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Sensitivity of some Australian animals to sodium fluoroacetate (1080): additional species and populations, and some ecological considerations

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Abstract

The sensitivity to fluoroacetate (1080) of a number of species of rodents and dasyurids with and without evolutionary exposure to fluoroacetate-bearing vegetation was determined. *Rattus fuscipes*, and species of *Pseudomys* from populations with exposure to this vegetation, were particularly tolerant to fluoroacetate. However, the level of tolerance varied among the different populations of each species, depending on the degree to which the toxic plants were present in their microhabitat. The tolerance of the F1 offspring of sensitive *R. fuscipes* (South Australia) crossed with tolerant conspecifics from Western Australia was mid-range between those of the parental populations. The sensitivity of introduced *R. rattus* and *Mus domesticus* from areas with fluoroacetate-producing plants in Western Australia was similar to that reported elsewhere for these rodents. This suggests that their relatively short coexistence with the toxic plants has had little obvious impact on their level of sensitivity to fluoroacetate. The dibbler, *Parantechinus apicalis*, which coexists with the toxic vegetation, was exceptionally tolerant for a native carnivore/insectivore (LD_{50} ~35 mg 1080 kg^{-1}). In contrast, however, *Phascogale tapoatafa* from southern Western Australia was more sensitive to 1080 than was expected, with an estimated LD_{50} of 7 mg 1080 kg^{-1}. Although the level of tolerance to fluoroacetate was seen to vary depending on the level of exposure of each species/population to fluoroacetate-bearing vegetation, our findings provide further evidence of the evolutionary impact that fluoroacetate-producing plants appear to have had on the genetic composition of indigenous Australian fauna.

Introduction

Sodium and potassium salts of fluoroacetic acid (henceforth referred to as fluoroacetate) are produced by a number of indigenous plants in Australia as part of a chemically mediated defence strategy against herbivory (Aplin 1971; Twigg and King 1991). Most of these plants (~40+ species identified) belong to the genus *Gastrolobium*, with the remaining two species being *Nemcia spathulata* and *Acacia georginae* (all genera are legumes, Order Leguminales). Most species, particularly those with high toxicity, are confined to the south-west of Western Australia (WA). However, although more patchily distributed, three less toxic species also occur in central (*G. brevipes*, *A. georginae*), or northern (*G. grandiflorum*) Australia (Aplin 1971; Twigg and King 1991; Twigg *et al.* 1999). Fluoroacetate-producing plants are predominantly found on acidic, heavier soils or sandy loams, and are rarely found on deep sands or soils calcareous in origin (Aplin 1971; Oliver *et al.* 1979). Fluoroacetate-producing plants also occur in southern Africa (Order Rosales, *Dichapetalum*, ~30 species: Vickery and Vickery 1975; Meyer 1994) and South America (Order Rubiales, *Palicourea marcgravii*: de Oliveira 1963). The Leguminales group is believed to have been derived from Rosales stock (Hutchinson 1973).

The concentration of fluoroacetate in fluoroacetate-producing plants in Australia ranges from <50 mg kg^{-1} of air-dried leaves up to 3500 mg kg^{-1} (see Table 1). However, its

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Table 1. Fluoroacetate (FAc) concentration in leaf samples of fluoroacetate-producing species, and the implication of these species in domestic livestock deaths
From Gardner and Bennetts (1956), Aplin (1971), Twigg *et al.* (1996, 1999)

Species	Common name	FAc conc. (mg kg^{-1})[A]	Livestock deaths
Gastrolobium villosum	Crinkle leaf poison	Low (0–100)	Yes
G. stenophyllum	Narrow leaf poison	90	Yes
G. grandiflorum	Wallflower poison	185	Yes
G. brevipes	–	50–300	Yes
G. velutinum	Stirling range poison	300	Yes (?)
G. spinosum	Prickly leaf poison	0–400	Yes
G. microcarpum	Sandplain poison	0–600	Yes (?)
G. callistachys	Rock poison	100–1000	Yes
G. calycinum	York road poison	400–2500	Yes
G. graniticum	Granite poison	900–1250	Yes
G. bennettsianum	Cluster poison	1300	?
G. parviflorum	Box poison	100–2500	Yes
G. bilobum	Heart leaf poison	500–3500	Yes
Nemcia spathulata	–	40–80	?
Acacia georginae	Gidyea	25	Yes

[A]Air-dried sample.

concentration can vary considerably among species, individuals within a stand, locality, season, and plant parts (Aplin 1971; Twigg *et al.* 1996, 1999). Fluoroacetate is found in all the major plant tissues, including the wood and roots, but ephemeral tissues, such as apical meristems, flowers and seed, contain the greatest amounts (Aplin 1971; Hall 1972; Vickery and Vickery 1975; Twigg *et al.* 1996, 1999). There is also a negative relationship between the presence of physical deterrents (e.g. spines, sclerified tissue) and the fluoroacetate concentration within the different species of *Gastrolobium* (Twigg and Socha 1996). All but two of the species of *Gastrolobium* are small to large shrubs (*G. bilobum* can be a small tree, *G. villosum* is a ground cover: Aplin 1971).

Many species of native Australian animals have coexisted with fluoroacetate-bearing vegetation for at least several thousand years and, consequently, have developed varying degrees of tolerance to this highly toxic compound. This is particularly so in populations in the south-west of Western Australia where relatively high levels of fluoroacetate tolerance are seen (Twigg and King 1991). However, the degree to which this tolerance has developed depends on the dietary and habitat preferences of individual species, and the characteristics of a particular genome (Oliver *et al.* 1979; King *et al.* 1981; Twigg and King 1991). Fluoroacetate tolerance is most pronounced in the herbivorous species, moderate in the omnivorous species, and generally least developed in the native carnivores. It also occurs across all animal groups, including insects, reptiles, birds and mammals (Oliver *et al.* 1977, 1979; King *et al.* 1981; McIlroy 1982*a*, 1982*b*; Mead *et al.* 1985; Twigg 1990; Twigg and King 1991; Martin and Twigg 2002). In combination with palaeontological records (e.g. Kirsch and Poole 1972), tolerance to fluoroacetate has been used to infer past radiation/speciation of some native species (e.g. *Macropus fuliginosus*, *Rattus fuscipes*: Oliver *et al.* 1977, 1979; Mead *et al.* 1985).

