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The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*

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Abstract

We described the diet of *Emydura macquarii*, an omnivorous turtle from south-eastern Australia, compared its digestive performance on diets of fish or plants at two temperatures, and related how both diet and temperature affect its food selection in nature. Filamentous algae constituted 61% of the stomach content of *E. macquarii*. The turtles rarely fed on motile prey, but selected carrion from the lagoon bottom and terrestrial insects (Diptera, Hymenoptera and Coleoptera) trapped on the surface of the water. Digestive efficiency of *E. macquarii* was affected little by body temperature, in contrast to consumption rates and rates of passage which were strongly influenced by both temperature and diet. In combination, these responses resulted in a slower rate of digestion at 20°C than at 30°C. Digestive efficiency of *E. macquarii* on a herbivorous diet at 30°C (49%) was about half that of turtles on a carnivorous diet (91%), but they had longer transit times (118 h on the plant diet versus 70 h). Lower consumption rates and longer mean retention times in turtles fed plants compared those fed fish relate to slower digestive processing of the plant. Rapid processing and higher consumption rates of fish by *E. macquarii* resulted in higher energy gains compared to turtles consuming plants (almost 100 times more energy at 30°C). The laboratory results suggest that fish carrion and aquatic and terrestrial invertebrates are probably essential dietary items of *E. macquarii* in the wild, because its metabolic requirements cannot be met from aquatic macrophytes alone.

Keywords: Diet; Digestive physiology; *Emydura macquarii*; Energetics; Freshwater turtle; Murray River

1. Introduction

The effect of temperature on the digestive capabilities of reptiles is poorly understood. Food type and body temperatures are important factors that affect energy assimilation rates and thus growth and reproduction in freshwater turtles [1,5,6,16]. For many reptiles an increase in body temperature increases the rates of food consumption [4,27], digestion [17] and digesta passage [35]. Digestive efficiencies, however, may decrease (e.g. *Trachemys scripta* [1]), or change very little (*Uta stansburina* [35]) with increasing body temperatures.

Emydura macquarii is a short-necked turtle found in the Murray River system in south-eastern Australia and may attain a mass of 4 kg and a carapace length of 320 mm [8]. Although species of *Emydura* are typically omnivorous, it is not known whether foraging is random or selective on their diet of aquatic macrophytes, carrion and aquatic arthropods [8,11]. Additionally, the relative nutritional values of the plant and animal material in the diet of *E. macquarii* are not known. Reptiles must rely on microbial breakdown of the cell wall fraction to digest plant material, as they lack their own cellulolytic enzymes [39]. Although plants make up a large proportion of the diet of *E. macquarii* [8], if the turtles are physiologically incapable of properly digesting plants their energy needs may not be met. Thus, augmentation of the diet with food of animal origin may be necessary.

Here we describe the diet of a population of *E. macquarii* from the River Murray, compare digestive

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efficiencies on diets of fish or plants at two temperatures, and relate the environmental constraints of diet and temperature to feeding regimes in nature. With this approach, we aim to understand the way that *E. macquarii* exploits the nutritional resources of its natural habitat.

2. Materials and methods

2.1. Determination of diet

Forty-seven *Emydura macquarii* were captured using hoop nets [23] from a permanent 32.5-ha (3.1 km long) oxbow lagoon (Snowdon's Lagoon) of the Murray River, near Albury (146° 90′ E, 36° 90′ S). Stomach contents were collected within an hour of capture by flushing [25], using a 12-V submersible pump (L.V. Motors model 105) to supply a steady flow of water into the stomach via a flexible plastic tube. The stomach contents passed up the oesophagus and were collected in a sieve. Five additional turtles yielded little or no material, either because their stomachs were empty or their stomach contents were only partially removed. Data from these individuals were not included in the analysis. Stomach contents were preserved in 70% ethanol and later identified under a stereomicroscope [37]. Bait consumed by the turtles was easily identified, and was removed before the sample was preserved. Sand and fragments of leaf litter were assumed to have been ingested accidentally and were also not included in the diet analysis.

