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ORIGINAL ARTICLE

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The risk of inter-specific competition in Australian short-necked turtles

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Abstract Freshwater turtles are threatened globally; however, short-necked turtles in Eastern Australia have been particularly successful in exploiting natural and man-made permanent water bodies. The catchments of eastern Australia offer a unique opportunity to compare the diets of species in habitats where both genera co-exist, but only one genus is usually locally dominant. We compared the diets of species of *Emydura* and *Myuchelys* and *Flaviemys* in inland and coastal catchments in eastern Australia to determine the breadth of diets. We also conducted a more in depth study of the ecology and habitat preferences of the Bellinger River Emydura (*Emydura macquarii macquarii*) and *Myuchelys georgesi*. We found that diets of short-necked turtles on the east coast of Australia are separated by water conditions, and largely independent of species and location. Species of *Myuchelys* and *Emydura* are omnivorous. A high proportion of their food is from benthic macro-invertebrate communities in clear water. Terrestrial invertebrates and filamentous algae are present more in the diets of species inhabiting turbid water. Competition between species of *Emydura* and *Myuchelys*/*Flaviemys* is likely to occur when in sympatry, because species of *Emydura* can adapt their diets to various habitats and water quality. *Myuchelys georgesi* is restricted to, but common in, the Bellinger River. Interspecific competition may occur between *E. m. macquarii* and *M. georgesi* because of similar habitat preferences, diets and life histories. *Emydura m. macquarii* is not unique to the Bellinger River and hybridization with the endemic *M. georgesi* is a threatening process.

Keywords Interspecific competition · Turtle *Myuchelys* · *Emydura* · Diet · Habitat preference

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Introduction

Globally, freshwater turtles are one of the most threatened animal groups, with many species already listed as critically endangered (Buhlmann et al. 2009). The longevity of turtles masks effects of increased mortality of eggs, and population numbers alone may not reflect true conservation status (Spencer and Thompson 2005). For example, despite high biomass densities, all Murray River turtles are now listed as threatened (*Chelodina expansa*: endangered; *Emydura macquarii*: vulnerable; *Chelodina longicollis*: data deficient; Vic DSE 2013) in the Australian state of Victoria because of sustained declines over a 35 year period (Chessman 2011). However, freshwater turtles inhabit a diverse array of natural and man-made aquatic ecosystems, including ponds containing effluent from sewerage and organic wastes (Cann 1998; Souza and Abe 2000) and there is considerable variation in dietary specialization among Australian turtles. Species of *Chelodina* (except *Chelodina burrungandjii*), *Reodytes leukops* and *Pseudemydura umbrina* are strict carnivores, whereas short-necked species (e.g. *Emydura*) are considered more opportunistic and tend toward omnivory (Legler 1978; Legler and Cann 1980; Burbidge 1981; Georges et al. 1986). However, even within short-necked genera (e.g. *Emydura* and *Myuchelys*) that are often sympatric, habitat and dietary requirements potentially differ. Species of *Emydura* are considered opportunistic and generalist omnivores, whereas species of *Myuchelys* are generally considered more specialists in terms of diet and habitat (Cann 1998; Spencer et al. 1998; Allanson and Georges 1999). Although both genera have exploited most permanent water bodies in eastern Australia and commonly coexist in many catchments, one genus is usually locally abundant, with interspecific competition potentially limiting population numbers of the other (Cann 1998).

Inter-specific competition between species of *Emydura* and *Myuchelys* may be a key factor defining the composition and abundance of turtles in east coast Australian drainages. Human water resource development and land use practices have changed the flow and nutrient levels of many Australian river systems. Removal of macrophytes, increased turbidity and sedimentation, clearing of riparian vegetation, altered flow regimes and the introduction of invasive species, such as European carp, have all altered habitat and the composition and abundance of food available to turtles and probably favoured the expansion of the *Emydura macquarii* (Williams 1980). Species of *Emydura* are classified as generalists and have exploited most permanent water bodies in eastern Australia. *Emydura macquarii* has a widespread distribution throughout central and eastern Australia (Cann 1998; Georges and Thomson 2010) and is extremely common in most catchments that they inhabit. In the Murray River, the species occurs at biomasses that are amongst the highest recorded in the world (Spencer and Thompson 2005). *Emydura macquarii* are conveniently divided into subspecies—*Emydura macquarii macquarii* in the Murray–Darling basin, and the adjacent coastal rivers of NSW north to the Pine Rivers of south-east Queensland; *E. m. emmottii* in the Cooper and Diamontina basins; *E. m. nigra* on Fraser Island and adjacent Cooloola Peninsula; and *E. m. krefftii* in coastal Queensland north from the Mary River to the rivers draining into Princess Charlotte Bay. Species of *Myuchelys* are considered dietary and habitat specialists, reflecting the contrasting phylogenetic relationships between the genera in the catchments of eastern Australia (Seddon et al. 1997). Several species of *Myuchelys* are catchment specific. (Georges and Thomson 2010).

The drainage systems on the east coast of NSW are in many ways unique; some are unregulated and relatively pristine, and most rivers are defined by the Great Dividing Range, having evolved ecosystems that are independent from one another and potentially allowing habitat specialization and catchment specific speciation over relatively short distances. One catchment system that is still unregulated and relatively pristine is the Bellinger River near Coffs Harbour on the east coast of NSW. *Myuchelys georgesi* and *Emydura m. macquarii* (Bellinger River) coexist within the River. The Bellinger River *Emydura* was considered one of the rarest turtles in Australia (Cann 1998). The number of animals within the Bellinger is still unknown but the population was thought to be small and restricted to two sites along a single stretch of the River, upstream of Thora (Cann 1994; Spencer 2002, unpublished data). However, Georges et al. (2011) identified a potential much larger distribution of *E. m. macquarii* and that the Bellinger *Emydura* was not a distinct sub-species, having been recently introduced into the Bellinger River. Disturbingly, hybridization between the endemic *Myuchelys georgesi* (restricted only to the Bellinger River and associated tributaries) and the introduced *E. m. macquarii* was considered a real possibility (Georges et al. 2011). Nest predation rates by foxes are high and dead adult turtles have been found on the banks of the River in these areas (Blamires et al. 2005). Recent analyses also suggests that *Myuchelys georgesi* is susceptible to predation by catfish and is primarily restricted to larger waterholes of the Bellinger River (Blamires and Spencer 2013). Hence, given its restricted range and the evidence of threats, *Myuchelys georgesi* is at risk of becoming endangered unless the factors threatening its survival cease to operate. Here we evaluate the potential threat to *Myuchelys georgesi* in the Bellinger River by the introduced *Emydura* m. *macquarii*. We present this case study in the context of broader dietary analyses of species of *Emydura* and *Myuchelys* in inland and coastal catchments, from the Murray River to Fraser Island. Many areas have been heavily impacted by agriculture or dams, whereas some coastal river systems have remained relatively pristine.