Sodium fluoroacetate, often referred to as 1080, is also the principal toxicant used in most vertebrate pest-control programs in Australia and New Zealand (Twigg and King 1991; Seawright and Eason 1994; Saunders *et al.* 1995; Williams *et al.* 1995). 1080 is

particularly target-specific in Western Australia because of the enhanced tolerance of native animals in this State (King *et al.* 1981; Mead *et al.* 1985; Twigg and King 1991; Martin and Twigg 2002). However, given their relatively small size compared with the target species, the sensitivity to fluoroacetate of relatively small-sized animals, such as many dasyurids and rodents, needs to be determined if more informed potential-risk profiles are to be developed with respect to 1080-baiting programs. Currently, limited information is available regarding the sensitivity of the dasyurids exposed to the toxic plants (see King *et al.* 1989; Twigg and King 1991).

In this paper we present further evidence of the impact that fluoroacetate-bearing vegetation appears to have had on the genetic composition of indigenous Australian fauna. This includes contrasting the sensitivity of a number of species of dasyurids and rodents with and without evolutionary exposure to fluoroacetate-bearing vegetation. In particular, we examine a number of populations of *R. fuscipes* with varying levels of exposure to the toxic plants, and speculate about the genetic processes likely to be involved in the development of fluoroacetate tolerance in these rats. The sensitivity to fluoroacetate of some introduced rodents (*Rattus* and *Mus*) from areas containing fluoroacetate-bearing vegetation is presented. We also provide brief comments regarding the role of enhanced tolerance to fluoroacetate in determining the target specificity of the pest-control programs that utilise 1080.

Methods

The data presented in this paper were often collected as the result of individual animals becoming available opportunistically, and, hence, not all individuals of each species (e.g. *Rattus* sp.) were tested at the same time. Most tests were undertaken between 1983 and 1986, although several species were also obtained (live-capture in the wild), and subsequently tested, up until mid-2000. The limited availability of some species used in our trials was largely caused by the associated cost and the difficultly with obtaining relatively large numbers of often scarce or rare species. The source locations for the species and populations used, and their potential exposure to fluoroacetate-bearing vegetation, are given in the Appendix. Except for the F1 *R. fuscipes* crosses, which were bred under controlled animal-house conditions, all other animals originated from free-ranging populations.

All animals were held in an animal house maintained at 23 ± 2°C with a 12 : 12 h photoperiod, and all animals were acclimatised to captivity for at least 2 weeks prior to dosing. Animals were fed *ad libitum* with appropriate commercially available foods. For herbivorous/omnivorous species this included a seed mix and fresh fruit (e.g. carrot, banana, avocado). Carnivorous species were fed live mealworms, euthanased mouse pups, portions of day-old chicks, scrambled egg, and tinned dog food. Water was provided to all animals *ad libitum*.

Sodium monofluoroacetate (NaFAc, 1080) was administered in aqueous solution by intraperitoneal injection. The purity of the 1080 powder used in these solutions ranged from 92 to 95% pure sodium monofluoroacetate, but the dosing solutions were not corrected for this. To enable ready comparison, the toxicity data presented have been standardised to values equivalent to 100% pure NaFAc (1080). For each group of trials, the same dosing solutions were used throughout. The dosing solutions were stored at 23°C. At the concentrations used, aqueous solutions of NaFAc are known to be stable under such conditions for at least 12 months (Mead 1980; L. E. Twigg, unpublished data). However, all dosing solutions were replaced once they had been in use for 12 months. Smaller animals were dosed using solutions containing between 0.10 and 10.0 mg 1080 mL^{-1}, with dose volumes ranging from 0.1 to 0.5 mL. The solutions used for the larger animals ranged from 1.0 to 20.0 mg 1080 mL^{-1}, with dose volumes of 0.2–1.0 mL. These volumes were generally <2% of the body weight of test subjects. Dose groups included only adult individuals but owing to difficulties in sexing some species, the sex of the animals used was not always known. Dosing was undertaken between 0830 hours and 1200 hours. Frequent observations were undertaken for the first 5–7 h after dosing, and all animals were then inspected at least daily for a further 9–13 days. Any mortality and signs of poisoning during this 14-day period were considered to have been caused by 1080. Signs of poisoning are usually apparent in less than 24 h (McIlroy 1982*a*, 1982*b*; Twigg and King 1991).

Two related procedures were used to determine the sensitivity of animals to 1080: (1) the 'standard' Lethal Dose$_{50}$ test protocol (LD_{50}, the amount of toxin that, theoretically, will kill 50% of test subjects) using a geometric dose multiplier (i.e. the multiplier remains the same between the dose levels within a given trial), and (2) the Approximate Lethal Dose procedure (i.e. ALD, the dose that kills 10% of test subjects, which usually corresponds with the lowest dose causing death: British Toxicology Society 1984; Calver *et al.* 1989*a*, 1989*b*). The ALD was adopted in mid-1984 because of the recommendations of the Animal Experimentation and Ethics Committee, Department of Agriculture, Western Australia regarding formal LD_{50} tests and animal welfare. The ALD procedure generally involves dosing animals at a set of predetermined dose levels until 10% of test animals succumb at a given level. A geometric progression factor is used, usually a 1.5 multiplier and, preferably, there are ~10 individuals per group. Although 'pilot trials' are sometimes used, all available animals are generally dosed at the first level before proceeding to the next (Calver *et al.* 1989*b*). However, in our study, restrictions were often placed on the number of animals that could be used, and severe signs of poisoning, as well as death, had to be used as an end-point when determining the sensitivity of individuals during some of the later trials. The number of animals available was also limited by the difficulty of obtaining some species (e.g. small dasyurids). These restrictions meant that, irrespective of which test procedure was employed, a staggered-entry dosing procedure was used for most species (see Twigg *et al.* 2002). That is, not all animals at a particular dose level were dosed on the same day, but rather, individuals were dosed ~24 h apart so that the preliminary outcome for the earlier-dosed animals could be ascertained. Any further dosing was based on the outcomes of the staggered-entry procedure. We used geometric progression factors in the range of 1.14–1.50, which was similar to that recommended by Calver *et al.* (1989*b*).

The starting dose for each species was based on the available information for closely related species (see McIlroy 1982*a*, 1982*b*; Calver *et al.* 1989*a*; Twigg and King 1991). The next dose level after the initial 'pilot' dose was either increased or decreased depending upon the outcome of the previous dose(s). To verify that the injection process itself had no obvious detrimental effect, some individuals of each species were administered equivalent amounts of deionised water only.