Percentage occurrence, abundance and volume [38] were used to evaluate the relative amounts of different foods eaten by *E. macquarii*. 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 abundance involved counting the number of items belonging to each food item for each turtle and then expressing it as a percentage of the total number of food items. The numerical method could only be used for food items that occur as discrete units; items such as filamentous algae and carrion did not occur as discrete units and were omitted from analysis. 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. Filamentous algae and periphyton were analysed together, as it was difficult to separate these items. Periphyton consisted predominantly of algae, with some protozoans.

Snowdon's Lagoon was divided into two 'regions', a deep region and a shallow region [31], approximately equal in size. To compare diet with food availability, eight plots in each of the littoral and profundal zones of each region were randomly chosen, and three samples within each plot were collected approximately 10 m apart. Eight samples of the water column were collected randomly from each region.

Samples were collected from the littoral and profundal zones by agitating the substratum by hand and passing a dip net (cross-sectional area 0.09 m^2) through the water five times over an area of approximately 0.4 m^2. Potential food items were emptied into a jar and preserved in 70% ethanol. Profundal zone samples were collected by a similar method to the collection of the littoral samples, but the substratum was agitated with a 3-m pole. Water column samples were collected by drawing a net (200 mm diameter circular aperture, 100 μm mesh size) horizontally through the water between the depths of 0.5 and 1 m, and samples were preserved in 70% ethanol. Comparisons between littoral and profundal zone samples within and between each site were analysed using a two-way ANOVA [30].

Percentage abundances of invertebrates within the lagoon were estimated for comparison with those in the diet of *E. macquarii* by assuming that the bottom of the lagoon had a surface area of 310000 m^2 (3.1 km long by 100 m wide). Numbers of dietary items in the water column were estimated by determining the volume of water sampled in relation to the volume of the water in the lagoon. The volume of the lagoon was estimated by assuming that the average depth of half the lagoon was 0.5 m and the average depth of the other half was 2.0 m [33]. Total numbers of each dietary item in the whole lagoon were expressed as a percentage abundance of each item.

The diet preference of *E. macquarii* was estimated using the Electivity Index [20]:

$$E_i = \frac{r_i - n_i}{r_i + n_i} \quad (1)$$

where E_i is Ivlev's electivity measure for dietary items, r_i is relative abundance of dietary item i in the stomach sample, and n_i is relative abundance of dietary item i in the lagoon. Electivity varies from -1.0 to $+1.0$; values between 0 and $+1$ indicate preference and values between 0 and -1 indicate avoidance [22].

2.2. Digestive performance

Sixteen adult *E. macquarii* (12 females with curved carapace lengths between 292 and 302 mm, four males with carapace lengths between 269 and 274 mm) were transported to the University of Sydney within 5 days of capture. The turtles were placed individually into glass aquaria ($900 \times 400 \times 400$ mm). Water was passed through a corner-aerating filter in each tank. Each filter was cleaned and the tank water replaced with water of similar temperature at weekly intervals.

With the constraint of one male assigned to each treatment, turtles were divided randomly into two temperature-controlled rooms at 20°C and 30°C. Four animals at each temperature were provided with small dead fish, *Engraulis australis*, to represent carrion consumed in the environment, and the other four turtles were fed the aquatic plant, *Valisnaeria spiralis*, a common dietary item of *E. macquarii* in parts of the Murray [9]. Turtles were acclimated to their assigned temperature and diet treatments for 3 months prior to the collection period.

A plastic bag (110 × 40 mm, 50 μm thick) was placed over the tail of each turtle and attached using waterproof, elasticised tape (Biersdorf, Germany) to collect all egested material. For 2 weeks prior to collection, turtles were treated as for the experimental period to allow them to become adjusted to handling and to reach a nutritionally steady state condition. Faecal collectors were checked for leaks during this period by filtering the water and checking for egested material. Feeding was halted for 7 days prior to the acclimation period to empty the digestive tracts. Food was then given ad libitum every 3 days to each turtle and any uneaten food (orts) was collected 24 h after feeding. Faeces were removed from the collection device within an hour of defecation, between 07:00 and 23:00 h for 3 weeks. Any collection device that had detached from the tail of the turtle was reattached and the time recorded.

