated the average absolute and directional residuals to determine model performance and bias, respectively. We included all sites in the posterior predictive test except for those not used to condition the model. We considered both Δ DIC ranking and residual reporting rates when determining the best overall models.

RESULTS

Model posterior predictive tests indicated that all models performed well and that model performance within demographics was very similar. The maximum average absolute residual of predicted reporting rate was about 20% (for males) while all models had a small bias towards over prediction. This bias is partly because of the logit transformation truncating possible predictions of reporting rate to slightly above 0. Between demographic classes, juveniles had the lowest average absolute residuals across all models (about 10%), males had the highest (about 20%) and females were in between (about 18%). According to DIC, accounting for platypus mobility substantially increased the plausibility of models for every demographic class: AI_{\min} , TI_{\min} and CA_{\max} were consistently more plausible predictors of reporting rate than AI, TI and CA, respectively (Table 1). There was spatial autocorrelation in reporting rates for all demographic classes. This effect was strongest for juveniles, and weakest for males (Fig. 2). Results were very similar for the two assessments of model quality; posterior predictive tests indicated that all models preferred by Δ DIC values performed the best (i.e. had the lowest residuals).

Adult female platypus reporting rate was most plausibly predicted by AI_{\min} . The average absolute residual for the AI_{\min} model was the lowest of all models for females at 17.6%, while reporting rate predictions were slightly biased to over prediction (average

Table 1. Difference between deviance information criteria (Δ DIC) and that of the best model (Δ DIC = 0) and average absolute and directional residuals of predicted reporting rate of each model for each demographic class

| Landscape variable | Females | | | Males | | | Juvenile | | |
|--------------------|--------------|-------------|-------------|--------------|-------------|-------------|--------------|-------------|-------------|
| | Δ DIC | Abs. Resid. | Dir. Resid. | Δ DIC | Abs. Resid. | Dir. Resid. | Δ DIC | Abs. Resid. | Dir. Resid. |
| AI _{min} | 0 | 17.6 | 3.4 | 0 | 19.7 | 7.1 | 2.6 | 10.3 | 1.9 |
| TI _{min} | 20.7 | 18.3 | 3.9 | 1.7 | 20.1 | 7.6 | 4 | 10.5 | 2.2 |
| AI | 56.4 | 18.3 | 3.5 | 28.4 | 20.5 | 7.4 | 11.4 | 10.6 | 2.1 |
| TI | 55.6 | 18.5 | 3.7 | 27.4 | 20.5 | 7.5 | 11.5 | 10.6 | 2.0 |
| CA _{max} | 70.2 | 18.6 | 3.4 | 31.6 | 20.7 | 7.4 | 0 | 10.5 | 2.1 |
| CA | 71.1 | 18.7 | 3.6 | 31.8 | 20.5 | 7.0 | 12.3 | 10.7 | 2.2 |

All models were the same structure, but differed in the predictor variable used. Subscripted min or max indicates the minimum or maximum values within 4 km downstream. Abs. Resid., absolute residual; AI, attenuated imperviousness; CA, catchment area; DIC, Deviance Information Criterion; Dir. Resid., directional residual; TI, total imperviousness.

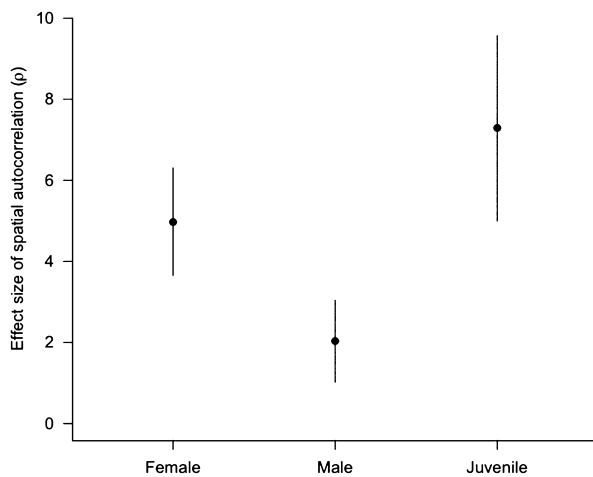


Fig. 2. Effect size of spatial autocorrelation (ρ) for each demographic class, averaged across all models, \pm 95% credible intervals. ρ was not statistically different (95% credible intervals overlapped) between females and juveniles.

directional residual = 3.4%). TI_{min} was a substantially less plausible predictor than AI_{min} according to Δ DIC and a comparable but still a weaker model according to model residuals (Table 1). This indicates that urban stormwater runoff impacts are a better predictor of adult female platypus reporting rate than is total urban density. After accounting for spatial autocorrelation, adult female platypus reporting rate declined steeply to near zero as AI_{min} increased from 0 to 10% (Fig. 3a).