As only a small number of individuals of some species were available, and because of the AEEC restrictions on the number of animals that could be used, some individuals had to be tested at more than one dose level (e.g. small dasyurids and some *Pseudomys* spp.). In these cases, a minimum of 3 weeks was allowed between doses, which is sufficient time for the animals to overcome the toxic effects of 1080, and to replenish their levels of glutathione, an important chemical involved in the detoxification of 1080 (see Twigg and King 1991). In endothermic animals, glutathione levels usually return to 'normal' within 24–48 h of dosing (Twigg and King 1991). Where animals were dosed at several levels, the number of dose levels used was generally 4 or less, which was within the maximum number of 'redoses' for a given individual as recommended by Calver *et al.* (1989*b*).

Where appropriate, the precise LD_{50} values and the 95% confidence limits were calculated using the moving-average method for unequal sample sizes, as described by Thompson (1947). In these cases, all animals were used once only. The moving-average procedure was chosen because it was used in earlier studies (e.g. McIlroy 1982*a*, 1982*b*; Twigg and King 1991). This procedure is also known to produce LD_{50} estimates that are similar to those obtained with probit analysis (Twigg *et al.* 2002). In most Australian species investigated, the LD_{50} is generally greater than the ALD value, by a factor of about 1.5 (Calver *et al.* 1989*b*), and we used this value when estimating a LD_{50} from a given ALD. Estimating standardised LD_{50} values enabled more realistic comparison between species and populations.

Changes in plasma citrate after administration of 1080 can be used as a reliable indicator of the relative sensitivity of individual animals to fluoroacetate (Oliver *et al.* 1979; King *et al.* 1981; Twigg and King 1991). Consequently, we reworked the data of Mead *et al.* (1985) to compare the citrate response of the tolerant (Pine Creek – Western Australia, WA), sensitive (South Australia, SA) and F1 cross (PCWA × SA) individuals of *R. fuscipes*. Changes in plasma citrate concentrations ($\mu g\ mL^{-1}$) in dosed rats were calculated as increases above the base-level (Time 0) concentration of the undosed rats (also see Twigg and King 1991; Martin and Twigg 2002). These increases were then compared (ANOVA: Zar 1984) between the individuals from the three groups of rats that had been administered 0.92 mg pure 1080 kg^{-1}.

Results

Rattus fuscipes

Rattus fuscipes from areas with fluoroacetate-bearing vegetation were 10–20-fold more tolerant to 1080 than were conspecifics outside the known range of the toxic plants

Table 2. LD_{50} values with 95% confidence limits for populations of *Rattus fuscipes*, primarily from Western Australia

Dose levels and LD_{50} values are in mg pure 1080 kg^{-1}. These data are from the present study unless otherwise indicated

Population	*n*	Lowest dose causing death	LD_{50}	95% confidence limits
Hellfire Bay[D]	23	14.28	17.39	13.98–21.62
Cape Arid[D]	38	31.1	42.61	36.00–50.42
Denmark[E]	26	18.4	~32.0	
Mt Ragged[D]	4	28.2	~23.5	
Salisbury Island	6	1.13	~1.7	
Daw Island	4	1.13	<1.1	
South Australia	2[A]	1.84	<1.8	
F1 – SA × PCWA[B]	16[C]	9.2	~9.0	
Canberra	20	0.78[F]	1.11	0.83–1.48[G]
Greenhead[E]	45	18.4	24.69	21.29–28.62[G]
Albany, mainland[D]	24	23.92	30.09	23.33–38.82[G]
Michaelmas Island[E]	22	14.17	24.58	21.62–27.95[G]
Cape Le Grand[D]	28	16.1	27.19	24.11–30.67[G]
Pine Creek, Manjimup[D]	20	36.31	36.31	34.01–38.78[G]
Mondrain Island[D]	33	68.36	79.66	72.69–88.63[G]

[A]In addition to the toxicity data, a number of other rats from South Australia (*n* = 12) were dosed with 1080 for the collection of plasma citrates. Most of these rats displayed obvious signs of 1080 intoxication within 1–4 h, and 3 of 7 (0.92 mg 1080 kg^{-1}), and 5 of 5 (9.2 mg kg^{-1}) rats did not 'survive' until the 6-h bleed.
[B]Western Australian (Pine Creek – Manjimup) population used.
[C]In addition to the toxicity data, a number of other F1 individuals (*n* = 62) were dosed with 1080 for the collection of plasma citrates. Few of these rats displayed obvious signs of 1080 intoxication at low doses, and 1 of 42 (0.92 mg 1080 kg^{-1}), 0 of 4 (4.6 mg 1080 kg^{-1}), and 7 of 16 (9.2 mg kg^{-1}) rats did not 'survive' until the 6-h bleed.
[D]Population coexists with fluoroacetate-bearing vegetation.
[E]Coastal sand-plain or island population, nearby mainland populations exposed to fluoroacetate-bearing vegetation.
[F]J. C. McIlroy, personal communication.
[G]Data from Mead *et al.* (1985).

(estimated LD_{50} ranges 17–43 and 1–2 mg 1080 kg^{-1}, respectively: Table 2). Two of the more tolerant populations are not directly exposed to the toxic plants (Michaelmas Island, Greenhead: Table 2), but, rather, appear to have received some gene flow from ancestral populations on the immediately adjacent mainland where fluoroacetate-producing plants are common (see Discussion). Interestingly, the F1 generation of a cross between the tolerant rats from Western Australia (Pine Creek – Manjimup) and the highly sensitive rats from South Australia, was mid-range in its tolerance with an estimated LD_{50} of 9.0 mg kg^{-1}. None of the South Australian rats survived a 9.2 mg kg^{-1} dose (Table 2). The increase in plasma citrate concentration, which can be used as an indicator of the toxic effects of fluoroacetate (Oliver *et al.* 1979; Twigg and King 1991), also differed among the South Australian, the Western Australian (Pine Creek – Manjimup) and the F1 cross rats (ANOVA: $F = 47.31$, d.f. = 2,9, $P < 0.001$ – data from Mead *et al.* 1985 reworked and analysed). Mean increases (±s.d.) in plasma citrate concentration above that of untreated rats (27.6 μg mL^{-1}, *n* = 16: Oliver *et al.* 1979) in *R. fuscipes*, following intraperitoneal

Table 3. Mortality data (number deaths/number dosed) for a variety of native animals from Western Australia administered 1080