Faeces, food samples and orts were frozen immediately after collection for later sorting and analysis. Faeces from each animal were bulked weekly, and the faeces and orts from each feeding were dried to constant weight at 60°C. A representative sample of the diet and faeces of each turtle, per week, was fully combusted in a muffle furnace for three hours at 500°C to determine the percentage of organic matter. The gross energy density of food and faeces, as well as filamentous algae collected from various parts of Snowdon's Lagoon, was measured in a Gallenkamp adiabatic bomb calorimeter [14]. Percentage of cell walls, or ash-free neutral detergent fibre, of *Valisnaeria* (cellulose, hemicellulose, lignin and cutin) was measured using the method of Goering and Van Soest [13].

Transit times and mean retention times of particulate digesta from each group of turtles were estimated using indigestible plastic markers. Twenty pieces of orange plastic tape (5 × 5 mm) and 40 pieces of pink plastic tape (1 × 1 mm) were placed in a small sample of fish and given to each turtle at the first feeding. Transit time was the time from the first feeding to the appearance of the first plastic marker in the egesta and mean retention time (MRT) of each size of plastic tape was calculated by the formula:

$$\mathrm{MRT} = \frac{\sum_{n=1}^{t} M_t T_t}{\sum_{n=1}^{t} M_t} \quad (2)$$

where M_t is number of particles excreted at time t, T_t is time in hours and ΣM_t is the total number of markers in the diet [36].

Gross energy intakes were calculated for each turtle over the first two weeks of the experimental period by:

$$C = (FE_\mathrm{d}) - (OE_\mathrm{d}) \quad (3)$$

where C is the gross energy intake (kJ per 2 weeks), F is dry mass of food offered (g per 2 weeks), E_d is gross energy density of diet (kJ g^{-1}) and O is dry mass of orts (g per 2 weeks) [1].

Assimilation rates (digestible energy intakes) were calculated for each turtle with:

$$D = C - (EE_\mathrm{f}) \quad (4)$$

where D is assimilation rate (kJ per 2 weeks), E is egestion rate (g per 2 weeks) and E_f is the gross energy density of the excreta (kJ g^{-1}) [1].

Digestive efficiencies (DE) were calculated for each turtle using [1]:

$$\mathrm{DE}\ (\%) = \frac{D}{C} \times 100 \quad (5)$$

The term 'digestive efficiency' in this study and other studies of freshwater turtles [1] is actually assimilation efficiency as the urinary products are included with undigested residues in the analysis.

The consumption rate, assimilation rate and digestive efficiency of dry matter, organic matter and energy for the first 2 weeks of the 3-week collection period were compared between temperatures and diets using a two-way ANOVA [30]. Paired t-tests within treatment groups revealed that both male and female turtles had similar consumption rates, assimilation rates and digestive efficiencies. Consumption rate and assimilation rate were ln transformed and digestive efficiency data were analysed with arcsine-transformed data. A Student–Newman–Keuls pairwise comparison test was used to distinguish significant differences among the means. All analyses were performed using the statistical package Sigmastat (Jandel Corporation, 1993).

3. Results

3.1. Diet

Emydura macquarii is omnivorous, with a diet composed predominantly of filamentous algae, plant debris and fish (Teleostomi) (Table 1). Of the main food items, filamentous algae, principally species belonging to the

Table 1
Percentage composition by occurrence, volume and abundance of the stomach contents of 47 *Emydura macquarii*

Food items	Occurrence (%)	Volume (%)	Abundance (%)
Filamentous algae	65.5	60.9	–
Plant detritus	46.8	16.6	–
Aquatic invertebrates			
Arthropoda: Crustacea			
Decapoda			
Macrobrachium australiense	8.5	0.3	11.1
Cherax destructor	14.9	0.6	1.9
Insecta			
Hemiptera	6.4	0.4	12.8
Coleoptera	2.1	<0.1%	15.6
Diptera	8.5	0.2	34.7
Trichoptera	4.3	0.1	10.4
Total aquatic invertebrates	81.2	1.7	86.5
Terrestrial invertebrates			
Arthropoda			
Arachnida: Areaneae	2.1	<0.1%	<0.1%
Insecta			
Coleoptera	6.4	<0.1%	3.8
Diptera	2.1	<0.1%	2.1
Hymenoptera	10.6	0.5	7.5
Undetermined	4.3	<0.1%	–
Total terrestrial invertebrates	22.7	0.9	13.5
Vertebrates: Chordata			
Teleostomi	25.5	19.9	–