Methods

Dietary analyses

Emydura macquarii is considered a generalist in most habitats (e.g. Spencer et al. 1998), but can reach very high abundances (Spencer and Thompson 2005) and potentially compete with other species that may more specific dietary requirements. We collected and compared empirical data from *Emydura m. macquarii* in south-east Queensland and *Emydura m. macquarii* and *Myuchelys georgesi* in northern NSW with previous studies on the diets of *Emydura m. macquarii* and species of *Myuchelys* (Georges 1982; Spencer et al. 1998; Allanson and Georges 1999).

South-eastern Queensland

We collected *Emydura m. macquarii* from six areas in the upper Darling catchment of the Murray–Darling Basin, the Brisbane and the Albert River drainage systems. The Kholo study area (KH) consists of a section of the Brisbane River, which runs adjacent to Kholo (27° 31′S 152° 45′E). Five different sites were sampled in this study area but only two sites were successful in trapping turtles. The first site was a bend in the river in which a small cove provided protection from the fast flow rate of the river. The second site was a shallow (~1.5 m depth) billabong with a dense mat of floating vegetation, including water hyacinth. We also sampled Lake Cooby (LC) (~35 km north of Toowoomba), which is part of the Murray–Darling Catchment (27° 23′S 151° 55′E). The lake has a depth of 22.3 m and a submerged area of 3.01×10^6 m. Lake Apex (LA) is a shallow lake located on the outskirts of the town of Gatton (27° 34′S 152° 16′E). The lake had dried over summer and more than 200 turtles were dredged out by Gatton council. Lake Galletly dam (LG) is situated on the University of Queensland, Gatton Campus (27° 33S′ 152° 20′E). It is approximately 210 m long and 145 m wide and has high volumes of waste run-off from nearby farms, which include pastoral paddocks and a piggery. We also sampled two tertiary effluent ponds (SP) situated on the outskirts of Gatton city (27° 32′S 152° 16′E) for turtles. Our last site was a 2 km section of the Albert River running through Kerry (near Beaudesert). The Albert River consisted of a series of sand and rock based pools, some of which were 3–4 m deep. Surrounding properties are mainly utilised for cattle grazing.

Each site was trapped (4–6 crab/hoop traps baited with ox liver) for 3–15 days from January–May 2003. Traps were cleared of turtles every 3–6 h. Turbidity was measured using a secchi disk (Cole 1994). Published data from *Emydura macquarii nigra* in an oligotrophic lake on Fraser Island in Qld was also included in the analyses (Georges et al. 1986).

Northern New South Wales

Two species of turtle were captured in the Bellinger River catchment (30°24′S, 152°41′E). *Emydura m. macquarii* (Bellinger River) and *Myuchelys georgesi* (Cann 1998) were captured by trapping and snorkelling in 2000. The sampling area was divided into three locations, the River between Bellingen and Thora (~20 km), the River upstream of Thora (~20 km), and the tributaries of the River (Rosewood and the Never Never), as well as the Kalang River. Locations above and below Thora were either snorkelled, trapped or both and locations of various lengths on the Rosewood, the Never Never and Kalang Rivers were searched systematically by snorkelling. Turbidity was measured using a secchi disk (Cole 1994). Published data for *Myuchelys gerogesi* in the Bellinger River (n = 31) and *Flaviemys purvisi* [see *Myuchelys purvisi* (Le et al. 2013)] in the Barnard (n = 22) and Manning River (n = 19) (see Allanson and Georges 1999) were also included in the analyses.

Southern NSW

Published data from *Emydura m. macquarii* from the Murray–Darling River catchment, near Albury NSW were included in the dietary analyses (n = 47) (Spencer et al. 1998).

Turtle and site data

We recorded curved plastron (CP) and carapace (CC) length (L) and width (W), straight plastron (SP) and carapace (SC) length (L) and width (W) of each turtle using a tape measure and callipers (See Spencer et al. 1998). Each turtle in northern NSW was given an individual mark by cutting unique notches in the marginal scutes (Thompson 1982) and, in south-eastern Qld, in accordance with QPWS protocols, we attached an aluminium chicken wing tags to the webbing of either hind foot between the 4th and 5th digit band tags. Turtles were released at point of capture within 12 h of capture.

Diets were determined through examination of gut contents. A soft rubber tube was passed down the oesophagus of the animal into the stomach. The stomach of the turtle was filled with water passed through the rubber tube by a small water pump and the ingested food passed up the oesophagus and out of the mouth (Legler 1977). Food items were collected on a fine nylon mesh on a small container and the contents were stored in 70 % ethanol. Dietary items were identified under a stereomicroscope. Bait that was consumed was easily identified and excluded from the analyses. We identified invertebrates to genus and percentage occurrence and volume were used to evaluate the relative amounts of different foods eaten by each species (Spencer et al. 1998). Percentage occurrence was determined by counting the number of turtles that had eaten one or more items of the particular food type and expressing the count as a percentage of the number of turtles examined. Percentage volume of each food category was represented as a percentage of the total volume of stomach contents within that sample. Volume of each food item was determined using water displacement.