Dose levels have been standardised to mg pure 1080 kg^{-1}. FRNP, Fitzgerald River National Park. Lake Magenta, Anderson Lake, and the FRNP are in the same general area

Species	Locality	Dose (mg 1080 kg^{-1})											Lowest dose causing 'death' (mg kg^{-1})[A]	Estimated LD_{50} (mg kg^{-1})[B]
		1.01–2.00	2.01–3.00	3.01–4.00	4.01–5.00	5.01–8.00	8.01–12.00	12.01–15.0	15.01–20.00	20.01–25.00	25.01–30.00	30.01–35.00		
Rodents														
Notomys mitchelli	Lake Magenta					–	0/3	0/3	–	0/5	–	1/2	33.96	50.9
Pseudomys albocinereus	Bernier I.	3/8											1.57	2.4
Pseudomys albocinereus	Bungalbin Hill	0/5	0/2										>3.00	
Pseudomys albocinereus	FRNP	–	0/5	–	0/4	0/4	0/4	0/4	–	1/4			21.34	32
Pseudomys albocinereus	Lake Magenta					–	0/1	–	–	0/1	–	0/1[S]	33.96	50.9
Pseudomys fieldi	Bernier I.	0/1	–	0/1	1/2	4/4	4/4						3.95	5.9
Pseudomys occidentalis	Anderson Lake/FRNP	0/4	0/5	–	0/5	0/5	0/5	0/4	–	0/4[S]			21.34	n.a.
Pseudomys occidentalis	Lake Magenta							0/2	–	0/2	–	1/2	33.96	50.9
Pseudomys shortridgei	FRNP	0/2	0/1	–	0/2	0/2	0/2	0/2	–	0/2	0/2		>30.00	n.a.
	Lake Magenta						–	0/4	–	0/4	–	1/4	33.96	50.9
Rattus tunneyi	Wyndham	0/1	0/5	1/2	2/2								3.4	5.1
	Rosemary/Enderby Is[C]	0/3	3/8	6/7	–								1.92	2.9
Zyzomys argurus	Fortescue River				–	0/2	0/2[S]						9.96	14.9
Dasyurids														
Dasycercus cristicauda	Shay Gap/Wiluna	0/2	0/2	0/2[S]									3.27	4.9
Parantechinus apicalis	FRNP	0/1	0/1	0/2	–	–	0/1	0/1	–	0/2[S]			23.5	35.3
Phascogale tapoatafa	Manjimup			–	0/4[S]	0/1[S]							4.84	7.3
Sminthopsis griseoventer	Esperance	0/3	1/3	–	1/1								2.82	4.2

[A]Includes the death of individuals and/or where severe signs ([S]) were evident such that death was highly likely at an increased dose level, and dosing was stopped under our AEEC approval. The lowest dose causing death approximates the Approximate Lethal Dose (ALD).

[B]LD_{50}s have been estimated from the ALD using a 1.5 multiplier according to Calver *et al.* (1989*a*).

[C]Modified from Calver *et al.* 1989*b*.

Table 4. LD_{50} values with 95% confidence limits for a variety of rodents from Western Australia administered 1080

1080 amounts are standardised to mg pure 1080 kg^{-1}

Species	Locality	LD_{50}	95% confidence limits
Rattus rattus	Kulikup	1.27	0.75–2.14
Rattus tunneyi	Wyndham	3.37	2.93–3.88
	Rosemary/Enderby Is[A]	2.34	1.99–2.76
Rattus villosissimus[B]	Kununurra	1.33	1.15–1.53
Pseudomys albocinereus	Bernier I.	1.57	1.43–1.73

[A]Modified from Calver *et al.* (1989*a*).
[B]From King (1994).

administration of 0.92 mg 1080 kg^{-1}, were: South Australia (n = 3), 80.7 ± 24.7 μg mL^{-1}; F1 s (n = 5), 18.6 ± 8.7 μg mL^{-1}; and Western Australia (Pine Creek, n = 4), 0.0 ± 4.1 μg mL^{-1}. Although we acknowledge that these sample sizes are small, the Tukey HSD *post hoc* tests (unequal n: Zar 1984) were: PCWA *v.* SA, $P < 0.001$, PCWA *v.* F1, $P = 0.099$; SA *v.* F1, $P < 0.001$. These results provide further indication of the differences in the sensitivity of these rat populations to fluoroacetate.

Other rodents

The tolerance to fluoroacetate of those native rodents that coexist with fluoroacetate-bearing vegetation, particularly in the Fitzgerald River National Park (FRNP) region in southern Western Australia, was high, with ALDs of 21.3–34.0 mg 1080 kg^{-1} (Table 3). The populations of *Pseudomys albocinereus* studied are particularly interesting in that the population from Bernier Island, which has had no known exposure to the toxic plants, was highly sensitive to 1080, with an LD_{50} of 1.57 mg kg^{-1} (Table 4). These mice were considerably more sensitive than their mainland conspecifics in the Fitzgerald River region (LD_{50} 32–51 mg 1080 kg^{-1}: Table 3). *Notomys mitchelli* from the FRNP region were also quite tolerant to 1080. *Rattus tunneyi* from Wyndham (limited possible exposure to fluoroacetate-bearing vegetation) were less sensitive than were conspecifics from Rosemary and Enderby Islands where the toxic plants do not occur, although all three populations were, nevertheless, relatively sensitive to 1080. As the 95% confidence limits do not overlap, this difference is significant at the 5% level (Tables 3, 4). *Zyzomys argurus* from the Fortescue region were also moderate in their tolerance to 1080 (Table 3).

In contrast, and although there was some regional variation, the sensitivity to 1080 of the introduced rodents appears to be relatively high, despite some of the tested populations coexisting with fluoroacetate-bearing vegetation. In particular, *R. rattus* were highly sensitive to fluoroacetate (Tables 4, 5). The LD_{50} for the population from Kulikup, which coexists with several highly toxic species of fluoroacetate-bearing plants, was 1.27 mg 1080 kg^{-1}. The LD_{50} for *Mus domesticus*, which are known to be less sensitive to 1080 than all other introduced rodents (see Discussion; McIlroy 1982*b*), was <13 mg kg^{-1} (Table 5).

