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Early response of the platypus to climate warming

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Abstract

Combining a climatic envelope modelling technique with more than two centuries (1800–2009) of distribution records has revealed the effects of a changing climate on the egg-laying monotreme, the platypus, *Ornithorhynchus anatinus*. We show that the main factor associated with platypus occurrence switched from aquatic habitat availability (estimated by rainfall) to thermal tolerances (estimated by annual maximum temperature) in the 1960s. This correlates directly with the change in the annual maximum temperature anomaly from cooler to warmer conditions in south-eastern Australia. Modelling of platypus habitat under emission scenarios (A1B, A2, B1 and B2) revealed large decreases (>30%) in thermally suitable habitat by 2070. This reduction, compounded by increasing demands for water for agriculture and potable use, suggests that there is real cause for concern over the future status of this species, and highlights the need for restoration of thermal refugia within the platypus' modelled range.

Keywords: climate change, climatic envelope modelling, MAXENT, *Ornithorhynchus anatinus*, platypus

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Introduction

Climate warming represents a major challenge for biota, particularly those that occupy habitats approaching their thermal maxima. Recent studies have shown reductions in population sizes (Thomas *et al*., 2004; Stork, 2010), latitudinal and altitudinal alterations in range (Parmesan, 1996, 2003) and changes in interspecific interactions (Walther *et al*., 2002) in response to a changing climate. However, although climatic changes in Australia are consistent with global trends, and some predicted impacts on biota have been described (see Williams *et al*., 2003; Fitzpatrick *et al*., 2008; Gibson *et al*., 2010; Yates *et al*., 2010) documented biotic impacts are limited. This is partly due to the lack of long-term datasets and phenological monitoring that have allowed the detection of climate-change-related trends in the Northern Hemisphere (Hughes, 2003). The extreme climatic variability which characterizes much of the Australian continent also renders trends more difficult to detect.

A comprehensive analysis of projected climate change for the east coast of Australia, taking into account the variability encompassed by multiple models, predicts both warming and drying trends (CSIRO, Australian Bureau of Meteorology, 2007). Even under low emission scenarios, temperatures are predicted to rise by between 1 and 2.5 °C, with a 7.5% decrease in rainfall by 2070. At high emission levels, 2.2–5 °C warming is predicted, with a 10% decrease in rainfall by 2070 (IPCC 2000). All scenarios predict an increase in extreme temperatures and rainfall events (Hennessy *et al*., 2008). Even where climate change scenarios indicate that rainfall may increase, higher temperatures will result in higher rates of evaporation, up to 8% per degree of global warming over most of Australia, resulting in a decrease in annual moisture balance (Hughes, 2003). This will result in a decrease in run-off into streams and, ultimately, a contraction of aquatic habitats (Bond *et al*., 2008). These scenarios present a high risk to the platypus (*Ornithorhynchus anatinus*, Shaw 1799).

The egg-laying monotreme, the platypus, is the sole species in the family Ornithorhynchidae, and together with four species of echidna, is one of the five extant monotremes in the mammalian subclass, Prototheria. The recent sequencing of the platypus genome has revealed a combination of reptilian, mammalian and unique characteristics (Warren *et al*., 2008), comprising a mosaic of plesiomorphies and apomorphies (Musser, 2003) and confirming its evolutionary importance amongst amniote vertebrates.

The species is endemic to the freshwater ecosystems of eastern Australia (Grant & Temple-Smith, 1998). It is usually nocturnal, feeds almost exclusively underwater on aquatic macroinvertebrates, and uses burrows in the banks of streams and pools for resting and nesting; see Grant (2007) for review. The obligate association of platypus with permanent freshwater environments, their dependency on both aquatic and riparian habitats (Grant, 1992a; Serena *et al*., 1998) and limited ability to travel overland (Grant, 1992b; Kolomyjec *et al*., 2009) render the species susceptible to a range of processes

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threatening Australian river systems (Grant & Temple-Smith, 2003).