–, no value, does not occur in discrete units.

chlorophyte genera *Cladophora* and *Spirogyra*, were present in 66% of turtle stomachs. All of the fish present in the diet was in the form of carrion, identified as small parts of large fish (predominantly European carp, *Cyprinus carpio*), and was present in 26% of the stomach samples. Plant detritus (seeds, bark, leaves and shoots) occurred in 47% of the stomach samples, but only constituted 17% of the volume of the stomach contents (Table 1). The crayfish *Cherax destructor* occurred in the diet of 15% of the turtles, but constituted less than 1% in volume. Aquatic dipteran larvae and Hemiptera (Notonectidae and Corixidae) were present in the stomachs of 9% and 6% of turtles, respectively. Terrestrial insects such as flies (Diptera), wasps and ants (Hymenoptera) were present in the stomach contents, but represented less than 1% of the total volume (Table 1).

Overall, there were few differences in the abundances of the major dietary items between the profundal and littoral zones or between the two regions of the lagoon. However, there were significantly more dipteran larvae in the profundal zone than in the littoral zone in both regions ($F = 61.12$, $P < 0.001$), and in the deep than the shallow region of the lagoon ($F = 15.68$, $P < 0.001$). Wasps (Hymenoptera) were only found in the shallow region of the lagoon in both littoral and profundal zones, and flies (Diptera) were present in small numbers in both regions. The prawn *Macrobrachium australiense* was detected only in the deep region with more in the profundal zones than in the littoral zones ($F = 97.25$, $P < 0.001$). No carrion or yabbies, *Cherax destructor*, were collected in any samples. Significantly more aquatic Hemiptera were sampled in littoral than in the profundal zones in both regions ($F = 16.77$, $P < 0.001$), but there was no difference between regions ($F = 0.18$, $P = 0.675$). There were no significant differences in numbers of coleopteran larvae between the littoral and profundal zones ($F = 2.57$, $P = 0.120$) nor between areas ($F = 2.26$, $P = 0.144$).

The Electivity Index [20] identified that turtles preferred the terrestrial insects Diptera ($+0.4$), Hymenoptera ($+1.0$) and Coleoptera ($+1.0$), and the crustacean *Macrobrachium australiense* ($+0.2$), as well as *Cherax destructor* ($+1.0$) (Fig. 1). Carrion (Teleostomi) ($+1.0$) was present in large volumes in the diet but was not detected in lagoon samples and thus was highly preferred by *E. macquarii* (Table 1). Turtles avoided the aquatic insects Hemiptera (-0.2) and coleopteran larvae (-0.2). Turtles neither selected nor avoided dipteran and trichopteran larvae (0.0).