Statistical analyses

We compared diets across genera, locations, and turbidity using multivariate statistics. Sites with a turbidity index of <2 m were considered turbid in south-eastern Qld. For areas where turbidity was not recorded (published data), we assessed habitat quality by whether turtles were captured by hand from snorkelling and from personal communication with the authors. We used percentage occurrence to compare diets because it was consistent across studies, and it provides an indication of the diversity of food items consumed by different species in different locations and habitats. Similarity of diet was compared using cluster analysis, using the Bray–Curtis similarity measurement. Nonmetric multi-dimensional scaling (nMDS) was used to compare dietary diversity between the sites. Differences in diet between sites were determined using analysis of similarities (ANOSIM), a multivariate non-parametric analogue of ANOVA (Clarke and Green 1988) and SIMPER (calculates the average Bray–Curtis dissimilarity between all pairs of inter-group samples) was used to identify discriminating features between species, locations and habitat quality. Data were square root transformed and standardised prior to analyses (Legendre and Legendre 1998).

Case study: Bellinger River turtles

A survey took place from 1/04/07–17/04/07 throughout the Bellinger River catchment. Turtles were collected from ~31 km stretch of the Bellinger River. The area was partitioned into three distinct sections (Thora upstream, Thora downstream and Kalang). The River upstream of the township of Thora is largely a series of waterholes with riffles or shallow flowing water in between waterholes. Downstream of Thora, the River widens considerably and distinct waterholes are far less frequent. The Kalang is similar to the upstream segment of the Bellinger River, with waterholes separated by riffles/shallow flowing water. A total of 26 waterholes (23 Bellinger River + 3 Kalang River) were sampled throughout the catchment. Most waterholes are < 1 ha in area. Sites were chosen by exploring the river on the ground, examining topographic maps, and by liaison with local landholders and other river-using locals. As much effort was made to sample waterholes on the whole river within potential turtle distribution, however logistical constraints meant that some more isolated parts of the river (upstream of Winch Flat) were not sampled.

Sites were snorkelled by 1–7 persons for a varied amount of time. In shallower, upstream sections of river, we were able to capture the majority of turtles in a waterhole, however in other sections of the River, snorkelling was stopped after 2 h, or when no new turtles were caught. Turtles were also captured using long-handled dip-nets off a small boat at night. To locate turtles, portable spotlights were used. This method was restricted to deeper waterholes around Bellingen, where the water was deep enough to operate a small flat-bottomed boat. Cathedral traps were set throughout the River. The upper parts of the traps were tied to overhanging trees for support and traps were placed next to bank in the vicinity of good microhabitat (e.g. logs, overhanging banks, aquatic vegetation). Traps were baited with sardines, with part of the bait held loosely in nylon mesh bags and available for the turtles to eat, and part of the bait held in perforated cans. Traps were checked at intervals of 4–10 h and re-baited after approximately 24 h. Traps were left in place for 24–48 h at each location.

Standard measurements on each turtle (see "Turtle and Site Data") captured were recorded. Mass was measured to the nearest 0.1 kg (turtles > 300 g) or 0.01 kg (turtles < 300 g) using an electronic and/or spring balance. Males were identified as having an elongated precloacal length relative to their body length. The minimum size of visually identifiable males (118 mm carapace length) was used as the upper size limit for all juveniles. All turtles were released after marking and measuring. Turtles with discernable growth annuli in the plastral scutes (Sexton 1959) had their annuli counted. Turtles were marked by drilling a small hole in the marginal scutes. Holes were usually placed close to the centre of the scute to prevent chipping of the edge of the scute, yet not to close to the flesh of the turtle. Digital photographs were taken of each turtle above the carapace, the top of the head, side of the head, and the plastron. The presence or absence of a cervical scute was recorded. For each *Emydura* captured, growth rings on the marginal scutes were counted so estimates could be made of the turtle's age.

Size-distribution curves were generated for adult males and females of each species, using straight plastron length as the standard measure, to enable direct comparison with other species (Spencer 2002). Size distributions were tested for normality using a Kolmogorov–Smirnov test. To assign age to size classes in *M. georgesi*, the relationship between size and age was estimated by fitting plastron lengths to a von Bertalanffy growth equation developed by Blamires et al. (2005). Growth curves have not been developed for the Bellinger River *Emydura*, however we compared size distributions of each sex with *M. georgesi* (paired t-tests) and applied the same growth equations to estimate age. These estimates were checked with data from growth annuli that were collected from each individual.

Length and mean width of each waterhole were estimated and water surface area was calculated from these measurements. Mean Number Alive (MNA) of *M. georgesi* and *E. m. macquarii* were calculated from populations that were sampled on multiple occasions. Only populations where at least one-third of turtles during the last sampling session were recaptures were included for density estimates. Densities were estimated by dividing MNA by the water surface area of each waterhole. We determined the relationship between the densities of *M. georgesi* and *E. m. macquarii* using non-linear regression techniques. Only waterholes where either species was present was included in the analyses.

Table 1 Habitat variables recorded at 26 waterholes to assess habitat preferences of both species of turtle

Variable
Subregion (Thora upstream/downstream/Kalang
Waterhole length (m)
Mean waterhole width (m)
Maximum waterhole depth (m)
Mean waterhole depth (m)
Water clarity (5 categories)
Percentage of waterhole substrate with sand (%)
Percentage of waterhole substrate with bedrock (%)
Percentage of waterhole substrate with gravel (%)
Percentage of waterhole substrate with rocks (%)
Water vegetation cover (Vallisneria) (%)
Water vegetation cover (*Hydrilla*) (%)
Water vegetation cover (other) (%)
Filamentous algae (present/absent)
Riparian vegetation score
Percentage of waterhole with overhanging trees (%)
Potential nesting substrate (sand) (present/absent)
Potential nesting substrate (grass/soil)
Morning sun (present/absent)
Distance to nearest bridge (m)
Basking habitat score (6 categories)
Number of *Myuchelys*
Number of *Emydura*

A range of physically and biologically relevant habitat variables were collected at sites both with and without turtles to determine habitat preferences of both species (Table 1). Distance variables were determined using a tape measure or Google Earth™ for longer measurements. Percentage estimates of variables were determined by a single observer (MW) to the nearest 10 % immediately after comprehensively snorkelling/boating a site. Non-metric multi-dimensional scaling (nMDS) was used to compare habitat variables between waterholes both with and without turtles. Differences in habitat preferences between waterholes were determined using analysis of similarities (ANOSIM), a multivariate non-parametric analogue of ANOVA (Clarke and Green 1988) and SIMPER (calculates the average Bray–Curtis dissimilarity between all pairs of inter-group samples) was used to identify discriminating features between species. Data were square root transformed and standardised prior to analyses (Legendre and Legendre 1998).

