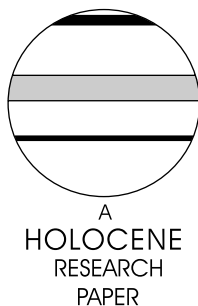


Carbon isotope evidence for an abrupt reduction in grasses coincident with European settlement of Lake Eyre, South Australia

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Abstract: Stable carbon isotopes in emu eggshell (EES) reflect emu diets and consequently the vegetation available for food sources. At Lake Eyre, South Australia, isotopic data suggest that there has been a rapid and dramatic change in vegetation at some point over the last 200 years when compared with the rest of the Holocene. The proportion of C₄ plants in emu diets has been reduced by approximately 20% in response to an overall shift in C₄/C₃ biomass at Lake Eyre. Isotopic measurement of the dominant plants at Lake Eyre indicate that the C₄ plants are almost entirely comprised of grasses and some chenopods and the C₃ plants are comprised of the dominant chenopods, shrubs, trees and forbs. We surmise that the ~20% reduction in C₄ plant biomass reflects landscape degradation and loss of C₄ grasses resulting from a combination of effects, including overgrazing by both introduced (e.g., sheep, cattle and rabbits) and native (e.g., kangaroos) animals, increasing drought and a change in fire regime beginning in the late 1890's. The magnitude of vegetation change that occurred in the last 200 years is as great as that which occurred during the last glacial maximum (~21 000 years ago), and provides the first evidence for major environmental change at Lake Eyre soon after Europeans settled the arid zone.

Key words: Australia, European settlement, environmental change, carbon isotopes, emu, eggshell, plants, grasses, historical change.

Introduction

Vegetation changes related to the most recent migration of humans into Australia (i.e., European settlement beginning over 200 years ago in AD 1788 (summarized in Flannery, 1994))

have been documented in the semi-arid regions of eastern Australia for the last century (summarized by Noble, 1997). For example, a decrease in perennial grass biomass resulting from the introduction of grazing animals (e.g., sheep and cattle) is thought to have led to a decreased fire frequency and a subsequent rise in woody shrubs in semi-arid western New South Wales (Harrington *et al.*, 1979; Duyker, 1983; Hodgkinson and Harrington, 1985; Noble and Grice, 2002). Isotopic evidence corroborating the aforementioned trends is relatively

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scant. While a significant decrease in C_4 grass biomass in the middle part of the twentieth century is measured in sheep faeces from a shearing shed in northern New South Wales, isotopic results on sheep faeces from a neighbouring shearing shed in southwestern Queensland suggest minimal C_4 grass uptake and biomass change over the same time period (Witt *et al.*, 1996; Witt, 2002). These and other studies illustrate the dearth of consistent and reliable evidence for short-term (century scale) vegetation change (Clark, 1990), particularly in the arid zone (reviewed by Lunt, 2002) and near Lake Eyre, South Australia.

In the aeolian landscapes of the arid and semi-arid zones of central Australia, the most abundant and best-preserved biogenic remains are eggshells of the large flightless birds, *Dromaius novaehollandiae* (emu) and the extinct *Genyornis newtoni*. Because eggshells can be dated directly by AMS ^{14}C and/or Amino Acid Racemization (AAR) (Brooks *et al.*, 1990; Miller *et al.*, 2000), and their carbon is derived from respiration of food products, these materials offer an opportunity to monitor vegetation change through time. There is a continuous record of emu eggshell deposition for the last ~200 000 years at Lake Eyre making it possible to use the same palaeovegetation proxy to compare historic and geologic records of environmental change. Here, we use stable carbon isotopes in emu eggshell (EES) to reconstruct emu diets and to evaluate changes in vegetation at Lake Eyre, South Australia, both prior to and after the arrival of the Europeans settlers.

