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Ecophysiology and conservation of wildlife in Western Australia

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Abstract

Ecophysiology is the study of the relevance of physiological processes in both plants and animals to ecological constraints imposed by their environment. My own research has focused on Australian animals, specifically reptiles, amphibians, birds and marsupials, but lately, plants have become important in working with the nectarivorous Honey possum. The discipline of physiology was created by the Frenchman Claude Bernard in the 19th century and he dealt with animals only as models for the human condition. It was only in the 20th century that physiologists began to study animals in their own right, not just as proxies for humans, and the developing discipline of comparative physiology laid the grounds for the emergence of ecophysiology. Animals adapt to changes in their environment, or they perish, and we are faced with an ever-lengthening list of species that are now threatened with extinction in Australia. A long-term study of the ecophysiology of the unique suite of native animals living on Barrow Island, for example, has revealed the extent to which they are amazingly adapted to survive in this difficult arid environment, but periods of stress have also been identified in some species when their ability to maintain physiological homeostasis is compromised. Our knowledge of the ecophysiology of the Western Australian fauna is limited to only a very small number of species but, in each case, it empowers us to identify those elements of the environment that are critical for their long-term survival. The challenges brought by climate change are ones that Australia's unique plants and animals must also face if they are to persist and it is through targeted ecophysiological studies that we will best be able to assist them in that process.

Keywords: ecophysiology, desert wallabies, desert kangaroos, Dragon Lizards, Honey Possums, quokka, Barrow Island, Rottnest Island, Shark Bay.

Introductory remarks

I am honoured to have been chosen as a recipient of the Medal of The Royal Society of Western Australia and, since becoming a member in the 1960s, I have long admired the substantial contribution that the Society has made to the study and understanding of our natural environment.

I served on the Council of The Royal Society of Western Australia in the 1970s and was pleased that the Society published a major two-part issue on research on Rottnest Island in 1983 (Bradshaw 1983). In that issue, my former supervisor, Bert Main contributed a paper on macropod ecophysiology, showing that the field of ecophysiology had well and truly arrived (Main 1983). It is amusing to note too that Bert later reports a physiologist telling him that ...*"it was quite improper to prostitute physiology as a field study in order to interpret the ecology of species."* (Main 1995)

The discipline of physiology was created by the Frenchman Claude Bernard in the 19th Century but he

dealt with animals only as models for the human condition (Bernard 1878). It was only in the 20th century that physiologists began to study animals in their own right, not just as proxies for humans, and the developing discipline of comparative physiology laid the grounds for the emergence of ecophysiology.

Physiology was taught as part of the medical curriculum at The University of Western Australia and any attempt to translate what was known about humans to animals, was actively discouraged, as I found to my cost when I included my own findings on frogs in a report dealing with the clotting times of blood!

Ecophysiology is the study of the relevance of physiological processes in both plants and animals to ecological constraints imposed by their environment. My own research has focused on Australian animals, specifically reptiles, amphibians, birds and marsupials, but lately, plants have become important in working with the nectarivorous Honey possum. I thought I might try in this talk to give you some examples from my own research showing how an ecophysiological approach can have great relevance to the problem of species conservation.



Figure 1. An adult colour-marked male Western netted dragon lizard, *Ctenophorus nuchalis* (formerly *Amphibolurus inermis*) basking on marker post in Shark Bay, some 900 km north of Perth in Western Australia.

Dragon Lizards in Shark Bay

My PhD was on dragon lizards, trying to find out how they contend with the problems of high diurnal temperatures and the lack of water in arid and semi-arid parts of Western Australia (Bradshaw 1970, 1971). I realised when I completed my degree, however, that I could not answer any of the ecological questions that I had posed without a knowledge of the animals' internal control systems – and that meant hormones. I thus spent the next 4 years in overseas laboratories, in Sheffield in the UK, in Paris in France and in Riverside in California, learning and developing new methods to measure steroid hormones from the adrenal glands in extremely small volumes of blood (Bradshaw & Fontaine-Bertrand 1968; Licht & Bradshaw, 1969; Bradshaw & Fontaine-Bertrand 1970). I then applied this in a 10-year study of the Western netted dragon, *Ctenophorus nuchalis*, at Shark Bay (Figure 1). To my amazement I found that these large 40–50g lizards only lived a single year and that they died each summer from a combination of dehydration and starvation to which they seemed ill adapted (Bradshaw 1981). The late Karl Zwicky, one of my colleagues in the Zoology Department, used to say to me ...”why bother studying desert animals because all you find out is that they are adapted to the desert!”. Well here was a case where they were not!

By measuring their rates of water turnover with tritiated water and their adrenal physiology at different times of the year I was able to show that they solved the problem of surviving in a fairly hostile environment, not by adapting their adult physiology, but simply by avoiding the problem. They are born in February each year, grow very rapidly and breed in the spring, lay their eggs in the soil and then die. By measuring rates of