Results

Dietary analyses

We collected diet samples from 128 *Emydura m. macquarii* in southeastern Qld (KH = Kholo lagoon, $n = 28$; LA = Lake Apex, $n = 15$; BD = Albert River Beaudesert, $n = 16$; LC = Lake Cooby, $n = 21$; SP = Sewerage plant, $n = 20$; LG = Lake Galletly (LG), $n = 28$), 43 *Myuchelys georgesi* and 22 *Emydura m. macquarii* in the Bellinger River. Diets differed between species in different water qualities ($R = 0.73, p = 0.001$). *Myuchelys* spp. were not captured in turbid water conditions, although diet differed significantly between *Myuchelys* spp. and *Emydura* spp. in clear water ($R = 0.39$, $p = 0.02$). More individual *Myuchelys* spp. consumed Lepidoptera and Odonata than *Emydura* spp., whereas *Emydura* spp. consumed more plant material and Crustacea (Table 2). *Emydura* spp. also consumed different dietary items in clear and turbid water conditions ($R = 0.82, p = 0.01$). The major dietary differences between *Emydura* spp. in clear and turbid conditions was the amount of filamentous algae. *Emydura* spp. In clear water conditions filamentous algae was rarely available, whereas almost three quarters of turtles in turbid conditions regularly consumed algae (Table 3). Vegetative matter was not eliminated completely from the diet of *Emydura* spp. in clear water conditions; aquatic macrophytes were present in the diet of 85 % of individuals compared to only 49 % of individuals under turbid conditions. *Emydura* spp. consumed a greater diversity of insects and crustaceans in clear water than they do in turbid water conditions (Table 3).

Table 2 SIMPER analysis of dissimilarity of diet between *Myuchelys* and *Emydura* in clear water conditions (Av. = Average)

	Myuchelys Av.	*Emdura* Av.	Cummulative contribution (%)
Lepidoptera	0.31	0.00	17.29
Odonata	0.58	0.32	29.83
Diptera	0.49	0.45	41.10
Ephemeroptera	0.18	0.06	51.48
Plant material	0.53	0.85	61.75
Crustacea	0.00	0.21	71.57
Coleoptera	0.34	0.25	79.43

Table 3 SIMPER analysis of dissimilarity of diet between *Emydura* spp. in clear and turbid water conditions (Av. = Average)

	Clear Av.	Turbid Av.	Cummulative contribution (%)
Filamentous algae	0.00	0.72	19.16
Trichoptera	0.62	0.00	35.49
Diptera	0.45	0.30	44.63
Crustacea	0.21	0.12	53.41
Odonata	0.32	0.00	61.46
Hemiptera	0.05	0.11	68.08
Plant material	0.85	0.49	73.97
Coleoptera	0.25	0.15	79.45

Cluster analyses clearly separate two sets of branches by water conditions (Fig. 1). The diets of *Myuchelys purvisi* in the Barnard and Manning Rivers are almost identical, and very similar to the diet of *Myuchelys georgesi* in the Bellinger River. *Emydura m. macquarii* in south-eastern Queensland (KH) and *Emydura m. macquarii* in the Bellinger River have similar diets, which are similar to the *Myuchelys* spp. The diet of *Emydura m. nigra* is less related to the other clear water populations, primarily because significantly more turtles consume Crustacea.

Populations under turbid conditions were further separated by the productivity of the environment. Diets of turtles in man-made environments (sewerage ponds or agricultural waste) were separate from natural populations. Populations were primarily separated by the ratio of plant material to filamentous algae consumed; however a greater proportion of Murray River turtles consumed Teleostomi, primarily European Carp (*Cyprinus carpio*) in the form of carrion (Fig. 1). The diet of the Lake Apex population of *Emydura m. macquarii* primarily consisted of Hymenoptera and Hemiptera. Diptera and Coleoptera were commonly consumed by *Emydura m. macquarii* in the sewerage ponds (SP) and Lake Galletly, which is used for agricultural waste. There was little difference in diet between different sexes or juveniles of *Emydura m. macquarii* in southeastern Qld (Global $R = 0.05$ $p = 0.34$).

Case study: Bellinger River Turtles

Distribution and density

A total of 360 *M. georgesi* and 76 *E.* m. *macquarii* were captured during the survey. Capture technique significantly influenced the proportion of species captured, with *M. georgesi* more likely to be captured by hand