Reporting rate of adult male platypus was equally plausibly predicted by TI_{min} and AI_{min} according to both Δ DIC and model residuals (Table 1) indicating there is not enough information in the adult male distributional data to isolate the impacts of urban stormwater runoff from those of total urban density. For both AI_{min} and TI_{min}, adult male reporting rate decreased with increasing imperviousness (Fig. 3b,c), suggesting that adult male platypus are sensitive to the impacts of catchment urbanization and urban stormwater runoff, but the effect is not as strong as it is for females (Fig. 4).

The effects of the predictor variables on juvenile platypus reporting rate were similar to those for adult males. According to model residuals, all models performed equally well and better than other demographic classes (Table 1). However, according to Δ DIC, the most preferred model was CA_{max}, but this was only slightly preferred over AI_{min} and TI_{min}. Reporting rate decreased with increasing imperviousness for both TI_{min} and AI_{min} (Fig. 3d,e), suggesting that juveniles are sensitive to the impacts of catchment urbanization and urban stormwater runoff. As was true for adult males, TI_{min} and AI_{min} were equally preferred juvenile models, indicating there was not enough information in the data to distinguish between the impacts of catchment urbanization and urban stormwater runoff. The most plausible predictor variable of juvenile reporting rate, according to Δ DIC, was a positive relationship with CA_{max} (Fig. 3f), although it was only marginally preferred to imperviousness models. In contrast, CA and CA_{max} were the least preferred predictors for both male and female adults.

DISCUSSION

Catchment urbanization and associated impacts of urban stormwater runoff influence the distributions of both adult and juvenile platypus living near Melbourne, and the negative effects are most limiting for adult females. Furthermore, the distribution of adult females is better predicted by impacts of urban stormwater runoff than the broader effects of catchment urbanization, indicating that urban stormwater runoff is a likely mechanism driving this limitation.

The relationship between stormwater impacts and the distribution of adult females plausibly reflects a strong underlying relationship between habitat productivity and female reproductive success. Adult platypus do not form lasting monogamous bonds and otherwise appear to be essentially solitary in their habits (e.g. Serena 1994; Gardner & Serena 1995;

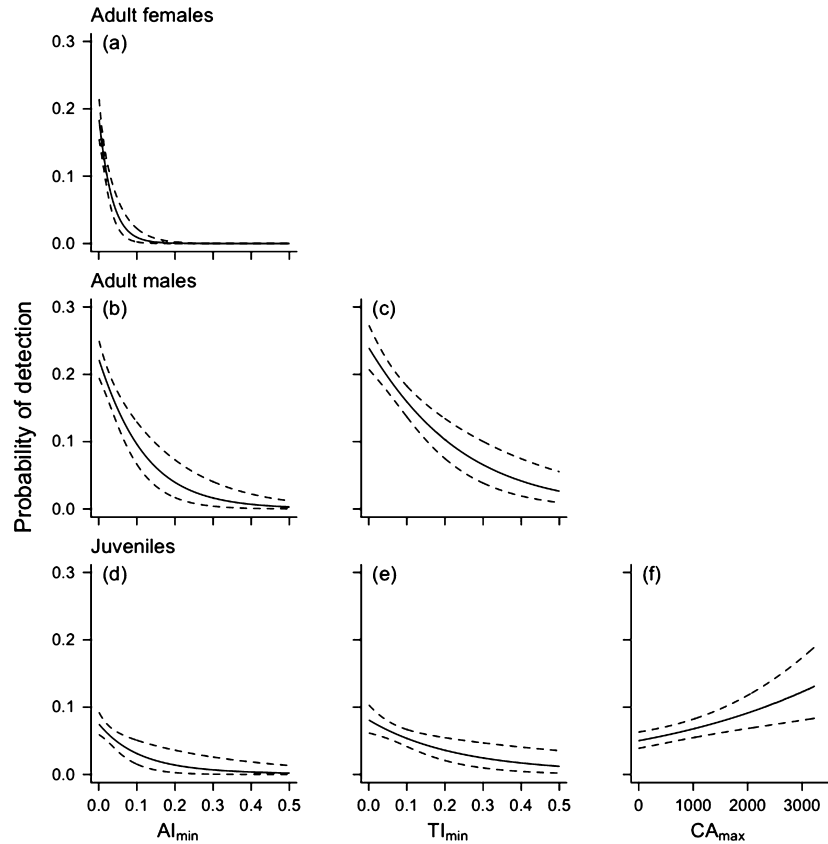


Fig. 3. Most plausible models of reporting rate for each demographic class of platypus. For each model, reporting rate along each predictor variable gradient was calculated by assuming zero reporting rate at neighbouring sites. (A) Adult females *versus* minimum attenuated imperviousness within 4 km downstream (AI_{min}). (B, C) Adult males *versus* AI_{min} and minimum total imperviousness within 4 km downstream (TI_{min}), respectively. (D, E, F) Juveniles *versus* AI_{min} , TI_{min} and maximum catchment area within 4 km downstream (CA_{max}), respectively. CA_{max} was the most plausible predictor of juvenile reporting rate, but AI_{min} and TI_{min} were almost as plausible. Solid line = median; dashed lines = 95% credible interval.