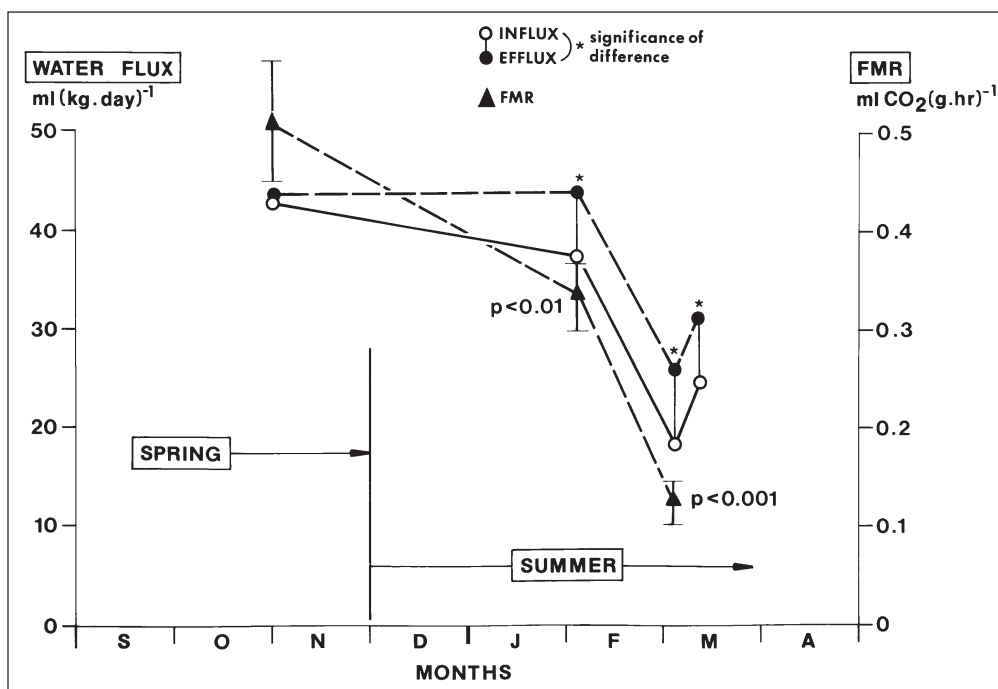


Figure 2. Seasonal changes in rate of turnover of water (influx and efflux) and field metabolic rate (FMR in ml CO₂ (g.hr)⁻¹) using doubly-labelled water of *Ctenophorus nuchalis* at Shark Bay showing a significant decline in both parameters in late summer (from Bradshaw 1986).

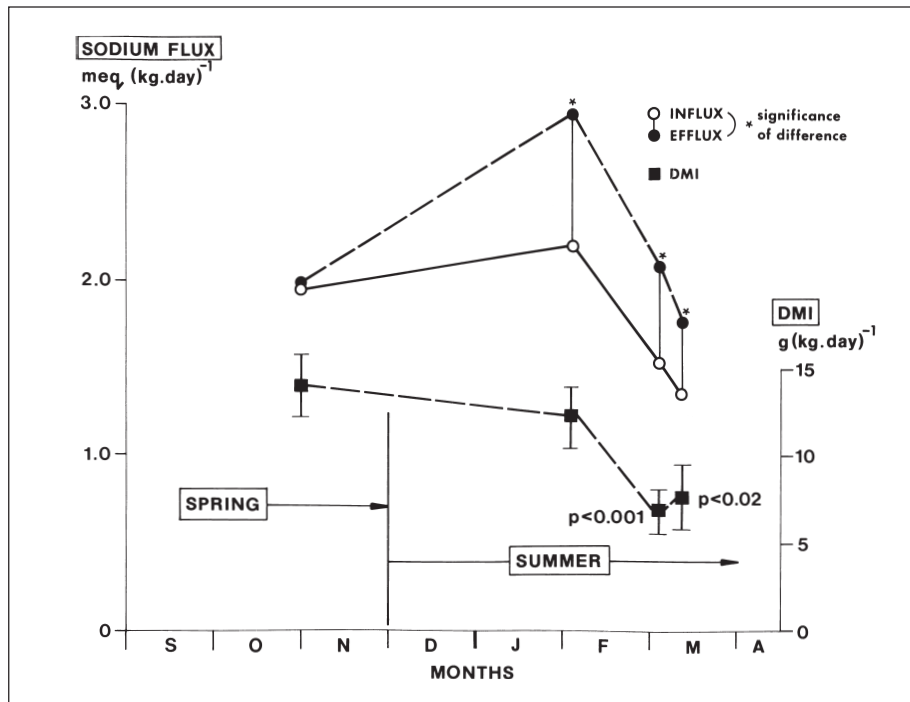


Figure 3. Seasonal variations in rate of sodium turnover (^{22}Na) and estimated dry-matter intake (DMI in g (kg.d)^{-1}) of *Ctenophorus nuchalis* at Shark Bay in Western Australia (from (Bradshaw 1986).

turnover of oxygen, water and sodium, I was able to show that their water balance becomes progressively more negative as summer progresses (i.e. efflux > influx) and their field metabolic rate (FMR) declines by more than 80% (Figure 2). Simultaneous measurements of rates of sodium turnover show that the lizards are feeding less and their dry matter intake (DMI) falls to starvation levels by late autumn (Figure 3). The population thus survives in the form of eggs over the hottest part of the year and the young emerge each year into an environment devoid of competing adults! (Bradshaw 1981, 1986; Nagy & Bradshaw 1995)

This was somewhat of an epiphany for me and I went on to look much more critically at the received wisdom – that reptiles represent the acme of vertebrate adaptation to a desert environment (Bradshaw 1987). My conclusion, which I expounded in my first book in 1986, was that reptiles worldwide do not show any specific adaptations to their preferred desert habitat – rather their basic reptilian constitution, with low rates of metabolism, a reliance on external sources of heat and low rates of water turnover, pre-adapt or ‘exapt’ them in the modern terminology to succeed in desert environments where vital resources are very limited (Bradshaw 1986, 1988).