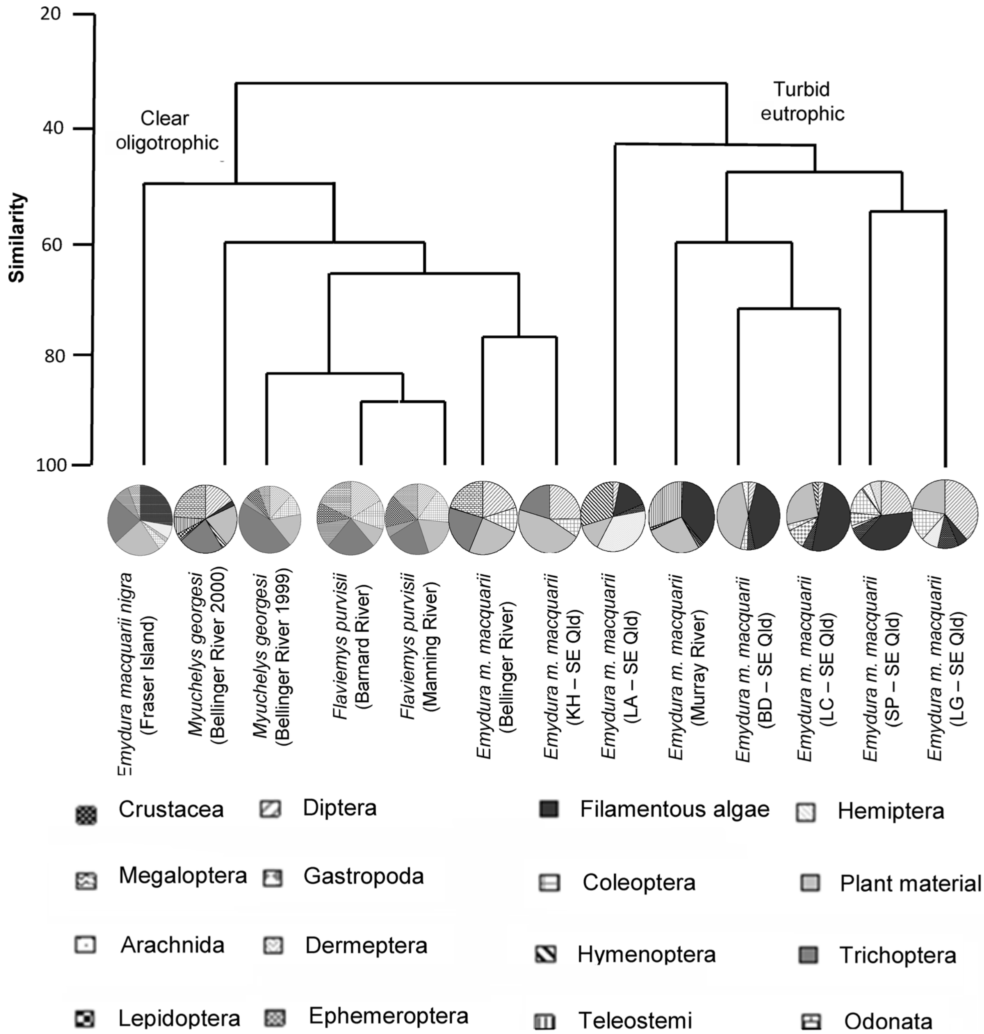

Fig. 1 Hierarchical cluster analysis comparing diet composition and abundances of the diets of each species in different locations. Fraser Island = Fraser Island Lakes (Qld); Bellinger = Belinger River (NSW); Manning = Manning River (NSW); Barnard = Barnard River (NSW); KH = Kholo lagoon (Qld); LA = Lake Apex (Qld); Murray = Murray River (NSW/Vic); BD = Albert River Beaudesert (Qld); LC = Lake Cooby (Qld); SP = Sewerage Plant (Qld); LG = Lake Galletly (LG). Bellinger River Species were sampled in 1999 [(see Allanson and Georges 1999), 2000 and 2007]. (Qld = Queensland, NSW = New South Wales, Victoria = Victoria)

while snorkelling than in traps or by dip net from a boat (Table 4. $\chi^2 = 135$ $p < 0.001$ d.f. = 2). Capture technique did not influence which sex was more likely to be captured in both species.

Both species were captured throughout the River. No turtles were caught within the tidal zone of the river and only one turtle was captured downstream of the Bellingen Bridge. Densities of turtles varied considerably throughout the River. *Myuchelys georgesi* occurred in high densities in the upper reaches of the River and although more *E. m. macquarii* were captured downstream (Table 5), densities were similar to upstream populations (Fig. 2).

Size and age distribution

The majority of female *E. m. macquarii* and *M. georgesi* had plastron lengths between 150 and 180 mm. Although the distributions of both species are negatively skewed, 50 % of individuals have plastron lengths smaller than the 150 mm size class. Consequently, over 30 % of turtles in the River are 15 years or younger. The size distribution of male *E. m. macquarii* and *M. georgesi* were significantly different with male *E. m. macquarii* growing to larger sizes.

A large proportion of *E.* m. *macquarii* were 6–10 years of age both up- and down-stream of Thora and almost 25 % of the upstream population of *E. m. macquarii* were in the 5 year old category. There was no difference in the age distributions of *M. georgesi* between up- and down-stream populations. The age structure of male *E. m. macquarii* was unable to be evaluated because the size structure was significantly different to that of *M. georgesi*, hence growth curve parameters developed for *M. georgesi* could not be applied to *E. m. macquarii*.

Table 4 Number of each species captured by different capture techniques

	Diving	Boat	Trap
Myuchelys georgesi	348	12	0
Emydura macquarii	39	26	11

Habitat preferences

From general observations, habitat preferences appeared to depend on species and time of day. *Myuchelys georgesi* was usually captured in deep water (> 3 m) on rocky substrate. *Myuchelys georgesi* generally remain motionless before capture (50 % of time) or attempt to flee (50 % of time). They were often found partly buried in sand, silt or leaves and they are usually found in the deepest part of the waterhole. *Myuchelys georgesi* was rarely captured using a dip-net from the boat at night; however, those captured were in deeper parts of waterholes than *E. m. macquarii*.

Emydura m. macquarii were usually found in shallower water (< 3 m), in any substrate including patches of vegetation. *E. m. macquarii* was generally captured while attempting to flee and they were often captured near submerged snags. *E. m. macquarii* were often observed feeding near the bank or under overhanging ridges of river banks. At night, *E. m. macquarii* were readily captured near banks with aquatic vegetation or snags. These areas were often very shallow water (< 1.5 m). *E. m. macquarii* were also regularly captured in patches of *Hydrilla verticillata*.