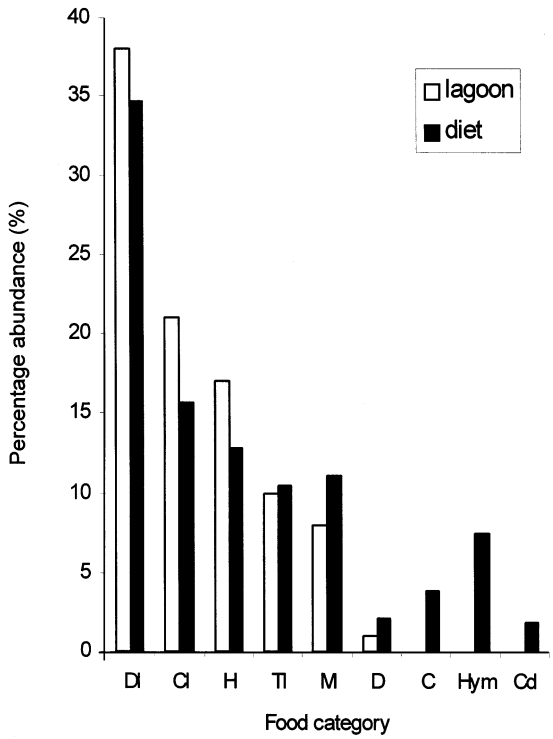

Fig. 1. Relative abundance of food items in Snowdon's Lagoon, compared to estimates of their numerical importance in the diet of *E. macquarii*. Dl, dipteran larvae; Cl, coleopteran larvae; H, Hemiptera; Tl, trichopteran larvae; M, *Macrobrachium australiense*; D, Diptera; C, Coleoptera; Hym, Hymenoptera; Cd, *Cherax destructor*.

3.2. Digestive energetics

Fish in the experimental diet had a higher gross energy density (22.1 ± 0.3 kJ g^{-1} dry mass) than the plant *Valisnaeria* (18.2 ± 0.4 kJ g^{-1} dry mass), and 60% of the total dry matter of the plant (Table 2) consisted of cell walls (fibre).

Temperature ($F = 25.27$, d.f. $= 1$, $P < 0.001$) and diet ($F = 334.92$, d.f. $= 1$, $P < 0.001$) significantly influenced gross energy consumption rates of *E. macquarii*. Turtles consumed greater amounts of fish and *Valisnaeria* at 30°C than at 20°C and there was no significant diet by temperature interaction ($F = 2.33$, d.f. $= 1$, $P = 0.155$).

The rate of gross energy assimilation by turtles was significantly affected by temperature ($F = 56.46$, d.f. $= 1$, $P < 0.001$) and diet ($F = 857.50$, d.f. $= 1$, $P < 0.001$), but the interaction of diet and temperature was not significant ($F = 1.46$, d.f. $= 1$, $P = 0.252$). Turtles offered fish assimilated over four times more energy at 30°C than those fed fish at 20°C, but turtles consuming the plant diet at 30°C assimilated less than 1% of the energy that turtles fed fish assimilated at the same temperature (Table 2).

Turtles consuming fish had a digestive efficiency at both 20°C and 30°C twice that of turtles consuming the plant diet ($F = 103.63$, d.f. $= 1$, $P < 0.001$). Temperature ($F = 0.290$, d.f $= 1$, $P = 0.601$) and the temperature by diet interaction ($F = 1.43$, d.f. $= 1$, $P = 0.256$) had no effect. Rates of consumption, assimilation and digestive efficiencies of dry and organic matter followed similar patterns to those of energy (Table 2).

On both diets, the transit time of the plastic markers at 30°C was shorter than at 20°C and, at both temperatures, transit times were shorter for the fish than for the plant diets (Table 3). Similarly, MRT of the plastic markers was significantly affected by temperature, diet

Table 3
Mean ($\pm$ S.D.) retention time and transit times of plastic markers through *E. macquarii* ($n = 4$ per treatment group) at 20°C and 30°C fed on fish and plants

Diet:	Fish		*Valisnaeria*	
Temperature:	20°C	30°C	20°C	30°C
Transit time (h)	89 ± 6	70 ± 3	260 ± 10	118 ± 8
Mean retention time (h)				
1 mm particles	115 ± 9	89 ± 51	310 ± 30	158 ± 12
5 mm particles	154 ± 12	123 ± 11	418 ± 25	180 ± 12

Table 2
Digestive performances of 16 ($n = 4$ per treatment group) *Emydura macquarii* at 20°C and 30°C, on a diet of fish and plant (mean $\pm$ S.D)