Quokkas on Rottnest Island

My predecessor, Harry Waring, catapulted the quokka to fame as one of the world’s most studied marsupials, with Rottnest Island its home. My interest was stimulated when John Iveson and I discovered that they were riddled with salmonellosis (Iveson & Bradshaw 1973) and that playing with quokkas could have serious health consequences! The story at that time was that quokka numbers had increased dramatically following a

devastating fire in 1956 and that the population was now controlled by starvation, with particularly young and old animals, dying over the summer months. In order to test this, I started monitoring the physiological condition of animals on Rottnest every 6 weeks, measuring particularly the level of adrenal hormones in the blood. A negative relationship between plasma steroid levels and body condition was the first indication that quokkas were experiencing stress over summer (Figure 4). We found that they did not die then, however, but at the break of the winter season when low plasma cortisol levels led to hypoglycaemia, with the quokkas unable to

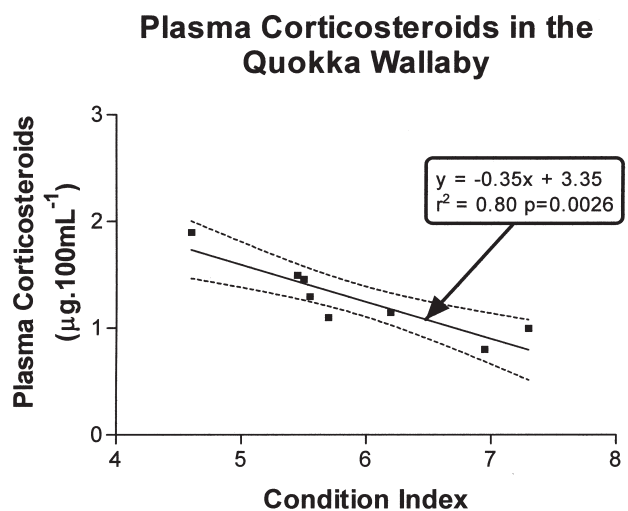


Figure 4. Regression of the concentration of plasma corticosteroid hormones against the body condition index of quokkas on Rottnest Island in late summer. The negative regression is statistically significant, with $r^2 = 0.80$ and $P = 0.0026$ (from Miller & Bradshaw 1979).



Figure 5. An adult quokka wallaby, *Setonix brachyurus*, drinking brackish water at a seep running into a hypersaline lake at Rottneest Island, 20 km off the coast of Western Australia. This supplementary supply of water considerably enhances their body condition in late summer.



maintain their normal body temperature in the cold weather (Miller & Bradshaw 1979).

A later study with a group of Honours students, in which we measured for the first time the levels of the pituitary antidiuretic hormone (ADH) that controls water loss from the kidney, showed the vital importance of even small quantities of brackish water for the long-term survival of quokkas in the degraded environment that is now Rottneest Island. Quokkas living around the fringes

of Lake Baghdad, with access to brackish water from fresh-water seeps flowing into the hypersaline lake (Figure 5), were in substantially better condition than animals from West End, which showed signs of dehydration in late summer (Table 1), despite maximally elevated levels of ADH and reduced rates of urine production (Jones *et al.* 1990).

This study led me to try to clarify the rather confused literature on what is stress and how to measure it. Stress

Table 1

Water and electrolyte balance of quokkas (*Setonix brachyurus*) in late summer on Rottneest Island, Western Australia (from Jones, Bradshaw, Fergusson and Watts 1990)

Parameter	West End	Lake Baghdad	Significance
Body Mass (kg)	2.09 ± 0.15	2.66 ± 0.13	P<0.01
Condition Index	5.33 ± 0.26	6.45 ± 0.25	P<0.01
Plasma ADH (pg.mL ⁻¹)	89.2 ± 19.5	35.6 ± 15.8	P<0.05
Urine Production (mL.kg ⁻¹ .day ⁻¹)	20.35 ± 2.75	58.18 ± 13.79	P<0.02
Urine Osmolality (mOsm.kg ⁻¹)	1253.1 ± 44.7	968.7 ± 101.3	P<0.02
Plasma Osmolality (mOsm.kg ⁻¹)	301.3 ± 6.0	279.8 ± 2.4	P<0.005



Figure 6. An aerial view of Barrow Island during the dry season of the year. The 30,000 ha island is located some 80 km off the arid Pilbara coast of Western Australia, approximately 1400 km north of Perth.

was originally defined, somewhat poetically, by Hans Selye in 1952 as “a state of non-specific tension in living matter” (Selye 1952) and later attempts at a definition have not been much better with “any factor that inhibits growth and reproduction in a population” (Brett 1958) or “an environmental condition that, when first applied, impairs Darwinian fitness” (Sibley & Calow 1986) – effectively confusing stressors with stress! I tried to simplify the dual problems of identifying stress when it occurs and then measuring its intensity by defining it as “the physiological consequences of demands that exceed an animal’s regulatory capacities” (Bradshaw 1997; Bradshaw 2003). This means that one should be able to identify stress by the presence of a significant perturbation of the animal’s *milieu intérieur* from whatever is considered to be the ‘normal’ state, despite the maximum deployment of regulatory systems (Bradshaw 2003). This operational definition turns out to fit in well with the new concepts of ‘allostasis’ and ‘allostatic load’ introduced by (McEwen 1998) and (McEwen & Wingfield 2003) and it corresponds to their case of ‘allostatic overload’ (Bradshaw 2007).