Potentially adverse impacts on platypus distribution include: poor water quality; loss of deep refuge pools, building of large dams (Grant & Temple-Smith, 1998; Grant, 2004), river regulation and impoundments; loss of riparian vegetation; stream bank erosion and channel sedimentation, introduced and invasive species (predation and competition), fisheries by-catch mortality and disease (Grant & Temple-Smith, 2003). Despite these impacts, the platypus still persists throughout much of its historical range, although there are no longer naturally occurring populations in South Australia and numbers have declined in the lower reaches of the Murray and Murrumbidgee Rivers in Victoria and NSW (Grant & Temple-Smith, 2003). The ability of the platypus to survive and reproduce in degraded environments is in marked contrast to the exceptionally high rate of decline and extinction of Australian mammals over the preceding 200 years (Burbidge & McKenzie, 1989; Johnson & Isaac, 2009). While the platypus has proven robust to many anthropogenic stresses, their specialized habitat requirements and limited dispersal ability may render them highly vulnerable to the impacts of a changing climate, particularly from loss of aquatic habitats due to drying and elevated water temperatures.

The fossil history of a diverse platypus-like fauna recorded in both Australia and South America (Grant & Temple-Smith, 2003; citing Musser, 1999) suggests a possible Gondwanic origin of the platypus. A late Cretaceous radiation of the platypus (Musser, 2003) indicates an evolutionary history dominated through the Cenozoic by considerable variation in thermal regimes. However, it is probably the increasing aridity of the Australian continent over the last 40 000 years (Bowler, 1982; Hill, 1994) that has progressively limited platypus to the wetter eastern and southern regions of the continent.

Given the iconic status of the platypus we sought to determine the likely impact of climatic warming on habitat availability using more than two centuries (1800–2009) of platypus distribution records and climatic envelope modelling. The long time series available for this modelling provided a unique insight into the potential response to climate change; most studies of species responses span only a few decades and so can be confounded by decadal scale climatic oscillations (Moritz *et al.*, 2008).

Materials and methods

A total database of 11 460 platypus records, covering the period from 1800 to 2009, and all Australian states and territories in which platypus occur (Table 1) was compiled from records held by Australian museums, state environmental management agencies and individual researchers (see Acknowledgements). Records of occurrence dated pre-1980 [when the Global Positioning System was introduced for public use (Macleod *et al.*, 2009)], may vary in accuracy. However, as all records were obtained from established databases these are considered to represent the most accurate available. Removal of duplicates resulted in a final set of 9570 individual records available for modelling. Climate and topographic Geographic Information Systems (GIS) layers covering the geographic extent of Australia were compiled. Geomedia (Intergraph 2011) was used to take a 'subscene' of the area of interest (eastern Australia) from all layers, restricted to the area bounded by −10°43′29″ to −43°58′30″S and 139°26′06″ to 154°3′7″E. Layers were then resampled to a resolution of 0.05° using ArcGIS (ESRI 2011) to ensure all layers were aligned and at the same resolution. Total annual rainfall (gridded data, 1900–2009) and annual maximum and minimum air temperatures (gridded data, 1911–2009) were obtained from the National Climate Centre, Australian Bureau of Meteorology (2010). These data were averaged for each decade. Maximum daytime temperatures were used as they are strongly correlated with water temperature and night time maxima. The digital elevation model (DEM) of eastern Australia, was sourced from Geoscience Australia (2010). We used variables at a landscape scale as they were the most appropriate to the questions for this study. The relatively large scale (catchment) variables are consistent with the spatial grain of the climate models, and with the degree of resolution of the platypus occurrence data.

Platypus distribution was modelled using Maximum Entropy Species Distribution Modeling Software (MAXENT) version 3.3.3e (Phillips & Dudík, 2008; Dudík *et al.*, 2010) which uses presence-only data to model and predict species' distribution. Climate and elevation were related to platypus location records to compare the factors influencing distribution for each decade. Platypus records for the period 1800–1911 were modelled using the 1910s climate data only, because no earlier climate data was available. MAXENTs default settings were used for all models run [regularization multiplier (1), convergence threshold (10^{-5}) and maximum number of iterations (1000)], as recommended by Phillips *et al.* (2006). To train the model, 75% of the location records were used and 25% were used for model testing.