Diet:	Fish		*Valisnaeria*	
Temperature:	20°C	30°C	20°C	30°C
Consumption rate of dry matter (g per 2 weeks)	34.4 ± 5	153 ± 15	1.0 ± 0.4	2.4 ± 1.6
Consumption rate of energy (kJ per 2 weeks)	761 ± 101	3377 ± 340	18 ± 7	44 ± 29
Assimilation rate of dry matter (g per 2 weeks)	32 ± 4	138 ± 16	0.4 ± 0.1	1.0 ± 0.5
Assimilation rate of energy (kJ per 2 weeks)	705 ± 93	3062 ± 355	6.2 ± 1	20 ± 11
Digestive efficiency of dry matter (%)	93 ± 1	80 ± 4	43 ± 12	45 ± 8
Digestive efficiency of energy (%)	93 ± 1	91 ± 4	40 ± 17	49 ± 7
Assimilation rate of organic matter (g per 2 weeks)	28 ± 4	118 ± 16	0.2 ± 0.1	0.7 ± 0.3
Digestive efficiency of organic matter (%)	98 ± 0.3	96 ± 2	45 ± 22	57 ± 0.6

and marker particle size. At 30°C, turtles consuming fish or plant had MRTs for both particle sizes that were less than those at 20°C. At both temperatures and on both diets, MRTs of the 25 mm^2 particles were longer than for the 1 mm^2 particles (Table 3).

4. Discussion

4.1. Diet

The majority of the diet of *Emydura macquarii* in Snowdon's Lagoon consisted of just two items, filamentous algae and carrion (Table 1). Similarly, in Lake Boga, also on the River Murray, the diet of *E. macquarii* is composed of filamentous algae (53% by volume) and carrion (Teleostomi) (21% by volume) [8], whereas *E. krefftii* on Fraser Island consumes little filamentous algae and no carrion. Plant material comprised only 30% of the diet, with crayfish (*Cherax robustus* and *Caridina indistincta*) being the major animal food (25% by volume) in this population of *E. krefftii* [11]. The clear lakes of Fraser Island presumably contain smaller quantities of filamentous algae compared to the eutrophic conditions of the Murray River. Moreover, the highly turbid waters of the Murray River system may prevent turtles from detecting prey by sight, in contrast to the clear waters on Fraser Island where *E. krefftii* can observe and capture motile benthic prey such as crayfish [12].

Emydura krefftii feeds mostly in the littoral zone of the lakes on Fraser Island and consumes freshly sprouted shoots of sedges (*Lepironia articulata* and *Baumea* sp.) and aquatic and terrestrial invertebrates [11]. *Emydura macquarii* consumes more plant material and smaller quantities of aquatic and terrestrial arthropods than *E. krefftii*. *Emydura macquarii* probably spends relatively more time than *E. krefftii* feeding in the profundal zone where the freshwater prawn *Macrobrachium australiense*, a preferred dietary item of *E. macquarii*, occurs most commonly.

Emydura macquarii feeds on the bottom of the lagoon because that is where the carrion and dipteran larvae occur, but they must feed on the water surface also to take trapped terrestrial arthropods such as flies, wasps and ants. The South American turtle *Podocnemis unifilis* skims particulate matter from the surface of the water and then evacuates excess water from the pharynx before swallowing in a process that has been called neustophagia [2]. Similarly, *E. macquarii* often bites at the surface, submerging after each bite, expelling pharyngeal water, and swallowing [24], probably taking the terrestrial insects detected in our samples of stomach contents.

Although selected by *E. macquarii*, the small fragments and low volume of the freshwater prawn, *M. australiense*, in the stomach contents suggests that they were consumed as carrion from the lagoon bottom and not captured alive by turtles in the water column. Unlike long-necked turtles such as *Chelodina expansa* and *C. longicollis* [8,12], *Emydura* are short-necked turtles that are probably unable to catch highly motile prey, especially in highly turbid water. However, *E. macquarii* has powerful jaws, which enables them to tear into dead material such as European carp (*Cyprinus carpio*) and to scrape algae from logs and rocks, explaining the prevalance of carrion and filamentous algae in the diet.

In summary, *E. macquarii* consumes large amounts of filamentous algae, as well as scavenging on the lagoon bottom for dead fish and at the surface for trapped terrestrial insects. However, it has difficulty catching fast moving prey due to its relatively short neck (compared to *Chelodina*) and the high turbidity of Murray River waters that make locating prey difficult.

4.2. Digestive energetics

4.2.1. Effects of diet

The rate and efficiency of assimilation of food in the digestive tract of turtles is a function of gastrointestinal enzyme activity, intestinal motility and the chemical composition of the food [27]. Plant material is generally less digestible than animal matter, and plant matter may be apportioned into two components, the cell wall, consisting of cellulose, hemicellulose and lignin, and cellular contents, which include cytoplasmic sugars, starch, protein and lipids [28]. Most cell contents are readily digestible, whereas the cell wall fraction is only partially digestible [19].