Desert Wallabies and Kangaroos on Barrow Island

Barrow Island off the Pilbara coast is Australia’s foremost A Class Nature Reserve with a total of 14 species of mammals, 8 of them marsupial and with 4 of these extinct, or virtually so, on the mainland of Australia

(Figure 6). I had a wonderful opportunity to study, with a group of colleagues, the ecophysiology of a whole suite of vertebrates on Barrow Island in the 1990s, courtesy of a grant from the Australian Research Council. By capturing and recapturing the same individuals, we were able to measure, simultaneously, the field metabolic rate (FMR) of a range of vertebrate animals with oxygen-18 and thus compare their metabolic footprints, using oxygen consumption as a common currency (Bradshaw 1992). Using this ecophysiological approach it was clear that the Golden bandicoot, *Isoodon auratus*, was by far the most important animal metabolically on the island (Bradshaw *et al.* 1994).

Attempts to recapture rock wallabies (*Petrogale lateralis*) on Barrow, which live in caves of the west coast of the island, were not overly successful and, with Keith Morris’ help, we initiated a study of the related species, *Petrogale rothschildi*, on Enderby Island in the Dampier Archipelago (Figure 7). Our aim was to compare their ecophysiology with Spectacled hare wallabies (*Lagorchestes conspicillatus*), which are very common on Barrow, and spend the daylight hours in spinifex tussocks where they are exposed to high environmental temperatures (Figure 8).

Our results were quite intriguing. Both species reduced dramatically their rates of water turnover and urine production in summer and both also showed no sign of any perturbation of their *milieu intérieur* or ‘internal environment’, even under the most trying conditions. The extent to which the Hare wallabies are



Figure 7. Rothschild's rock wallaby, *Petrogale Rothschildi*, disappearing over a hill on Enderby Island in the Dampier Archipelago following a physiological interrogation.



Figure 8. The Spectacled hare wallaby, *Lagorchestes conspicillatus*, on Barrow Island and a section of habitat showing the clumps of spinifex (*Triodia* spp.) in which the wallabies shelter during the heat of the day

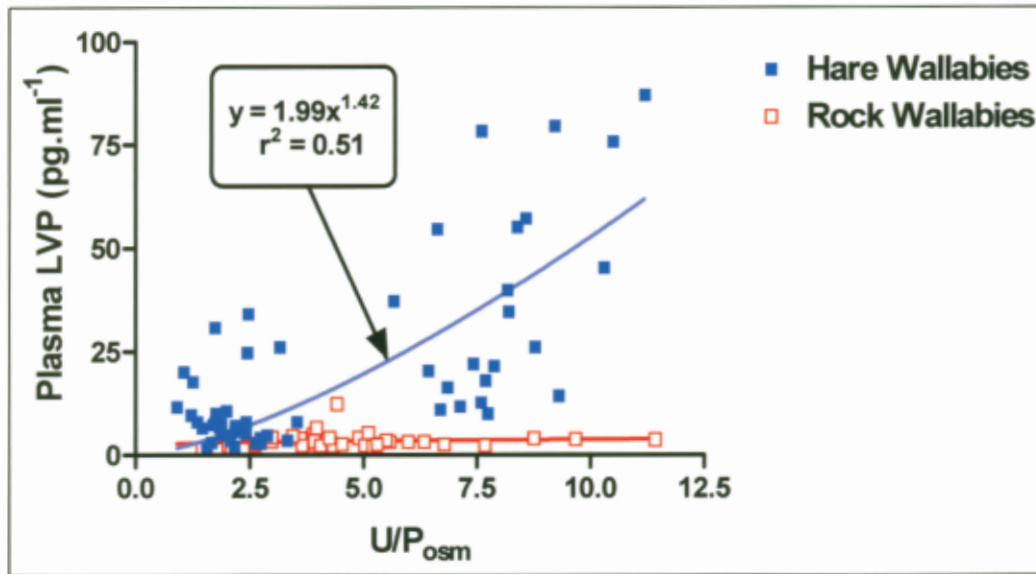


Figure 9. Variation in circulating levels of lysine vasopressin (LVP) in Hare wallabies and Rock wallabies as function of the concentrating activity of the kidney (U/P_{osm}) (from Bradshaw, Morris & Bradshaw 2001).

able to conserve water is quite remarkable and their rate of water turnover is the lowest of any desert mammal measured worldwide (Bakker & Bradshaw 1989; Nagy & Bradshaw 2000; King & Bradshaw 2008). It was when we looked in detail at the means by which the two species were conserving water loss from their kidneys that an amazing difference emerged (Figure 9). The Hare wallabies displayed a typical mammalian response to lack of water. Plasma levels of ADH increased (as in quokkas on the West End of Rottnest), urine volume declined and its osmotic pressure increased as water was abstracted by the renal concentrating mechanism (Table 2). When we looked at the Rock wallaby on the other hand, we found that ADH levels did not change from wet to dry season and, although urine volumes declined in the dry season, the urine did not get more

concentrated (Table 3). What the Rock wallabies were doing was responding somewhat like reptiles and simply reducing their rate of urine production by cutting down blood flow to the kidneys. Less urine was thus being produced, and less water being lost, but without any change in its concentration. We thus appear to have discovered the first instance of a mammal completely lacking an hormonally-controlled regulation of kidney function as shown in Figure 9, (Bradshaw *et al.* 2001). This discovery serves to underline the vital importance of the cool and humid cave environment in which the Rock wallabies shelter during the heat of the day. If this were to be destroyed they lack the physiological adaptations that would enable them to survive in this arid environment (King & Bradshaw 2008).