Future climates for A1B, A2, B1 and B2 emission scenarios (Arnell, 2004) were modelled using CSIRO Mk 3.5 data (Gordon *et al.*, 2010) generated by OzClim (CSIRO 2010). The CSIRO Mk 3.5 model was chosen as it represents a conservative scenario for warming and can be closely validated to historical data (Gordon *et al.*, 2010). The A1 scenario depicts rapid economic growth and introduction of new technologies, with A1B representing a subcategory which balances future energy usage across both fossil intensive and nonfossil energy sources and technologies. The A2 scenario depicts a more heterogeneous world with a continuously increasing population, whereas the B1 scenario depicts a convergent world with the same population as scenario A1. Scenario B2 is focused on sustainability, with a slightly lower population growth rate than A2 and less rapid, yet more diverse technological changes

Table 1 Platypus records by Australian state, 1800–2009

State	QLD	NSW	VIC	TAS	SA	ACT
No. records	731	6591	1797	1877	16	478
First record (year)	1770	1800	1870	1890	1894	1945
Last record (year)	2009	2009	2009	2009	1996	2009

Records of occurrence (sighting or capture) of the platypus (*Ornithorhynchus anatinus*) in each Australian state and territory where it occurs.
QLD, Queensland; NSW, New South Wales; VIC, Victoria; TAS, Tasmania; SA, South Australia; ACT, Australian Capital Territory.
Total number of records = 11 489. Number after removal of duplicate localities = 9570.

than A1 and B1 scenarios. None of these scenarios assume execution of the United Nations Framework Convention on Climate Change or the emissions targets of the Kyoto Protocol (IPCC 2000).

Future platypus distributions were projected from the current decade (2000–2009) of platypus data. All future climate projection layers were resampled to the 0.05° resolution of the current climate layers. Future scenario models were run in the same manner as the current climate models. An image analysis program, Image J (National Institute of Health 2010) was used to analyse the change in climatically suitable habitat modelled for each emission scenario. We used a threshold of 0.5 probability of occurrence at a spatial location to define suitable habitat (i.e. if the modelled probability of platypus occurrence in a location was <0.5 then we considered the habitat unsuitable). As the models determined that in most areas probability was either very low (0–0.25) or moderate to high (0.50–0.75), the effect of variation in selecting this threshold was low.

Results

Climatic envelope modelling, based on historical records of platypus occurrence (Fig. 1), a DEM, and long-term meteorological data revealed a change in climatically suitable habitat over two centuries. Model performance, as indicated by the area under the receiver operating characteristic curve (AUC) values (0.844–0.993) which ranged from very good to excellent, indicating that climatic variables are a good descriptor of platypus distribution. Total annual rainfall made the highest percentage contribution to predicting platypus distribution over the pre-1910 to 1950 time period, followed by annual maximum air temperature, annual minimum air temperature and elevation (Fig. 2). From the 1960s a switch occurred, with annual maximum air temperature making a greater contribution to the prediction of platypus occurrence than annual rainfall (Fig. 2a). This change coincided with an increase in the annual maximum air temperature anomaly for southeastern Australia (Fig. 2b). In contrast, a slight decrease occurred in the annual rainfall anomaly for southeastern Australia over the same time period (Fig. 2c).

Modelling of the distributional data from the most recent decade (2000–2009) and future climate projections for all emission scenarios (A1B, A2, B1 and B2), for 2020 and 2070, revealed a reduction in the current modelled distribution under every scenario (Fig. 3a–i). A predicted reduction in suitable habitat of approximately 31% by 2070 will occur under the A1B scenario, with the main losses occurring at the northern and most inland extent of the platypuses range (Fig. 3f). A similar range reduction (~30% by 2070) was also evident under the most optimistic scenario (B2) (Fig. 3i).

Discussion

Although rainfall and maximum air temperature are both important factors influencing the distribution of platypus (Fig. 2a) our modelling indicates an increase in the importance of temperature coincident with an increase in the annual maximum air temperature anomaly for southeastern Australia (Fig. 2b). Although there have been a greater number of records compiled since