Gust & Handasyde 1995; Serena *et al.* 1998). This implies that female reproductive fitness depends directly on the ability to wean young. The home range of an adult female therefore needs to provide adequate food resources in the form of benthic macroinvertebrates to support both her and an annual litter of up to three juveniles (Burrell 1974). Lactation lasts approximately 4 months (Holland & Jackson 2002; Grant *et al.* 2004; Hawkins & Battaglia 2009), with food consumption in captivity increasing over the course of lactation to a peak daily value of around 80% of maternal body mass (Holland & Jackson 2002). Platypus diet is dominated by disturbance-sensitive invertebrate taxa that are sensitive to urban impacts (Faragher *et al.* 1979; Grant 1982; Munks *et al.* 2000; McLachlan-Troup *et al.* 2010). The loss of these preferred platypus prey items from streams receiving urban stormwater runoff (e.g. Walsh 2004) may potentially drive the steep decline in reporting rate of females with increasing AI_{min} . However, urban stormwater runoff has many varied effects on stream ecosystems, such as altered geomorphology and

reduced water quality, and these effects are confounded. We have not attempted to disentangle them because the overarching threat is urban stormwater runoff and addressing this issue will address all impacts of urban stormwater runoff.

The relationships of TI_{min} and AI_{min} with reporting rate of adult males and juveniles do not decline as sharply as that of females, indicating that these demographic classes are less affected by catchment urbanization and urban stormwater runoff. In the case of adult males, the weaker relationship could be a result of greater mobility. Male reproductive success in solitary mammals is limited in the first instance by the number of females that are successfully inseminated. This commonly results in males behaving as 'area maximisers' (*sensu* Hixon 1987), that is, occupying home ranges larger than needed to satisfy food requirements in order to improve access to mates. Adult male platypus occupy areas that are, on average, three times larger than those occupied by adult females (Serena & Williams 2012b), so that each male home range characteristically overlaps two or more

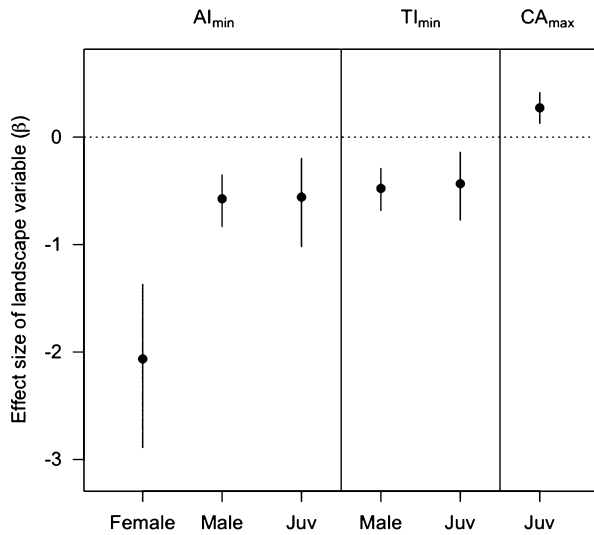


Fig. 4. Effect size (β) of predictor variables (AI_{\min} , minimum attenuated imperviousness, TI_{\min} , minimum total imperviousness and CA_{\max} , maximum catchment area, all within 4 km downstream) in the most plausible models for adult female and male, and juvenile (Juv) platypus.

adult female ranges (e.g. Gardner & Serena 1995; Serena *et al.* 1998). Resident adult males plausibly spend more time at suboptimal sites than females as a by-product of patrolling territorial margins frequently (Gardner & Serena 1995), or because male home ranges encompass non-contiguous female home ranges. In addition, male platypus may potentially be encountered in a suboptimal habitat when travelling outside their normal home ranges. In other species of solitary mammal, extraterritorial movements may be undertaken either to locate additional mates adventitiously during the breeding period (Sandell 1989), or to update information on the distribution of both males and females in neighbouring areas prior to breeding (Dahle & Swenson 2003). In the case of platypus in a Tasmanian lake system, males deemed to be transient based on recapture frequency were most commonly recorded during the spring breeding season (Bethge *et al.* 2009). Lengthy movements by an adult male between stream catchments have also been observed outside the platypus breeding season (Gardner & Serena 1995). Finally, less dominant males may be forced into poorer quality habitats as an outcome of intrasexual aggression, particularly during the breeding season. Adult males have been observed fighting in the wild at this time of year (Gust & Handasyde 1995; Easton *et al.* 2008), with spatial segregation among males increasing during the breeding season (Gust & Handasyde 1995).