Table 2

A summary of kidney function in the Spectacled hare wallaby, *Lagorchestes conspicillatus*, on Barrow Island in wet and dry seasons (from Bradshaw, Morris and Bradshaw, 2001)

Season	C_{PAH}	C_{IN}	C_{OSM}	C_{H2O}	V	FR_{H2O}	U/P_{OSM}	ECFV (%)	LVP
DRY	6.0 ± 0.4	1.5 ± 0.1	57.5 ± 3.2	-50.5 ± 2.8	6.9 ± 2.2	99.6 ± 0.1	8.4 ± 0.3	18.3 ± 0.7	32.7 ± 5.6
WET	9.0 ± 1.3	2.7 ± 0.2	91.6 ± 6.9	-39.6 ± 3.9	50.2 ± 4.5	97.8 ± 0.3	2.0 ± 0.1	18.2 ± 1.4	10.7 ± 1.8
<i>P</i> =	0.04	0.001	0.001	0.059	.001	0.001	0.001	NS	0.001

Table 3

A summary of kidney function in Rothschild's rock wallaby, *Petrogale rothschildi*, on Enderby Island in wet and dry seasons (from Bradshaw, Morris and Bradshaw, 2001)

Season	C_{PAH}	C_{IN}	C_{OSM}	C_{H2O}	V	FR_{H2O}	U/P_{OSM}	ECFV (%)	LVP
DRY	5.8 ± 0.1	0.8 ± 0.1	34.8 ± 6.7	-28.1 ± 5.4	6.7 ± 1.4	99.4 ± 0.1	5.4 ± 0.7	12.2 ± 0.5	3.5 ± 1.5
WET	7.9 ± 0.5	1.3 ± 0.1	59.2 ± 6.2	-46.3 ± 4.5	14.3 ± 2.1	99.2 ± 0.1	5.4 ± 1.1	18.8 ± 1.1	6.0 ± 0.9
<i>P</i> =	.008	0.005	0.02	0.02	0.01	NS	NS	0.001	NS

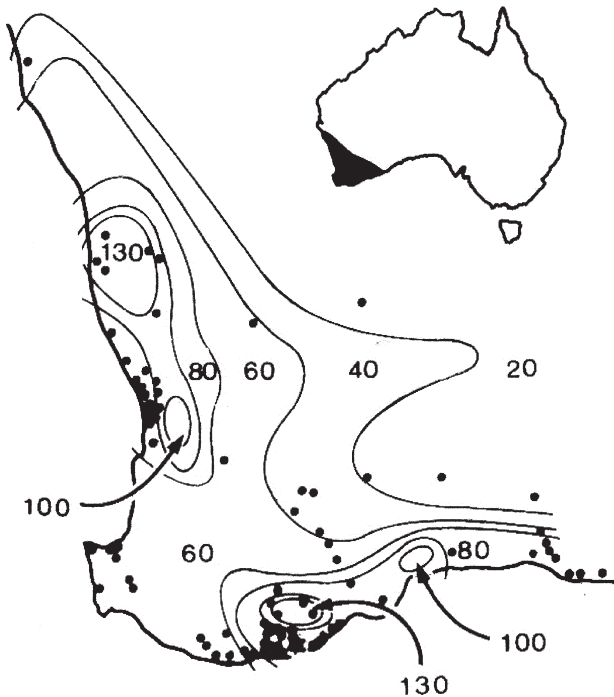


Figure 10. The past and present distribution of the Honey possum, *Tarsipes rostratus*, in south-western Western Australia (from Wooller, Russell and Renfree, 1984). Each dot indicates a specimen in the Western Australian Museum collection and the lines are isoflors joining points of equal plant species richness within the family Proteaceae (after Hopper 1979).

Although the Barrow Island fauna displays an impressive level of physiological adaptation to the exigencies of its arid environment, our study did reveal one instance of probable stress in the dwarf euro kangaroo, *Macropus robustus isabellinus*. Evidence was found of a significant change in the animal's *milieu intérieur* on one occasion on Barrow Island: in November 1994, following a protracted 8-month drought when a total of only 54 mm of rain was recorded on the island. Euros had significantly elevated levels of plasma osmolality, cortisol, ADH, and a reduced eosinophil count (King & Bradshaw 2010). This suggests that these animals may have been dehydrated, despite the operation of appropriate physiological responses to water deprivation. Lower eosinophil counts also suggest that immune function may have been suppressed as a result of the elevated corticosteroid levels. Comparisons with the mainland sub-species of the euro also revealed the presence of a non-generative normocytic hypochromic anaemia in Barrow Island euros that potentially compromises their aerobic capacity (Billiards *et al.* 1999; Ogawa *et al.* 2000) and adds to their vulnerability.