There was a significant difference between habitats with and without *E. m. macquarii* ($R = 0.18$ $p = 0.04$). *E. m. macquarii* were more likely to be found in long waterholes with a rocky substrate (Table 6). Waterholes with *E. m. macquarii* had a reasonable amount of *Hydrilla* and also a high density of *M. georgesi* (Table 6). *E m. macquarii* occurred less commonly in waterholes far from bridges with a sandy substrate. Waterholes with and without *M. georgesi* also differed significantly ($R = 0.21$ $p = 0.006$). *Myuchelys georgesi* was more likely caught in waterholes with a rocky substrate; reasonable vegetation cover of *Hydrilla*; and with a medium level of basking habitat (rocks and logs) (Table 7). *Myuchelys georgesi* was captured less in waterholes that were far from bridges and with a gravel or sandy substrate (Table 7).

The relationship between the densities of the two species were best described by linear polynomial equation ($R^2 = 0.22$ $F_{1,20} = 5.2$, $p = 0.03$). In waterholes where turtles were present, there was a positive relationship between the densities of *E. m. macquarii* and *M. georgesi* (Fig. 3). We captured seven turtles with morphological features of both *M. georgesi* and *E. m. macquarii*. Morphological characters useful in identifying instances of hybridization between *E. m. macquarii* and *M. georgesi* were the head shield extending laterally and posteriorly toward the tympanum (present in *M. georgesi*, absent in *E. macquarii*), a plastron clear of darker blotches, darker striations and darkening of the margins of the plastral and ventral marginal scutes (uniform grey or cream in *E. m. macquarii*, grey cream or yellow with the markings in *M. georgesi*), a cervical scute (present except as a rare variant in *E. m. macquarii*, commonly absent or reduced in *M. georgesi*). Readily identifiable

Table 5 The number captured, average plastron length (PL ± S.D.) and average age of both species in different regions of the catchment

Species	Sex	Location	No	PL (mm)	S.D (mm)	Age (years)
Myuchelys georgesi	Female	Thora downstream	65	151.1	21.4	19.0
		Thora upstream	40	151.8	17.6	17.2
		Kalang	0	0	0	0
		Catchment	105	151.3	20.1	18.4
	Male	Thora downstream	140	126.2	9.9	21.1
		Thora upstream	96	127.1	6.3	20.6
		Kalang	0	0	0	0
		Catchment	236	126.6	8.7	20.9
	Juvenile	Thora downstream	12	90.5	12.5	5.2
		Thora upstream	7	85.0	10.3	4.8
		Kalang	0	0	0	0
		Catchment	19	88.6	11.8	5.1
Emydura m. macquarii	Female	Thora downstream	28	149.5	23.2	19.1
		Thora upstream	7	139.2	20.0	12.6
		Kalang	5	141.7	21.4	12.8
		Catchment	40	147.1	22.4	17.0
	Male	Thora downstream	15	133.0	17.1	20.1
		Thora upstream	9	133.1	10.9	20.2
		Kalang	4	107.2	6.0	7.2
		Catchment	28	129.2	16.5	18.6
	Juvenile	Thora downstream	4	98.0	12.4	5.9
		Thora upstream	3	80.8	50.1	5.1
		Kalang	1	91.1	0.0	5.2
		Catchment	8	90.7	29.3	5.5

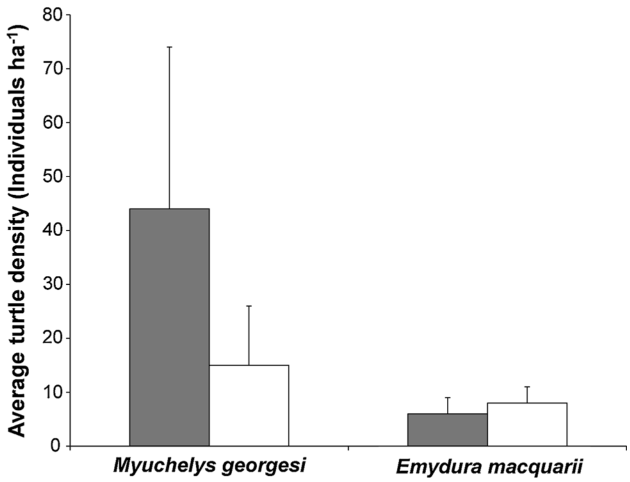

Fig. 2 Turtle densities in the upper (*filled*) and lower (*open*) regions of the Bellinger River

hybrids have the head shield of *M. georgesi* but the clear plastron and ventral marginal scutes of *E. m. macquarii*. All suspected hybrids were adults with plastron lengths >130 mm (>15 years of age).

Discussion

The diets of omnivorous turtles on the east coast of Australia can be separated by water conditions, irrespective of species and location. Diet is related to resource availability; the ability to acquire different prey; and patterns of feeding under different conditions. Species of both *Myuchelys* and *Emydura* are short-necked turtles that are probably unable to catch highly motile prey, especially in highly turbid water. However, both genera have a powerful jaw to consume large dead material, such as European carp (*Cyprinus carpio*), but it also that enables them to scrape algae from logs and rocks, which is prevalent in in the diet of turtles in turbid conditions (Spencer et al. 1998).

A high proportion of the diet of both *Myuchelys* and *Emydura*.is from benthic macro-invertebrate communities, but with some terrestrial fruit and aquatic vegetation consumed. Both genera could be considered omnivorous in clear water conditions, with *Myuchelys* tending towards carnivory in some populations. Most species consume live prey associated with the substratum, such as caddis-fly larvae (Trichoptera) (Allanson and Georges 1999). Trichopteran larvae are the most common carnivorous dietary item consumed by all species, except for *Emydura m. nigra,* where Crustacea are better represented. Ribbon weed (*Valisnaeria* sp.) is the primary sources of vegetation for each species in clear water conditions, but a high proportion of *Myuchelys georgesi* also consume figs (Legler 1976). Aquatic insects are less prevalent in the diets of species in turbid water conditions. For example, 81 % of turtles on the Murray River ingest aquatic insects (Spencer et al. 1998), compared to over 95 % in *M. georgesi* and *F. purvisi* (Allanson and Georges 1999). Terrestrial invertebrates that fall on the surface of the water become increasingly important in the diets of species inhabiting turbid water, with almost a quarter of turtles in the Murray River consuming terrestrial insects and spiders (Spencer et al. 1998).