Dasyurids

Phascogale tapoatafa was found to be more sensitive to 1080 than expected, with an estimated LD_{50} of ~7 mg 1080 kg^{-1}. The dibbler, *Parantechinus apicalis*, was quite exceptional in its tolerance for a native carnivore, with an estimated LD_{50} of ~35 mg

Table 5. Mortality data (number deaths/number dosed) for introduced rodents from Western Australia administered 1080

Dose levels have been standardised to mg pure 1080 kg^{-1}

Species	Locality	Dose (mg 1080 kg^{-1})									Lowest dose causing death (mg kg^{-1})
		<0.50	0.51–1.00	1.01–2.00	2.01–3.00	3.01–4.00	4.01–5.00	5.01–8.00	8.01–12.00	12.01–15.00	
Rattus rattus	Perth	3/5	2/3	2/2	1/1						0.24
	Dwellingup		2/4	6/7							0.84
	Kulikup	1/3	3/8	2/3	1/3	2/2					0.42
	Barrow I.			2/3							1.89
	Middle I.			2/6			1/6	4/4			1.41
Mus domesticus	Millstream									6/8	13.16
	Yuinmery									1/1	<13.16
	Thevenard I.								2/2		<9.40

1080 kg^{-1} (Table 3). The tolerance of *Dasycercus cristicauda* and *Sminthopsis griseoventer* was relatively low and similar between these two species (Table 3).

Discussion

We acknowledge that the number of individuals used for determining the sensitivity of some of the species during our trials was small. However, in general, low sample sizes have less impact on the ranking of the sensitivity of a given species than does the variability in the response of individual animals to administered 1080. Provided that their response is relatively homogeneous, as few as three individuals per species can be used to rank the sensitivity of populations and/or species (Calver *et al.* 1989*a*, 1989*b*; Martin *et al.* 2002). In some cases, our toxicity data were also supported by the observed changes in plasma citrate concentration in response to administration of 1080. The plasma citrate technique is a well accepted procedure for determining the relative sensitivity of individuals to 1080 (Oliver *et al.* 1979; King *et al.* 1981; Twigg and King 1991). We are therefore confident that our procedures were appropriate for comparing the relative sensitivity of animals to 1080, given the constraints on the number of animals available for some species. The LD_{50} estimates for *Pseudomys albocinereus*, *P. occidentalis*, *P. shortridgei* and *Parantechinus apicalis* given here supersede the values given for these species in Calver *et al.* (1989*a*), as the latter estimates were based on preliminary investigation only, with a small number of animals.

The relatively high level of tolerance to fluoroacetate exhibited by those species that coexist with fluoroacetate-bearing vegetation provides further evidence of the impact that fluoroacetate-bearing vegetation has had on the evolution of the native fauna associated with these plants. With two exceptions, the level of tolerance seen was comparable to that reported previously for animals with evolutionary exposure to fluoroacetate-bearing plants (see Oliver *et al.* 1979; King *et al.* 1981; Twigg and King 1991).

The exceptions were *Phascogale tapoatafa* and *Parantechinus apicalis*. Given that the population of *P. tapoatafa* studied was from an area with several species of *Gastrolobium* (e.g. *G. bilobum*, *G. calycinum*, *G. villosum*, *G. spinosum*), some of which are highly toxic (see Table 1), we expected that the tolerance of *P. tapoatafa* (LD_{50} ~7.3 mg kg^{-1}) would be similar to that of *Phascogale calura* (LD_{50} 16.5 mg kg^{-1}: Twigg and King 1991). *P. calura* is endemic to Western Australia and coexists with highly toxic *G. parviflorum*, *G. microcarpum*, *G. calycinum* and *G. spinosum* (Table 1). The lower tolerance of *P. tapoatafa* is even more perplexing in that this species in Western Australia is now believed to be a different species to the 'conspecifics' found in eastern Australia. The Western Australian species would probably be more accurately referred to as *Phascogale* sp. nov., an undescribed species from south-western Australia (Rhind *et al.* 2001). Species endemic to Western Australia with exposure to fluoroacetate-bearing vegetation usually have exceptional tolerances to fluoroacetate (Twigg and King 1991). The foraging behaviour of *P. tapoatafa* suggests that these animals may spend little time foraging at ground level (Scarff *et al.* 1998); nevertheless, they should still encounter insects (their main prey) that have fed upon fluoroacetate-bearing plants (Twigg 1990; Twigg and King 1991).

In contrast to *P. tapoatafta*, *Parantechinus apicalis* exhibited unusually high tolerance to fluoroacetate, and *P. apicalis* from the FRNP region (LD_{50} ~35 mg 1080 kg^{-1}) has by far the greatest tolerance to fluoroacetate of any dasyurid (i.e. native carnivore) studied (McIlroy 1981; King *et al.* 1989; Twigg and King 1991). This suggests that some of its prey must contain reasonably high amounts of fluoroacetate, or that a considerable portion of its

daily food intake contains some fluoroacetate. Further support for this notion is suggested by the relatively high sensitivity of dasyurids from outside the range of the toxic plants (Table 3; McIlroy 1981; King *et al.* 1989; Twigg and King 1991). Differences in their dietary preferences may also contribute to the toxicity differential observed in those dasyurid species that coexist with the toxic plants (e.g. *P. apicalis* and *P. calura v. P. tapoatafa*, *Antechinus flavipes* (LD_{50} ~12 mg 1080 kg^{-1}) and *Dasyurus geoffroii* (LD_{50} ~7 mg 1080 kg^{-1}): King *et al.* 1989; Twigg and King 1991). However, both unadapted dasyurids and bandicoots without any known exposure to fluoroacetate-bearing vegetation have an innate 'tolerance' to fluoroacetate such that their relative sensitivity is less than that of similar-sized, unadapted eutherians (McIlroy 1981; King *et al.* 1989; Twigg *et al.* 1990). This 'tolerance' is believed to result from differences in the metabolic rates between these two mammalian groups (marsupials *v.* eutherians). The reduced metabolic rate of the marsupials probably results in a reduced rate of conversion of fluoroacetate to fluorocitrate (the ultimate toxin) within the mitochondria, enabling more of the ingested fluoroacetate to be detoxified in the liver before the toxic effects can be induced (Twigg and King 1991).

Given that most native rodents in Australia include some seeds in their diet (Watts and Aslin 1981), it is not surprising that they appear to ingest some fluoroacetate with their food where populations coexist with fluoroacetate-bearing vegetation. The relatively high levels of tolerance seen in such species and/or populations (Tables 2, 3; Twigg and King 1991) reflect this exposure.