Honey Possums

I should like to close with a brief mention of our current research project on the tiny nectarivorous Honey possum, *Tarsipes rostratus*, in Scott National Park in the extreme southwest of Western Australia (Figure 10). The southwest corner of Western Australia contains

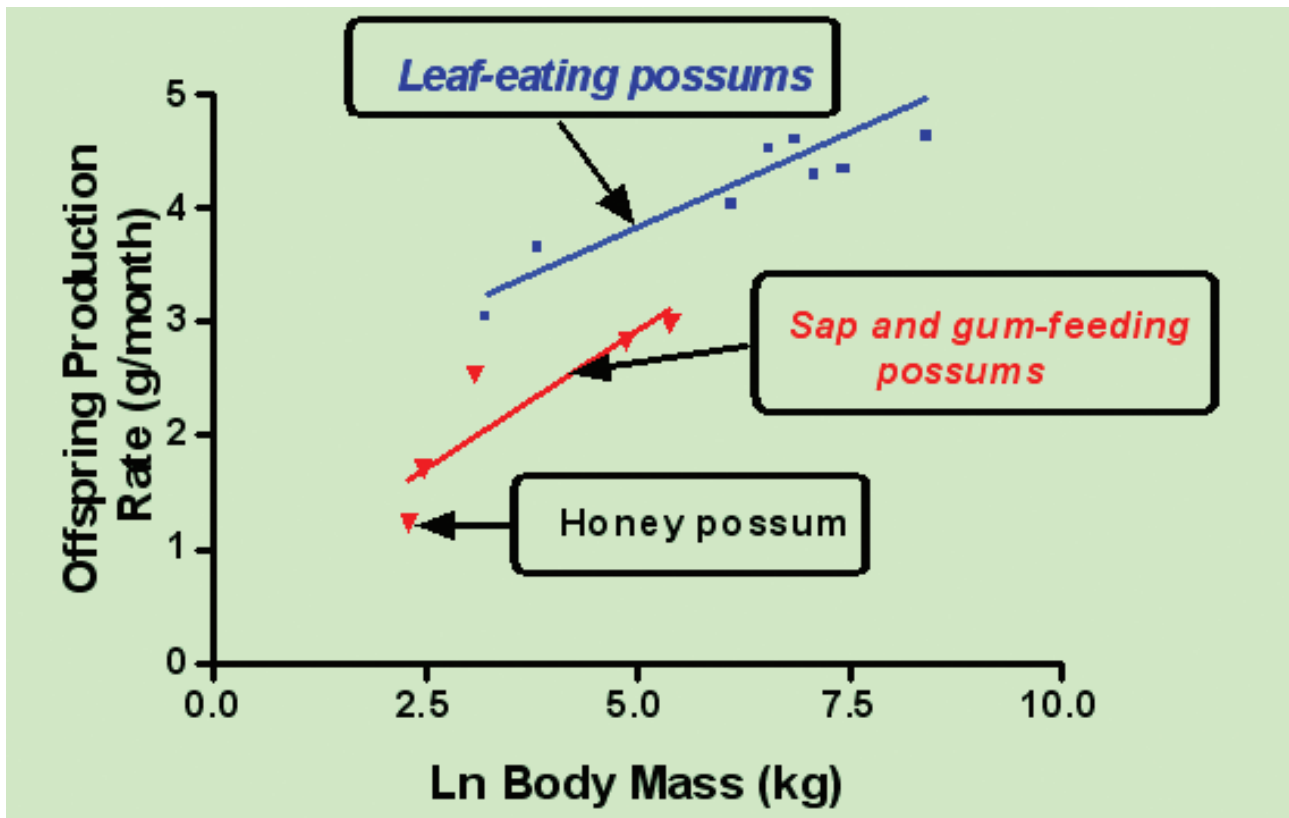


Figure 11. Relationship between the offspring production rate, in grammes per month, and female adult body mass in leaf-eating versus sap, nectar and gum-feeding possums (from Smith & Lee 1984).