Emydura macquarii must rely on microbial fermentation to break down the cell wall fraction of a plant diet [32]. In turn, microbial fermentation influences consumption rates and rates of passage as the rate of digestion is dependent on the number of microbes in the gut [39]. The low intake and long marker MRTs for *E. macquarii* on the herbivorous diet probably stem from the longer digestive processing, possibly through fermentation, of the plant compared to the fish diet. These dietary differences were reflected in the higher energy gains of turtles fed fish compared to those fed plants.

The digestive efficiency for energy of *E. macquarii* on the fish diet (93% at 20°C) is towards the top of the range of values measured for a number of reptiles fed carnivorous diets (54–94% [39]). For example, the painted turtle, *Chrysemys picta*, has a digestive efficiency of 89% at 30°C when fed raw meat [21]. Low digestive efficiencies for energy of *E. macquarii* consuming plants (49% at 30°C) may be attributed to the refractory nature of plant cell walls.

When fed duckweed, the turtles *Trachemys scripta* and *Pseudemys nelsoni* have digestive efficiencies for energy of 29% and 25% respectively, but when fed the aquatic plant *Hydrilla*, the digestive efficiency of *T. scripta* is 80% and of *P. nelsoni* is 75% [6]. Compared with *Hydrilla*, duckweed has a thick waxy cuticle that is difficult for turtles to digest [6]. Similarly, the digestive efficiency for organic matter by *E. macquarii* on a plant diet (45% at 20°C) is less than the digestive efficiencies for organic matter of *P. nelsoni* (80%) and *T. scripta* (84%) fed *Hydrilla*. *Valisnaeria* does not have a thick cuticle like duckweed, but it has a cell wall content of 60% compared to 36% in *Hydrilla*. Moreover, duckweed fronds often pass through the digestive tracts of *P. nelsoni* and *T. scripta* intact [5]. Large pieces of *Valisnaeria* were passed intact in the faeces of *E. macquarii*.

Regulation of movement along the gut is a complex physiological process, with retention of the digesta in a given segment of the gut allowing for storage, enzymatic digestion, absorption of nutrients and water and microbial fermentation [15]. Different particle sizes of the digesta are retained in various parts of the gut for different lengths of time. In both treatments of temperature and diet, the 1-mm^2 plastic markers appeared in the faeces before the 25-mm^2 pieces. The surface area of food particles available for microbial attachment influences the rate of digestion [5]; larger particles have a lower surface area:volume ratio and so their digestion is slower and less complete than that of small particles.

4.2.2. Effect of temperature

Body temperature had a large and significant effect on the consumption rate of food. *Emydura macquarii* had a consumption rate Q_{10} of 4.4 between 20°C and 30°C when consuming fish but only 2.5 for *Valisnaeria*. The lower Q_{10} value on *Valisnaeria* relates to the quality of the diet. The consumption and assimilation of the fish is limited only by the direct thermal responses of the digestive physiology of the animal, whereas a large proportion of the plant diet is subject to fermentation by microbial attack. Even with increases in body temperature, the exposed surface area and chemical composition of the plant material in the gut limit the rate of fermentation.

Mean retention time and rate of passage are significantly influenced by body temperature. As for other species, transit time and mean retention times of *E. macquarii* are longer at lower body temperatures due to a direct thermal effect on the rate of digestion [26]. The rate of passage at 20°C for the lizard *Uta stansburiana* is ten times slower than it is at 32°C [35]. A slower rate of passage at low temperatures may be due to a reduced bulk flow of digesta resulting from a decrease in the consumption rates of food [39].

Although body temperature affects rates of food consumption and passage in *E. macquarii*, it has little affect on digestive efficiency of either diet (Table 3). Similarly, the digestive efficiency of the rusty lizard, *Sceloporus olivaceus*, on a diet of insects rises only 8% between 15°C and 30°C, even though the consumption rate more than doubles [18]. Any increase in digestive efficiency at higher temperatures, due to increased enzyme activity, could be counterbalanced due to increased bulk flow from greater consumption rates.