Rattus fuscipes

Rattus fuscipes mainly feeds on the seeds and leaves of a variety of plant species (Wheeler 1970). However, the seeds of *G. bilobum* can contain up to 6000 mg of fluoroacetate per kilogram of seed (Hall 1972; Twigg and King 1991), and the young leaves of many species also contain significant amounts of fluoroacetate (Table 1; Twigg *et al.* 1996). Animals that feed on this toxic plant material would therefore need the appropriate biochemical mechanisms to enable them to deal with the relatively high amounts of fluoroacetate likely to be ingested. Among other things, the development of such mechanisms will be influenced by the level of exposure to the toxic plants (i.e. to the selective 'agent').

The effect of the habitat on the selection for fluoroacetate tolerance is best illustrated by comparing the sensitivity to fluoroacetate of the various populations of *R. fuscipes*. Populations from eastern Australia (Canberra: McIlroy 1982*b*) and South Australia are not exposed to the toxic plants and were found to be highly sensitive to fluoroacetate (Table 2). The tolerance of island populations of *R. fuscipes* from Western Australia that have not been exposed to the toxic vegetation is also low (except for Michaelmas Island – see below), and is similar to that of unadapted populations from eastern Australia. Populations from the Western Australian mainland, which coexist with fluoroacetate-bearing vegetation, however, have moderate to high levels of fluoroacetate tolerance. When the tolerances of these populations are loosely grouped according to the locality of each population, then adjacent populations are reasonably similar in their tolerance. These groups are: Cape Arid, Mt Ragged and Mondrain Island in the south-east of Western Australia, Hellfire Bay and Cape Le Grand near Esperance, the Albany mainland, Michaelmas Island and Denmark populations in the south, the Pine Creek population in the south-west, and the Greenhead population on the central coast. The heterogeneity is least in those populations that have had a direct association with the fluoroacetate-bearing plants (Table 2). Although the Greenhead and Michaelmas Island populations are outside the known distribution of the fluoroacetate-bearing vegetation, the nearby *R. fuscipes* populations coexist with the toxic

plants. Thus it appears, and it has been argued (Oliver *et al.* 1979; Mead *et al.* 1985; Twigg and King 1991), that ancestral gene flow has occurred between the Greenhead and Michaelmas Island populations and the other nearby rat populations with exposure to the toxic plants; hence the mid-range level of tolerance in the Greenhead and Michaelmas Island rats. The Mondrain Island population is of particular interest, however. These rats coexist with *G. bilobum*, one of the highly toxic fluoroacetate-producing plants (Table 1, Appendix). The extremely high tolerance of these rats (~80 mg 1080 kg^{-1}: Table 2) reflects the intense selection pressures that may be evoked when food choices for island populations become limited. These findings also provide further support for the suggestion that *R. fuscipes* radiated from eastern to western Australia (Oliver *et al.* 1979; Mead *et al.* 1985).

The sensitivity to fluoroacetate of the F1 generation for the SA/PCWA *R. fuscipes* cross was mid-range between those of the sensitive and tolerant parental conspecifics. This suggests that at least two different genes or alleles are likely to be involved in the development of tolerance to fluoroacetate in these rats. The regulation of these genes may be by a single gene or, more likely, by the multi-control of two or more codominant genes (multiples of two). Homozygous alleles would lead to either tolerant or sensitive individuals depending on parentage, and offspring, that are heterozygous for this trait, would be mid-range in their sensitivity (as seen in our F1s). However, the F1 × F1 backcross would be required to provide further insight into how fluoroacetate resistance is inherited. For example, it is possible that selection pressure could disfavour a dominant gene if it expresses an adverse phenotype, or there may be limited inhibition by a dominant 'suppressor' gene inherited from 'sensitive' individuals, or the 'fluoroacetate-tolerance' gene(s) may be dominant.

Various animal phyla, with past or present exposure to fluoroacetate-bearing vegetation, exhibit considerable and varying degrees of tolerance to fluoroacetate, and this includes insects, reptiles, mammals and birds (Twigg and King 1991). This provides further support for the notion that the development of tolerance to fluoroacetate (i.e. the impact of fluoroacetate-bearing plants on animal populations) is an important selection pressure on the genome of those populations/species with evolutionary exposure to these toxic plants. An indication of the importance of this selection pressure on the overall gene pool of Australian animals can be seen by the high level of tolerance retained by some island populations of several native Australian species. In such cases, the tolerance remains high, and is similar to that of the exposed mainland conspecifics, even though the island populations have been isolated from the selection pressure for 7000–10000 years (Twigg and King 1991). It is less likely that tolerance to fluoroacetate would persist in animal populations no longer exposed to the toxic plants if the genes resulting from the original selection pressure, and which ultimately maintain this trait, were recessive. However, these conclusions are provisional and, as stated above, there are a number of possibilities as to how this trait is inherited. It is possible that the current level of expression of the 'tolerance' genes in populations exposed to the toxic plants may result from their phenotypic interaction with the environment rather than the ongoing effects associated with a particular genotype *per se*. Further investigation is therefore required to clarify the influence and importance of such factors. However, any selection for the development of tolerance to a toxin such as fluoroacetate will be a 'passive' process dependent on the characteristics of a particular genome, its degree of homozygosity, and its plasticity or ability to undergo evolutionary change. The level of tolerance will also depend on dietary and habitat preferences of each species, and the extent of their exposure to the fluoroacetate-producing plants (Oliver *et al.* 1979; King *et al.* 1981; Twigg and King 1991).

Other rodents

Notomys mitchelli from the FRNP region (LD_{50} ~51 mg 1080 kg^{-1}) coexist with the fluoroacetate-bearing vegetation and this population is more tolerant of fluoroacetate than are conspecifics from the pastoral region of Western Australia. Two pastoral populations have been studied: one from Yuinmery (LD_{50} 28.2 mg pure 1080 kg^{-1}) which may have had limited exposure to the toxic plants, the other from Officer Basin, Kalgoorlie (LD_{50} 14.1 mg pure 1080 kg^{-1}) which is outside the known range of the fluoroacetate-bearing vegetation (LD_{50} estimated from Calver *et al.* 1989*a*). The tolerance of the Officer Basin population is similar to that of other non-adapted populations from South Australia (LD_{50} ~19.0 mg pure 1080 kg^{-1}: McIlroy 1982*b*).