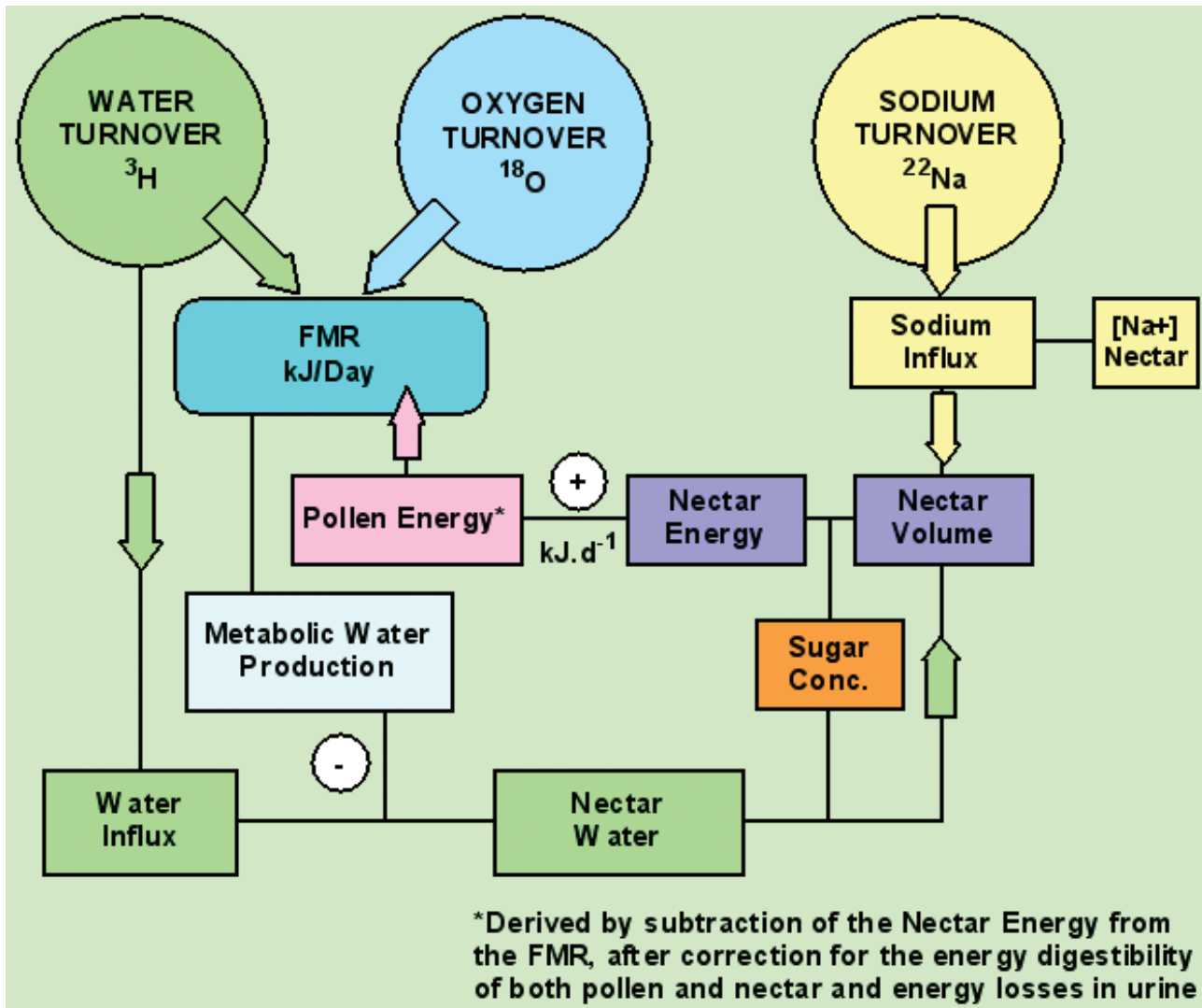
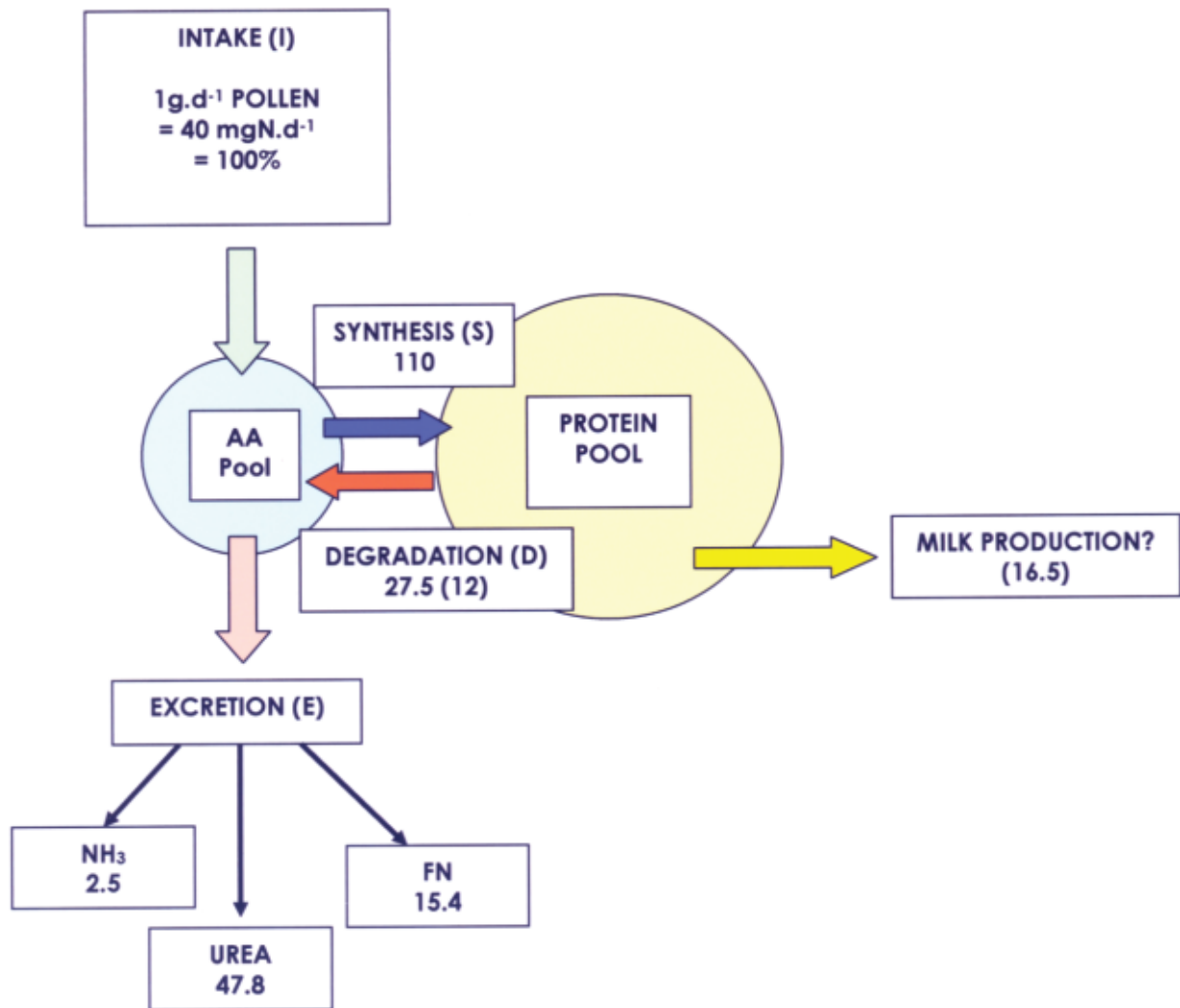


Figure 12. Schema of the rationale used to measure rates of pollen and nectar intake using stable and radioactive isotopes in free-ranging Honey possums (*Tarsipes rostratus*) in Scott National Park. Nectar intake is estimated independently from influxes of sodium-22 and tritium, the latter corrected for metabolic water production (MWP) and averaged. Pollen intake is estimated by subtraction of the nectar energy intake from the field metabolic rate (FMR) (from Bradshaw & Bradshaw 1999).