Rate of digestion, which is related to the rate of passage and digestive efficiency, is ecologically important as it reflects how much resource the animal uses [39]. The omnivorous turtle *T. scripta* has a longer transit time and a lower digestive efficiency on duckweed than on *Hydrilla*, between 24–27°C, and is thus able to process more food per unit time with a greater digestive efficiency on *Hydrilla* compared to duckweed [6]. Similarly, *E. macquarii* is able to process more fish per unit of time than *Valisnaeria* at both temperatures. Digestive efficiency of *E. macquarii* is affected little by body temperature while the rate of passage is strongly influenced by temperature and diet. The combination means that the rate of digestion of *E. macquarii* is slower at 20°C than at 30°C.

4.3. Energy use and nutrition

Emydura macquarii inhabits the thermally variable habitat of the Murray River and associated water bodies, like Snowdon's Lagoon [7]. During summer, the lagoons inhabited by *E. macquarii* are thermally stratified [10,33]. Thermophilic behavior by *E. macquarii* may be essential for maintaining high consumption and assimilation rates. *Emydura macquarii* may increase its rate of digestion by maintaining high body temperatures through aquatic basking in the warm top layer of the water,

By using the inter-specific metabolic rate/body mass equation for turtles [3] and assuming that 1 l of O_2 is equivalent to 18.8 kJ of energy [29], we estimate the standard metabolic energy requirement of an average 2.5 kg *Emydura macquarii* [34] at 20°C is 5.4 kJ day^{-1}. Thus on a diet of *Valisnaeria* alone, *E. macquarii* would be in a negative energy balance as it assimilates only 1.4 kJ day^{-1} (20 kJ 2 weeks) at 30°C and 0.44 kJ day^{-1} (6.2 kJ per 2 weeks) at 20°C on this diet. *Emydura macquarii* must consume food, such as carrion and insects, that have higher energy densities than *Valisnaeria* to maintain activity, growth and reproduction. On a diet of fish, *E. macquarii* is in a positive energy balance at 30°C (219 kJ day^{-1}) and at 20°C (50 kJ day^{-1}) and presumably can accumulate energy stored as fat in preparation for the non-feeding period over winter. *Emydura macquarii* ceases to feed at water temperatures below 16.3°C [10]), but may be active at

cooler temperatures during winter [33] when it must rely on energy accumulated during the warmer months when food is consumed.

Valisnaeria is a common component of the diet of *E. macquarii* in many parts of the Murray River system [8], however it does not occur in Snowdon's Lagoon where it is replaced by filamentous algae. Although filamentous algae have a similar gross energy density to *Valisnaeria* (19.1 ± 0.5 kJ g^{-1} dry mass and 18.2 ± 0.4 kJ g^{-1} dry mass respectively), algae have less hemicellulose than many aquatic macrophytes and can potentially provide more energy to *E. macquarii* than *Valisnaeria* [32].

Although *E. macquarii* cannot sustain a positive energy balance consuming solely *Valisnaeria*, and possibly filamentous algae, associative effects may be important to the nutrition of *E. macquarii*. Although the digestive efficiency for energy of *T. scripta* eating duckweed is only 29%, consumption of beetle larvae together with duckweed increases the digestive efficiency for the duckweed to over 61% [5]. Thus, the direct energy gains of consumption of dipteran and coleopteran larvae by *E. macquarii* may be relatively small, but their consumption may increase the accessibility of energy in plants such as filamentous algae.

In conclusion, *E. macquarii* has a better digestive performance when consuming meat than plants, with greater consumption rates, assimilation rates and digestive efficiencies on a carnivorous diet. In the wild, *E. macquarii* may rarely be able to capture fast moving prey such as fish and prawns and so must rely on plant material and carrion as the main dietary components. Although unable to meet its energy needs solely on a diet of plant, associative effects between the plant material and insects may increase digestive efficiency and assimilation rate enough to meet basic energy requirements, at least until other more nutritious foods, such as carrion, are available.

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