Populations of *Pseudomys* from the FRNP were also highly tolerant to fluoroacetate, with estimated LD_{50}s ranging from 32 mg 1080 kg^{-1} (*P. albocinereus*) to 51 mg 1080 kg^{-1} (*P. shortridgei*) (Table 3). In contrast, *P. albocinereus* from Bernier Island, which is not exposed to fluoroacetate-bearing plants, was highly sensitive to fluoroacetate (LD_{50} 1.57 mg kg^{-1}: Tables 3 and 4). Again, those species outside the range of the toxic plants are reasonably sensitive to fluoroacetate (e.g. *P. albocinereus*, *P. fieldi* from Bernier Island: Table 3; *P. higginsi* from Tasmania, LD_{50} 8.8 mg pure 1080 kg^{-1}: McIlroy 1982*b*). Other *Pseudomys* species with limited exposure, or possible gene flow from exposed ancestral populations, are mid-range in their tolerance (e.g. *P. nanus* – Arnhem Land, LD_{50} 14.5 mg pure 1080 kg^{-1}: McIlroy 1982*b*; *P. nanus* – east Kimberley region, Western Australia, LD_{50} ~9.5 mg kg^{-1}: Martin and Twigg 2002). In contrast, *Rattus villosissimus* from the east Kimberley are highly sensitive to fluoroacetate (Table 4; King 1994). However, the 'old endemics' (subfamily Hydromyinae), such as *Pseudomys*, have been present in Australia for much longer than the 'new endemics' (subfamily Murinae), such as *Rattus* (Watts and Aslin 1981), and this may partially explain the differences in the fluoroacetate-tolerance of these rodents. Although the differences in the tolerance of these subfamilies of rodents do not appear to be correlated with differences in their diet, metabolism or ecology (McIlroy 1982*b*), it is possible that past 'bottle-necks' during times of abiotic stress may have increased the need for these animals to consume plants containing fluoroacetate.

The common rock rat, *Z. argurus*, from the Fortescue River region was less sensitive to fluoroacetate than are populations of these rats from Enderby and Rosemary Islands (LD_{50} values 14.9 and 4.0–5.1 mg pure 1080 kg^{-1}, respectively: Table 3; Calver *et al.* 1989*a*, 1989*b*). The corresponding lowest doses causing death were 9.96 and 4.42 mg 1080 kg^{-1}. The island populations are not exposed to fluoroacetate-bearing vegetation, and their level of tolerance suggests that there has been limited/little gene flow from any tolerant ancestral populations on the mainland. Although the level of exposure of the Fortescue population is unclear, they are likely to have had limited exposure to the toxic plants, either directly or through gene flow from exposed ancestral populations. Fluoroacetate-bearing plants (*G. grandiflorum*) occur in the Fortescue botanical district but not in the Dampier district (i.e. Enderby and Rosemary Islands (Dampier Archipelago and adjacent mainland): Aplin 1971). *Rattus tunneyi* from Wyndham, which may have had limited exposure to fluoroacetate-bearing vegetation (*G. grandiflorum* occurs in the nearby Hann botanical district: Aplin 1971), was less sensitive to fluoroacetate than are populations of these rats from Enderby and Rosemary Islands (LD_{50} ~5.1 *v.* 2.9 mg 1080 kg^{-1}: Table 3). Whether this difference results from differing exposures to the toxic plants is unknown.

The sensitivity of other populations of *Rattus* without exposure to the toxic plants ranges from 0.74 to 1.68 mg pure 1080 kg^{-1} (McIlroy 1982*b*). *R. rattus* from Kulikup (Table 4) was

within this range, even though this population occurs in an area with several highly toxic species of *Gastrolobium*. However, most of the introduced rats are commensal in habit, and are not usually found in large numbers away from human settlements (Watts and Aslin 1981). This behaviour would limit their potential exposure to fluoroacetate and hence they would not be expected to develop a tolerance to this toxin. *R. rattus* from Perth and Dwellingup were also from areas with fluoroacetate-bearing vegetation, but the sensitivity of these rats appears no different from that of unexposed rats in eastern Australia. Irrespective of their potential exposure to fluoroacetate-bearing vegetation, house mice (*M. domesticus*) are known to be less sensitive to fluoroacetate (1080) than are other unadapted rodents [LD_{50} values range from 8.2 (*M. domesticus*: McIlroy 1982*b*) to 12.8 (*M. musculus*: Emlen and Strecker 1951) mg pure 1080 kg^{-1}]. For reasons yet to be understood, house mice seem to be more tolerant of a range of chemicals than are most other commensal rodents (Hone and Mulligan 1982). Although the results are preliminary, the sensitivity to fluoroacetate of the three mouse populations we examined suggests that sensitivity of house mice in Western Australia appears to be similar to that reported elsewhere in Australia. However, we are yet to determine the sensitivity of this species from areas containing the highly toxic species of *Gastrolobium*.

It has been recently demonstrated that free-ranging rabbit (*Oryctolagus cuniculus*) populations with a long and intense history of exposure to 1080 baits used for routine rabbit-control programs are becoming significantly ($P < 0.05$) less sensitive to 1080 (LD_{50} has increased ~2.5-fold: Twigg *et al.* 2002). The selection for tolerance to fluoroacetate has also been demonstrated in the laboratory in house flies (*Musca domestica*: Tahori 1963) and in *Rattus norvegicus* (Howard *et al.* 1973). Fluoroacetate tolerance increased 7-fold over 25 generations in the flies, and by 1.8-fold over 5 generations in the rats. This suggests that mechanisms exist for the potential development of tolerance in species exotic to Australia, but there is no evidence that this has occurred in introduced rodents that coexist with naturally occurring fluoroacetate. These rodents may be unable to eat the fluoroacetate-producing plants, their commensal habitat may limit their exposure to the toxic plants, insufficient time may have elapsed for any enhanced tolerance to become obvious (an unlikely scenario – see above), or they may fail to recognise these plants as food. A number of native species are able to detect fluoroacetate in their food (Sinclair and Bird 1984; Mead *et al.* 1985; Calver *et al.* 1989*a*; Twigg and King 1991). For example, fluoroacetate-bearing plants comprise only ~25% of the diet of free-ranging western grey kangaroos (*M. fuliginosus*) in southern Western Australia, and these kangaroos also consume more of the less toxic species (Mead *et al.* 1985). Individuals of *Z. argurus*, *Pseudomys hermannsbergensis*, *R. rattus* and *M. domesticus* all reduced their food consumption significantly ($P < 0.01$) in the laboratory once 1080 was included in their food (Calver *et al.* 1989*a*).