Australia's only biodiversity hotspot threatened by habitat loss and degradation (Myers *et al.* 2000; Mittermeier *et al.* 2004) and the Honey possum is extremely vulnerable, depending as it does on kwongan vegetation now threatened by fire and spreading *Phytophthora cinnamomi* infections.

We set out to test an old hypothesis in the literature that the relatively low reproductive rate of Honey possums, compared with leaf-eating species, may be due to their high carbohydrate diet (nectar) that could be deficient in protein (Figure 11) (Smith & Lee 1984). We needed to know how much nectar and pollen Honey possums actually consume daily in their natural habitat and, after much work at Lucas Heights, we developed an isotopic method to determine this (Figure 12) (Bradshaw *et al.* 1987; Bradshaw & Bradshaw 1999). We found that a 9 g possum consumes, on average, 7 ml of nectar and 1 g of pollen – virtually its own body mass daily. Although pollen had been thought in the literature to be

indigestible, it is a rich source of nitrogen and 1 g of pollen per day provides approximately 10 times the Honey possum's minimum requirement for nitrogen balance (Bradshaw & Bradshaw 2001). We then went on to measure rates of protein metabolism using ^{15}N -glycine in lactating females and were able to establish that they divert the very small amounts of nitrogen needed to sustain the developing young *via* the milk by decreasing rates of protein degradation, rather than increasing rates of synthesis when lactating (Bradshaw & Bradshaw 2009) (Figure 13). The Honey possum joey is the size of a grain of rice when born and only weighs 4 mg – only minute amounts of nitrogen are thus needed to be diverted from the mother's diet through the milk to sustain its development. We can calculate that the total amount of nitrogen needed to produce a young of 2.5 g at weaning is only 128 mg, and contrast this with the mother's daily intake of nitrogen on its pollen diet of approximately 40 mg (Bradshaw & Bradshaw 1999).



URINARY N (50.3) + FAECAL N (15.4) = TOTAL N EXCRETION = 65.7

N BALANCE = 34.3

Figure 13. A model of nitrogen flow in relation to dietary intake of 1 g of pollen of 4% nitrogen content for the Honey possum *Tarsipes rostratus*. Dietary intake is set at 40 mg per day and taken as 100% with all other parameters shown as percentage values of this. I = nitrogen intake, E = nitrogen excretion, S = rate of nitrogen synthesis to the protein pool and D = rate of nitrogen degradation from the protein pool. FN = faecal nitrogen excretion, urea = urinary urea excretion and NH₃ = urinary ammonia excretion. The value for D in parentheses (12) represents the lower whole body degradation rate measured in females carrying pouch young (from Bradshaw & Bradshaw 2009).

Although one can never prove hypotheses in science, we have shown that the one initiating this study is false – i.e. that their high carbohydrate diet is deficient in protein and that this accounts for the Honey possum’s relatively low reproductive rate when compared with leaf-eating possums (Smith & Lee 1984). It also highlights the fact that this was the wrong question to ask in the first place. Because an animal has a lower rate of reproduction than another does not necessarily mean that its diet is wanting. Rates of reproduction of different species are attuned to their particular environment as a result of natural selection and, unless the population is in

obvious decline, the reproductive rate will be adequate to balance mortality and emigration (Stearns 1992). The Honey possum is unusual amongst marsupials in retaining its young with the mother for a longer period of time than similar-sized phalangeroids (Russell 1982; Wooller *et al.* 1984), suggesting that this enhanced parental care involves a longer learning experience that increases their probability of survival and thus compensates for a lower offspring production rate than other small possums.

We now have a quantitative measure of the amounts of energy needed to sustain Honey possums in their

kwongan habitat, and the flower resources needed to provide these daily amounts of carbohydrate and nitrogen. The Honey possum is not yet listed as vulnerable or threatened, but it will be soon if the current loss and destruction of its habitat continues unabated. Fire is also one of its main enemies and our long-term study in Scott National Park has shown that recovery after fire is very slow with an estimate of 15–20 years to recover pre-fire population densities (Bradshaw *et al.* 2007).

In summary

I hope that these few examples will give an idea of the power of the ecophysiological approach – bridging two established disciplines to better understand the vital nexus between an animal and its environment – and opening vistas for effective conservation of our unique biodiversity legacy in Western Australia.

Acknowledgements: I have been most fortunate in that my research over the years on sometimes obscure native animals has been generously funded by the Australian Research Council (ARC), and its forerunners ARGC and ARGS. An important group of colleagues, both in Australia and overseas, have greatly assisted me in my researches, as have the many graduate students that I have had the privilege to supervise over a period of forty years at The University of Western Australia. My greatest thanks though go to my most valuable colleague and collaborator, my wife Felicity, and I express my love and thanks to her for her unwavering support in everything I do.

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