The weaker effect of catchment urbanization and urban stormwater runoff on the distribution of juvenile platypus compared with adult females could be a result of dispersal. Live-trapping studies in Victoria

suggest that many juvenile platypus initiate dispersal from their natal home range at the age of about seven months, roughly 3 months after they first emerge from a nesting burrow (Serena & Williams 2012a), with immature males sometimes moving >40 km (Serena & Williams 2012b). Accordingly, many juvenile platypus moving through an urban landscape are likely to spend time in suboptimal habitats. The proposition that captured juveniles included dispersers could also help to explain the positive relationship observed between juvenile reporting rate and maximum catchment area within 4 km of capture sites (CA_{\max}), and a clumped spatial distribution as indicated by strong positive spatial autocorrelation. Young platypus may be most likely to persist in larger rivers where the likelihood of agonistic encounters with older animals is reduced.

The superiority of AI_{\min} over AI as a predictor of female platypus distribution points to the likely importance of channel morphology as a driver of platypus habitat quality. In our dataset, female platypus were found in the lower reaches of only two urban streams with high levels of AI (Mullum Mullum and Ruffey creeks: Fig. 1), both of which are within 4 km of the large, predominantly rural Yarra River. The lower reaches of these streams remain well vegetated, with undercut banks providing habitat for platypus burrows. However, catchment urbanization has grown in both catchments over the last 20 years, and both streams are actively eroding (Geoff Vietz, University of Melbourne, pers. comm., 2012). In the mid-1990s, platypus captured in one of these streams allocated nearly half of their foraging effort and time spent in burrows to nearby parts of the Yarra River (Serena *et al.* 1998). We hypothesize that the occurrence of platypus in the lower reaches of these streams is a result of persistence of important habitat features such as undercut banks (Serena *et al.* 1998), along with the availability of neighbouring river habitats less impacted by stormwater runoff. However, the active erosion of these stream channels suggests that these features may be temporary, as geomorphic response to urbanization can occur over decades (Chin 2006).

More generally, the universally superior performance of models that accounted for platypus mobility (i.e. those using AI_{\min} , TI_{\min} and CA_{\max}) demonstrates the importance of accounting for mobility in species distribution models of vagile animals. Other studies, particularly of terrestrial animals, have considered species mobility indirectly by incorporating spatial autocorrelation to deal with non-independence of occupancy observations at neighbouring sites, and was included in our models (e.g. Wintle & Bardos 2006). This is often referred to as the neighbourhood effect. However, studies rarely consider mobility in the context of habitat complementarity, that is, non-uniform usage of the home range driven by local habitat heterogeneity, where some areas might be favoured over others. Our results suggest the predictive power of species distribution models may be improved

by explicitly including animal mobility in model and data formulation. Our modelling framework, which accounts for both animal mobility and spatial autocorrelation in sample data likely to be induced by such mobility, could be easily adapted to other vagile species and to assess the effects of other catchment-scale drivers of species distributions.

Past considerations of mechanisms limiting platypus in urban streams have focused on poor sediment or water quality (Serena & Pettigrove 2005). Our identification of urban stormwater runoff as a strong predictor of platypus reporting rate suggests that platypus are potentially limited by the multiple impacts of urban stormwater runoff, for example, water quality, sediment quality, hydrology and geomorphic change (Walsh *et al.* 2005b; Burns *et al.* 2012). These effects of urban stormwater runoff are highly confounded and are likely to defy any attempt at disentanglement (Walsh *et al.* 2005b). However, they need not be considered in isolation to inform management of streams in urban catchments for the conservation of platypus. If urban stormwater runoff is adequately managed through retention for loss through evapotranspiration or human use, with some infiltration to restore reduced baseflows (Walsh *et al.* 2012), all potential mechanisms resulting from urban stormwater runoff can plausibly be addressed.

This approach of identifying the ultimate source of multiple potential mechanisms of degradation is useful for identifying the scale of remedial actions required. In particular, platypus conservation measures that concentrate on local-scale protection or restoration of habitat features without addressing urban stormwater runoff are likely to be of limited benefit. Sustainable restoration or maintenance of platypus habitats in urban streams will require catchment-scale management of stormwater runoff to more closely approximate pre-urban flow regimes and water quality (Burns *et al.* 2012). This will require dispersed retention of urban stormwater runoff by harvesting and irrigation, both to reduce total volumes and promote infiltration to restore lost baseflows (Walsh *et al.* 2010).

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