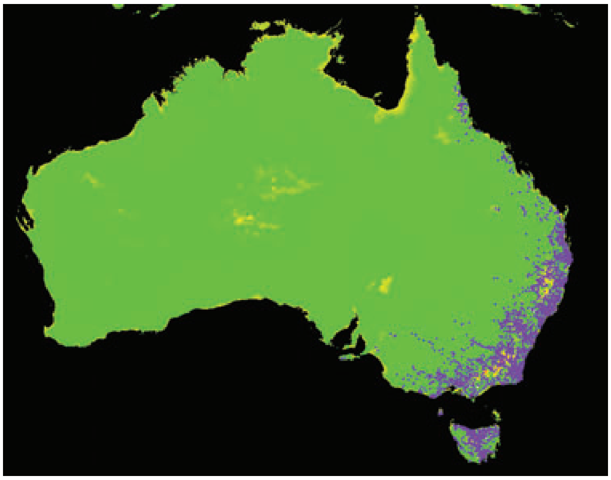

Fig. 1 Records of occurrence (sighting or capture) of the platypus (*Ornithorhynchus anatinus*) (n = 9570) mapped on a digital elevation model of Australia.

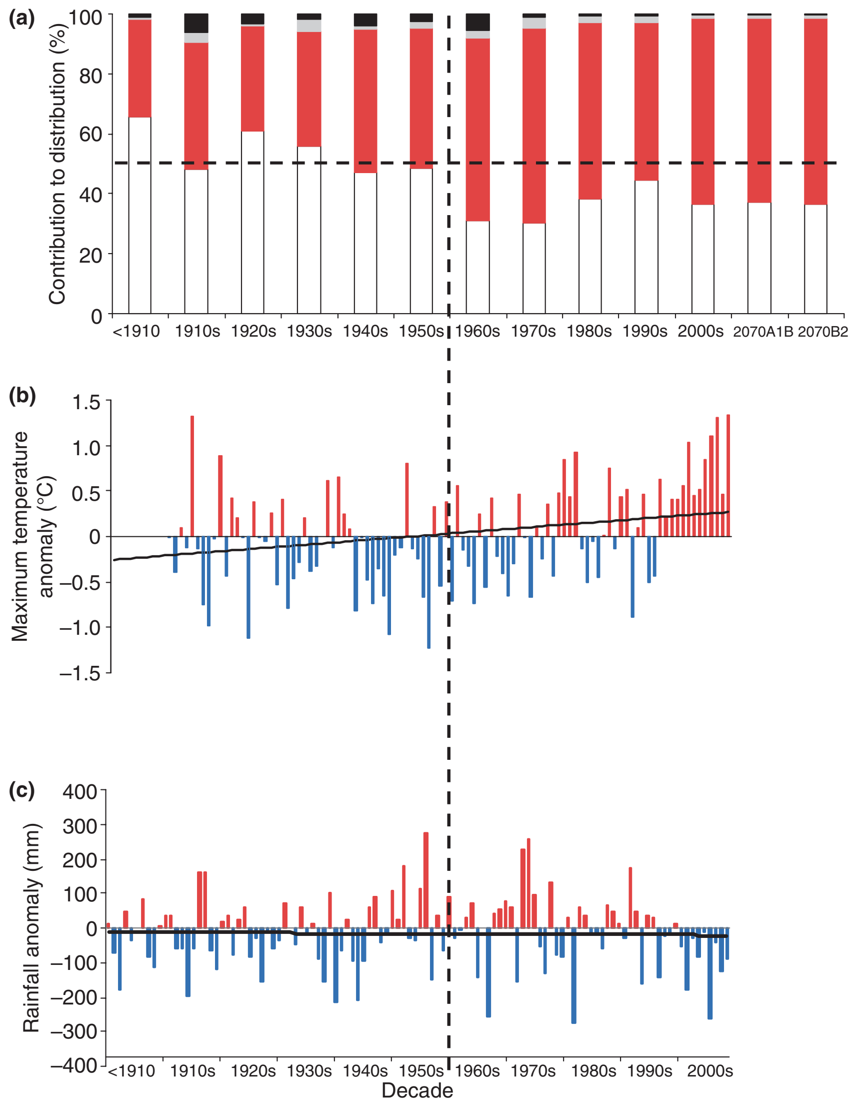

Fig. 2 The 1960s climate switch: (a) percentage contribution of environmental factors; average annual rainfall (white), average annual maximum temperature (red), average annual minimum temperature (grey) and elevation (black), to the modelled distribution of the platypus on a decadal basis since records began, and predicted future distribution of the platypus under A1B and B2 emissions scenarios), (b) annual maximum temperature and (c) annual rainfall (bottom panel) anomalies for southeastern Australia (Australian Bureau of Meteorology 2010).