Our current data further demonstrate the target-specificity of pest-control programs that utilise 1080 in areas where animals have enhanced tolerance to 1080. However, it is important to realise that 1080 can still be used effectively and safely in pest-control programs outside these areas, provided that a common-sense approach is used (Saunders *et al.* 1995; Williams *et al.* 1995; Martin *et al.* 2002). Furthermore, the theoretical risks to non-target species during 1080-based pest-control programs, as determined by laboratory-based data (i.e. sensitivities only), rarely equate to a real hazard to native wildlife in the field (Calver *et al.* 1989*a*; King 1989; Morris *et al.* 1995; Martin *et al.* 2002). The actual field risk potentially faced by non-target species will depend on the sensitivity of the non-target animals to the poison used (e.g. 1080), their size relative to that of the

target species, the toxic loadings of the baits used, the location of the toxin within the bait, which part of the bait is eaten (edge versus centre), the rate at which individuals encounter baits, and whether sufficient bait is consumed for adverse effects to occur. We recognise that these factors will vary for different species and individuals. However, we advocate that any potential impacts of any pest-control program on non-target species should be assessed at the population level for the species of concern (Twigg and King 1991; Martin and Twigg 2002; Martin *et al.* 2002).

Conclusions

Our findings provide further evidence of the evolutionary impact of highly toxic fluoroacetate-bearing vegetation on the genetic composition of indigenous animals that coexist with it . The degree to which this tolerance is developed in individual species and/or populations depends on the dietary and habitat preferences of these animals, the extent to which the toxic plants occur in their environment, and the ability of their genome to undergo evolutionary change. The enhanced tolerance of these adapted animals, and the reduced sensitivity (i.e. innate 'tolerance') of some unadapted animals such as dasyurids and bandicoots, together with appropriate baiting practices (e.g. type of bait, bait placement, timing, etc.: Saunders *et al.* 1995; Williams *et al.* 1995), further enhance the target-specificity of 1080 baiting programs in Australia.

At present, there is limited information on the sensitivity to fluoroacetate of animals indigenous to the other continents where plants produce significant amounts of fluoroacetate. In south-western Africa, the LD_{50} values for two species of antelopes (*Taurotragus oryx* and *Tragelaphus strepsiceros*) that coexist with toxic species of *Dichapetalum* are ~5–8 mg fluoroacetate kg^{-1} (Basson *et al.* 1982). Spider monkeys (*Ateles geoffroyi*) and Virginia opossums (*Didelphis marsupialis*), which often coexist with *Palicourea marcgravii* in South America, have LD_{50} valuesof 15 (Chenoweth and Gilman 1946) and 60 mg 1080 kg^{-1} (cited in Atzert 1971), respectively. These sensitivities are considerably less than those of most non-adapted mammals ($LD_{50} < 2$ mg 1080 kg^{-1}: Atzert 1971). Thus, it appears that tolerance to fluoroacetate has evolved on all three continents where some native plants contain significant amounts of this potent toxin. Interestingly, Australia, Africa and South America once formed part of Gondwanaland; so, given the apparent restriction of fluoroacetate-bearing plants to these three continents, it is likely that the development of fluoroacetate tolerance in indigenous animal populations represents a co-evolutionary event that has occurred on all three continents.

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Appendix. Details of the locations for the origin of the experimental animals, and an indication of whether each population coexists with fluoroacetate-bearing vegetation

Nearby ancestral populations have coexisted with this vegetation in some instances. Detailed maps of the distribution of fluoroacetate-bearing vegetation in Australia can be found in Aplin (1971) and Twigg and King (1991). Perth: Includes animals from the greater Perth metropolitan area, with animals mainly collected from Forrestfield and the Murdoch University Veterinary Farm. Hellfire Bay, Cape Le Grand, Cape Arid, Salisbury Island, Mt Ragged, Mondrain Island, and Daw Island are all in the vicinity of the Recherche Archipelago east of Esperance

Location	Latitude	Longitude	Exposure to fluoroacetate-bearing vegetation
Albany	35°00′S	117°52′E	Yes
Anderson Lake/Tambellup	34°02′S	117°38′E	Yes
Barrow Island	20°46′S	115°24′E	No, but on adjacent mainland
Bernier Island	24°52′S	113°08′E	No
Bungalbin Hill, WA	30°24′S	119°38′E	Yes
Canberra	35°17′S	149°13′E	No
Cape Arid	33°45′S	123°30′E	Yes
Cape Le Grand	33°55′S	122°30′E	Yes
Daw Island	33°51′S	124°06′E	No
Denmark	34°58′S	117°21′E	Yes
Dwellingup	32°43′S	116°04′E	Yes
Enderby Island	20°36′S	116°30′E	No
Esperance	33°52′S	121°54′E	Yes
Fitzgerald River National Park	33°45′S	120°10′E	Yes
Fortescue River	21°22′S	116°11′E	No?
Green Head	30°05′S	114°58′E	Not on coastal sand-plain, but nearby inland populations exposed
Hellfire Bay	33°50′S	122°40′E	Yes
Kulikup	33°50′S	116°40′E	Yes
Kununurra	15°47′S	128°44′E	*G. grandiflorum*, low toxicity
Lake Magenta/Ongerup	33°24′S	119°16′E	Yes
Manjimup	34°15′S	116°09′E	Yes
Michaelmas Island	35°03′S	118°02′E	No
Middle Island	21°29′S	115°21′E	No
Millstream	21°30′S	117°15′E	Yes?
Mondrain Island	34°08′S	122°15′E	*G. bilobum*, highly toxic
Perth	31°57′S	115°51′E	Not on coastal sand-plain, but several species on the adjacent escarpment
Pilbara	21°15′S	118°19′E	No
Pine Creek (Manjimup)	34°20′S	116°20′E	Yes
Rosemary Island	20°29′S	116°35′E	No
Salisbury Island	34°22′S	123°33′E	No
Shay Gap (Wiluna)	20°30′S	120°10′E	No
Thevenard Island	21°28′S	115°00′E	No
Wiluna (Wanjarri Nature Reserve)	27°23′S	120°45′E	No
Wyndham	15°28′S	128°06′E	*G. grandiflorum*, low toxicity
Yuinmery	28°34′S	119°01′E	Yes, but limited

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