The difference in invertebrate dietary items between species in clear and turbid water conditions represents a fundamental difference in feeding patterns. There are large variations in turbidity in Australian river systems; inland rivers tend to be naturally more turbid than coastal rivers. Turbidity is affected by rainfall and catchment runoff, bed disturbance, e.g. by introduced fish species such as carp, excessive algal growth, which is often associated with highly eutrophic conditions, and water flow (Williams 1980; Fletcher et al. 1985). The water flow was low in all the locations with turbid water and several locations were eutrophic because of agricultural (Murray River and Lake Galletly) and sewerage treatments (SP). Large mats of algae were common throughout summer in most of these water bodies. Other than filamentous algae and periphyton ingested by most

Table 6 SIMPER analysis of dissimilarity of habitat variables between waterholes with and without *Emydura m. macquarii*

Variable	*E. m. macquarii*, absent Av. Abundance	*E. m. macquarii,* present Av. Abundance	Av. dissimilarity (Diss.)	Diss./SD	Cummulative contribution (%)
Substrate-sand	31.21	15.85	2.64	1.24	10.58
Substrate-rocks	29.89	51.23	2.58	1.23	20.93
Substrate-gravel	18.58	19.46	2.52	1.20	31.01
Substrate-bedrock	19.21	13.31	2.35	1.22	40.40
No. *Myuchelys georgesi*	6.63	11.46	2.02	1.40	48.49
Vegetation cover-vallisneria	4.21	7.00	1.82	1.25	55.79
Vegetation cover-*hydrilla*	6.32	10.77	1.82	1.17	63.09
Vegetation cover-other	2.79	0.77	1.10	0.76	67.51
Basking habitat-rocks	1.53	2.00	1.09	1.14	71.86
Potential nesting substrate-sand	0.63	0.46	1.00	1.16	75.85

The average value for each variable at waterholes with turtles absent (Absent Average) and present (Present average). The contribution of each variable to describing variance or differences between factors (i.e. turtles present or absent at a waterhole is shown by Cumulative contribution %). (Av. = Average)

Table 7 SIMPER analysis of dissimilarity of habitat variables between waterholes with and without *Myuchelys georgesi*

Variable	*M. georgesi* absent Av. Abundance	*M. georgesi* present Av. Abundance	Av. Dissimilarity (Diss.)	Diss./SD	Cummulative contribution (%)
Substrate-Gravel	30.25	12.15	2.98	1.40	11.50
Substrate-Rocks	21.92	48.55	2.73	1.18	22.04
Substrate-Sand	33.58	19.80	2.59	1.20	32.07
Substrate-Bedrock	12.50	19.40	2.39	1.17	41.32
Veg. Cover-*Hydrilla*	4.17	10.50	2.09	1.29	49.41
Veg. Cover-Vallisneria	5.00	5.55	1.79	1.17	56.34
Basking Habitat-Rocks	1.08	2.10	1.50	1.61	62.14
Veg. Cover-Other	3.83	0.85	1.24	0.81	66.92
No. *Emydura m. macquarii*	0.17	1.65	1.22	1.12	71.63
Potential Nesting Substrate-Sand	0.67	0.50	1.02	1.15	75.59

The average value for each variable at waterholes with turtles absent (Absent Average) and present (Present Average). The contribution of each variable to describing variance or differences between factors (i.e. turtles present or absent at a waterhole is shown by Contribution % (Av. = Average)

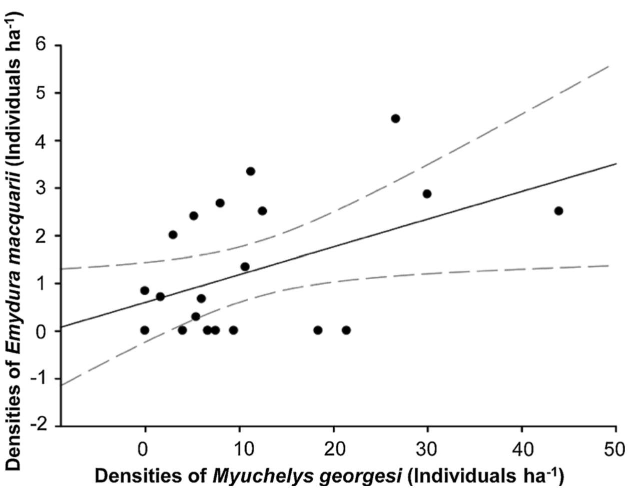

Fig. 3 Relationship between densities of *Emydura macquarii macquarii* and *Myuchelys georgesi* described by a linear polynomial model (2-parameter) ($R^2 = 0.55$ $F_{1,20} = 23.5$, $p < 0.001$). *Dashed lines* show 95 % confidence intervals

species in turbid conditions, other plant material consisted mainly of plant detritus.

Aquatic vegetation in clear water systems is an important resource for all freshwater turtles. It is used for food, either through direct consumption or indirectly to feed on prey associated with vegetation (e.g. Caddisfly larvae), and it is used for refuge by juveniles (Congdon et al. 1992). Both genera rarely consumed large prey items. The lack of carrion or fish in the diet of short-necked species was surprising. Although fish represents an extremely good resource in terms of energy assimilation for *Emydura,* only *Emydura m. macquarii* in the Murray River regularly consumed Teleostomi in the form of carrion (Chessman 1986; Spencer et al. 1998). European carp is extremely common in the Murray River, particularly in the backwaters, and *E. m. macquarii* was regularly observed close to shore feeding on the remains of carp (pers. obs.). *Emydura m. nigra* is the only other species to consume large prey, in the form of large macro-invertebrates (Crustacea), in a resource limited oligotrophic lake on Fraser Island (Georges 1982).