1960, and especially since 1990, mapping the records for occurrence through time revealed no obvious systematic bias in sampling but rather an increase in sampling intensity across the platypus' entire range. MAXENT is relatively robust to variation in the number of records used to generate the models (Phillips & Dudík, 2008) and so the increase in sampling intensity should not have influenced the model outcomes.

Increased temperatures are likely to have direct physiological impacts on the platypus. It is covered in highly insulating fur, but cannot pant or utilize saliva spreading for thermoregulation, and can only cool itself by immersion in cool water, seeking refuge in burrows or through limited sweating (Grant & Dawson, 1978a,b; Brice, 2009). Although homeothermic and able to maintain their body temperature around 32 °C (Grant, 1983), even while foraging for extended periods in very cold waters (<5 °C) (Grigg *et al.*, 1992), it is likely that their upper lethal environmental temperature will increasingly be exceeded under a warming climate. Their main mechanism for surviving extreme temperatures is to remain within stream-side burrows, buffered from elevated temperatures by the surrounding soil (Grant & Dawson, 1978b; Grant, 1983). Their dependence on aquatic invertebrates as their food source (Grant, 2007) means that under prolonged warm periods this strat-

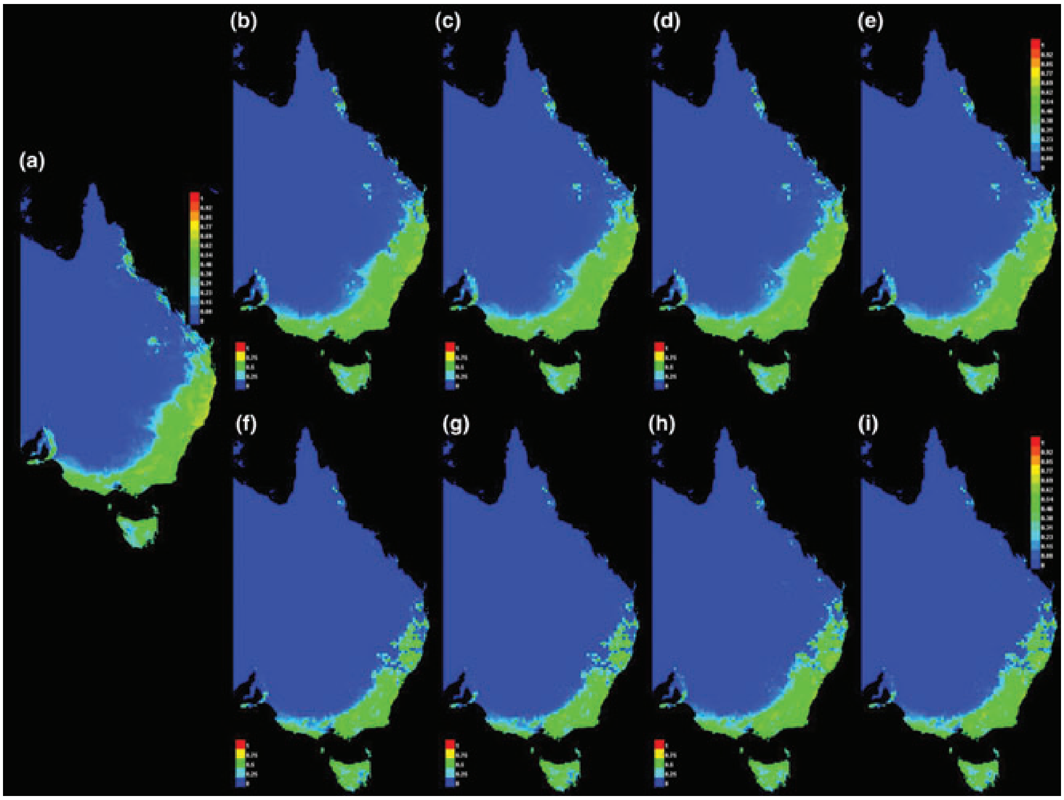

Fig. 3 Modelled platypus distribution based on presence records (2000–2009, n = 4232), elevation data and current or future modelled meteorological data (maxent): (a) current decade climatic conditions, (b) A1B emissions scenario for 2020, (c) A2 emissions scenario for 2020, (d) B1 emissions scenario for 2020, (e) B2 emissions scenario for 2020, (f) A1B emissions scenario for 2020, (g) A2 emissions scenario for 2070, (h) B1 emissions scenario for 2070 and (i) B2 emissions scenario for 2070. All scenarios used data with a moderate rate of global warming based on the CSIRO Mk 3.5 global climate model, obtained from Ozclim (CSIRO, 2010). Suitable habitat is indicated by warmer colours (orange, yellow, green) while unsuitable habitat is indicated in blue.

egy could result in a greatly reduced food intake due to a reduction in foraging opportunities.

As most exposure to ambient air temperature occurs when the platypus moves between its burrow and water, often under the cover of overhanging riparian vegetation, their exposure may be limited to seconds or minutes. It is the thermal regimes present within the aquatic environment that are of greater concern. Cooler temperatures at night, when platypus usually forage, and the thermal buffering provided by deeper water, provide some optimism with respect to the persistence of suitable habitat under a warming climate. However, the combination of a warming and drying climate provides a less optimistic scenario. Drying of previously permanent river systems into a series of pools, as recorded in the recent decade-long ‘millennium’ drought in southeastern Australia (Bond *et al*., 2008), will increase the exposure of platypus to warmer air temperatures when they travel overland between pools.

Not only will the areal extent of aquatic habitats decrease under lower annual rainfall, decreased water availability and higher rates of evaporation will create shallower systems where water temperatures more closely follow air temperatures. Further research is needed to relate predicted changes in air temperatures to water temperatures within suitable platypus habitats. Calculations of burrow temperatures, for a range of modelled surface temperatures and soil types, are needed to determine the potential for burrows to continue to provide thermoneutral refugia for resting platypus. The depth to which burrows might need to extend, and whether platypus could dig burrows to greater depths, are questions for future research.

The negative impacts of a warming climate are likely to be much greater when other major stressors on the platypus, and more broadly on aquatic habitats, are considered. These include loss of riparian vegetation, degradation of water quality, changes in sediment regime and alteration of hydrology (primarily through increased extraction for irrigated food crops and domestic consumption) (Carpenter, 1992; Sala *et al*., 2000; Palmer *et al*., 2008). The complexity of modelling and predicting the possible consequences of climate change is confounded by the possibility that novel ecosystems will become increasingly common (Willis & Bhagwhat, 2009). The predicted contraction of many southeastern Australian rivers into hydrologically disconnected pools (Bond *et al*., 2008) will create new ecosystems with an increased risk of predation by foxes (*Vulpes vulpes*), dogs (*Canis familaris*) and feral cats (*Felix catus*) as the frequency of platypus travelling along shallow or dry riverbeds between pools increases. Predation of platypus by foxes and cats was recorded by Brown & Triggs (1990; in faeces), Grant (1993) and Serena (1994). The wedge-tailed eagle (*Aquila audax*) has also been noted as a likely predator (Marchant & Higgins, 1993; Rakick *et al*., 2001).

The impact of a warming and drying climate on the aquatic resources sustaining platypus populations also needs consideration. Warm, shallow, drying waterbodies typically exhibit poor water quality (decreasing concentrations of dissolved oxygen and increasing conductivity/salinity and nutrient concentrations) with stagnation/stratification increasing the risk of toxic algal blooms and a corresponding negative impact on aquatic invertebrate and fish communities (Bond *et al*., 2008).

Analysis of the occurrence of stream macroinvertebrate assemblages in NSW over a period of increasing air and water temperatures, and declining rainfall and river flows (1994–2007) revealed a decline in the families that favour cooler waters and faster flows (Chessman, 2009). These families often form the major component of the platypus diet (Grant, 2007). The recorded decline in river flows was more severe than the decline in rainfall (Chessman, 2009). This was attributed, in part, to the relationship between rainfall and runoff: a 1% change in annual rainfall results in a 2.5–3% change in mean annual streamflow in Australian catchments (Chiew, 2006); and partly to the impacts of water impoundment and extraction for irrigation use (Chessman, 2009). Chessman's (2009) surprising find of stream water temperature rising at a higher rate (+0.12 °C per annum) than air temperature (+0.09 °C per annum) over the same period (1994–2007) was attributed to greater radiant heating in the shallower streams. The latter were the product of lower flows and reduced inputs of cooler groundwater (Chessman, 2009).