There is no difference in the diet between male and female *Emydura m. macquarii* in south-eastern Queensland. Diets differ between male and female *Emydura m. nigra* on Fraser Island, with females consuming more plant material and large macro-invertebrates than males, which generally consume more aquatic insects, such as dipteran and trichopteran larvae (Georges 1982). Even in turbid conditions on the Murray River, there is a significant difference between large adult females and males, with large females rarely consuming terrestrial invertebrates and plant material (Chessman 1986). Dietary differences in the Murray River and Fraser Island species may relate to size (i.e. females are larger than males) rather than sex because we found no difference in the average size of male (168 ± 31 mm PL) and female (160 ± 39 mm PL) *E. m. macquarii* in SE Qld. and male and female *Emydura m. macquarii* of similar size on the Murray River have similar diets (Chessman 1986).

Omnivorous short-necked turtles in eastern Australia are well adapted to exploit most resources in all water conditions and drainage systems. Most species rely on aquatic macrophytes and filamentous algae, which has important life history consequences. Although species like *E. m. macquarii* in the Murray River, cannot sustain a positive energy balance consuming solely aquatic macrophytes and filamentous algae (Spencer et al. 1998), associative effects may be important to their nutrition. The digestion and assimilation of plant material is greatly enhanced in *Trachemys scripta* when consumed with Coleoptera larvae (Bjorndal 1991). Thus, the direct energy gains from consuming aquatic and terrestrial arthropods may be relatively small, but their consumption may increase the accessibility of energy in bulk items, such as plants and filamentous algae, which has important life history consequences for growth and reproduction in freshwater turtles (Congdon 1989; Congdon and Gibbons 1989; Rowe et al. 2003).

Given the similarity between diets of *Emydura* and *Myuchelys* spp. in eastern Australia, essentially defined by water quality, there is a real possibility that interspecific competition is a major factor affecting the distribution and abundance of both species from each genera in these habitats. We have shown that there is a positive association between *E. m. macquarii* (Bellinger River) and *M. georgesi* in the Bellinger River, suggesting that there is probably no direct, or aggressive competitive interactions occurring. Ribbon weed (*Vallisneria gigantea)* is an important dietary source for both genera and *Hydrilla* may also be important for both species in the Bellinger River. Both species in these clear water conditions tend towards carnivory, with a high proportion of their food coming from benthic macro-invertebrate communities associated with aquatic vegetation. Densities of both *E. m. macquarii* and *M. georgesi* in the Bellinger River appear defined by substrate type and the presence of aquatic macrophytes. Rocky substrates are preferred by both species and *M. georgesi* avoids areas with gravel and sand, however both species are present when aquatic macrophytes are present in a waterhole.

Myuchelys georgesi is restricted to, but common in, the Bellinger River. Its restricted distribution and habitat requirements make it a species potentially at risk to human induced or natural perturbations, despite relatively large densities in some sections of the River. *Myuchelys georgesi* are highly adapted to exploit the upstream regions of the Bellinger River, preferring deeper waterholes with a rocky substrate that is surrounded by bedrock (Table 7 and Blamires and Spencer. 2013). Like many *Myuchelys* spp. on the east coast of Australia, *M. georgesi* consume live prey associated with aquatic vegetation, such as caddis-fly larvae (Trichoptera) (Allanson and Georges 1999). *Myuchelys georgesi* were affected by major floods in the Bellinger River catchment in March 2001, which removed much of the upper river aquatic vegetation. In some waterholes, 100 % of plant beds were removed after the floods and consequently, dietary analyses revealed that the guts of five *M. georgesi* and one *E. m. macquarii* were empty. There were also indications that reproduction did not occur throughout the catchment, with no gravid female *M. georgesi* captured in October–November 2001 (8 months after the flood).

There is another factor to consider when comparing the population status of *E. m. macquarii* and *M. georgesi*. Recent molecular work by Georges et al. (2011) indicates that the majority of the Bellinger River population of *E. m. macquarii* is a very recent introduction from neighbouring catchments. It is highly likely that the once rare Bellinger River *E. m. macquarii* is possibly an invasive species establishing and increasing in abundance. The steep increase in the rate of capture in 2007 most likely relates to different modes of capture, but there is a strong possibility that this potential invasive species increasing in abundance given the relative high numbers of juveniles in the population. The presence of hybrid *E. m. macquarii* and *M. georgesi* turtles opens the possibility of such introgression and the contamination of the genotype of *M. georgesi* by horizontal transfer of genes from *E. m. macquarii*. Similar preferred habitat and overlapping diet in both species is conducive for further hybridization and introgression. There is a clear need to determine whether hybridization between the species is an evolutionary dead-end (offspring are sterile) or if introgression between the introduced *E. m. macquarii* and endemic *M. georgesi* can occur. *Myuchelys georgesi,* although locally abundant, is only found in the Bellinger River catchment and it meets the criteria for being listed as a vulnerable species under the Threatened Species Conservation Act of NSW. It's limited population distribution and the suite of generic environmental threats that were used to list the (former) Bellinger River Emydura (including: competition between turtle species, fox predation, extraction of river sand and gravel, construction of bridge and ford crossings upstream of the species location, low intensity grazing and agricultural activities in downstream reaches of the Bellinger River, logging of native forests leading to water pollution and soil degradation, and line fishing) all apply to *M. georgesi*. The present situation in the Bellinger River is currently manageable. *Emydura m. macquarii* can easily be caught; having established the best technique (dip netting by boat) in this study; and the densities of hybrids are low. However, the time to assess the impact of hybridization and manage the population is limited. The life cycle of freshwater turtles in this population, and Australia more generally, means that females do not mature until 8–12 years of age (Blamires et al. 2005; Spencer et al. 2006) and the levels of fox predation on turtle nests have probably limited the spread impact of hybridization in the Bellinger River. However, it is only a matter of time before the hybrid population reach a critical level before back-crossing with *M. georgesi* and polluting their gene pool; if not already occurring. Hybridization and introgression over the last 200 years between dingoes and domestic dogs has led to the near extinction of the pure bred dingo in Australia (Corbett 1995).

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