There is an increasing awareness that the most extreme impacts of climatic changes may occur in systems already subject to other stressors. Mitigating the effects of these other stressors provides credible management options for platypus populations in the face of climate change. Habitat manipulation or artificial habitat restoration (Webb & Shine, 2000) may prove to be viable options for maintaining suitable microhabitats in climatically suitable locations. The replanting of riparian vegetation has the potential to reduce stream water temperatures and 'over-restoration' by increased riparian plantings at a catchment scale has been suggested as a strategy to protect the aquatic Gondwanic fauna of southwestern Australia (Davies, 2010). A similar approach would do much to provide local thermal refugia for platypus, especially in the northern and western portions of their range where their vulnerability to warmer conditions is greatest. The shading provided by riparian plantings would have the double advantage of cooling both the aquatic and riparian habitats (burrows) utilized by platypus. Similarly, provision of environmental flows, which allow streams to persist through dry periods, could facilitate platypus dispersal, support their persistence in refugia and simultaneously maintain their invertebrate food resources (Bond *et al*., 2008; Chessman, 2009). For example, building of small weirs (<5 m high) or diversion of water from large pools to storage sites has been shown allow water supply access for stock, while still providing suitable platypus habitat (Grant & Temple-Smith, 1998; Grant, 2004).

The significant role of predation by the introduced red fox in the decline of many Australian mammals (Johnson & Isaac, 2009), suggests that the importance of islands as predator-free refugia for platypus must also be considered. The presence of healthy platypus populations on the fox-free, cool temperate islands: King Island; Kangaroo Island (the latter a successful introduction) (Fleay, 1980; Grant, 1992a); and Tasmania (not withstanding the evidence for the recent presence of an unknown number of red foxes: http://www.dpiw.tas.gov.au) could indicate the importance of predator control in the conservation of the platypus. Alternatively, the presence of healthy platypus populations could be attributed to the cooler climates experienced on these southern islands.

The predictions of climate mapping programs such as MAXENT, although useful, are based on the assumption that climate is the only factor affecting a species distribution. Accordingly, their predictions must be considered as indicators of potential change, rather than accurate forecasts (Hughes, 2003). Comparison of the actual distribution (Fig. 1) of the platypus with the current (2009) modelled distribution (Fig. 3a) reveals a larger area of climatically suitable habitat in southeastern and western South Australia, parts of the central western plains of NSW and parts of southwestern Queensland than is evident from actual records. In contrast, the documented occurrence along the lower Murrumbidgee and Murray Rivers (Grant, 1992a; Carrick *et al*., 2008) is not predicted.

The former discrepancies can probably be explained by habitat and life history requirements additional to suitable climatic conditions, especially the need for longitudinal connectivity between aquatic habitats and the provision of suitable riparian conditions, including well-vegetated riverbanks. In contrast, the presence of platypus in the lower reaches of the Murrumbidgee and Murray Rivers suggests that these large rivers provide suitable aquatic and riparian habitats within potentially unsuitable (semiarid and arid) climatic regions. The modelled 'larger than actual' area of climatically suitable current (2009) habitat (Fig. 3a) suggests that the predicted reductions under varying climate change scenarios (Fig. 3b–i) are conservative indicators. The potential reduction in platypus distribution, under the multiple stressors of climate change, hydrological change and land use impacts, may be far greater.

Although platypuses are common throughout much of their historical range, and are IUCN-listed as of 'least concern' in terms of global conservation status (Lunney *et al.*, 2008) our modelling shows that their vulnerability should not be underestimated. The apparent crossing of a threshold from aquatic habitat limitation to physiological limitation signals an early response to climate warming. The next step may be an 'ecological surprise' in the form of a catastrophic decline in platypus distribution and abundance. Facing this scenario, climate adaptation strategies must give highest priority to ensuring the enduring conservation of this globally significant animal.

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