Background

Stable isotopes in plants and animals

Australian plants utilize either the C_3 (Calvin) or the C_4 (Hatch-Slack) photosynthetic pathways (Hattersley, 1983; Takeda *et al.*, 1985; Nicholls, 1991). These pathways differ in their ability to fractionate CO_2 during synthesis of plant carbohydrate, which results in characteristic stable carbon isotope ($\delta^{13}C$) values of the plant tissue (reviewed in Farquhar *et al.*, 1989; Fogel and Cifuentes, 1993) (All isotopic data are presented in delta rotation, or parts per thousand deviation from the vienna PeeDee Belemnite (VPDB) standard, where: $\delta^{13}C = \{[(^{13}C/^{12}C)_{\text{sample}} / (^{13}C/^{12}C)_{\text{VPDB}}] - 1\} \times 1000$). The average $\delta^{13}C$ value of C_3 plant tissue approximates -27‰ (with a range of 12‰), and the average $\delta^{13}C$ value of C_4 plant tissue approximates -13‰ (with a range of 10‰) (O'Leary, 1988; Ehleringer, 1991). The range in $\delta^{13}C$ values of C_3 and C_4 plants can be attributed to differences in the $\delta^{13}C$ values of local atmospheric CO_2 , available moisture, light intensity and edaphic properties (Farquhar *et al.*, 1989; Tieszen, 1991; Lajtha and Marshall, 1994).

The primary environmental controls on C_4/C_3 plant distributions are growth season temperature and light intensity (reviewed in Sage *et al.*, 1999). C_4 plants are adapted to warm growing seasons with moderate to high light intensities, and include most tropical and warm-temperate grasses and some sedges. In Australia they typically grow where precipitation has a summer dominance, such as the monsoon-dominated north and central regions. C_3 plants include those grasses adapted to cool-temperate climates and most trees and shrubs. In Australia, there is an increase in C_4 grass and sedge abundance with decreasing latitude (Hattersley, 1983; Takeda *et al.*, 1985), in response to the increased summer monsoonal influence to the north.

Secondary environmental controls on C_4/C_3 plant distributions are summarized in Sage *et al.* (1999). These include (1) other elements of climate (e.g., precipitation variability and seasonal drought), (2) soil characteristics (e.g., nutrient avail-

ability, salinity and texture), (3) biotic disturbances (e.g., grazing pressures, disease), and (4) frequency and intensity of fire.

The stable isotope composition of animal tissue (e.g., bone, shell, muscle, hair, etc.) reflects the animal's diet, offset by an isotopic fractionation factor unique to each tissue (reviewed in Ostrom and Fry, 1993; Koch *et al.*, 1994; Koch, 1998). For herbivorous birds, it is possible to discern the relative percent of C_3 to C_4 plants consumed by measuring the $\delta^{13}C$ of the eggshell and then using a two end-member mixing model as follows:

$$\delta^{13}C_{\text{eggshell}} - \Delta^{13}C = \Delta^{13}C_{C_3}(X) + \delta^{13}C_{C_4}(1 - X) \quad (1)$$

where $\Delta^{13}C$ is a fractionation factor and is equal to $\delta^{13}C_{\text{eggshell}} - \delta^{13}C_{\text{diet}}$; $\delta^{13}C_{C_3}$ is the average isotopic composition of C_3 plants; X is the proportion of C_3 plants in diet; $\delta^{13}C_{C_4}$ is the average isotopic composition of C_4 plants; and $(1 - X)$ is the proportion of C_4 plants in the diet (von Schirnding *et al.*, 1982; Johnson *et al.*, 1998, 1999). Fractionation factors are typically measured under controlled settings with captive-raised animals (e.g., zoos, farms, laboratories) where the isotopic composition of the diet and the resultant animal tissue can be measured (DeNiro and Epstein, 1978; von Schirnding *et al.*, 1982; Hobson, 1995).

Various components of the avian eggshell can be used for isotopic analysis, each of which has diagnostic fractionation factors. The two major components include the inorganic, crystalline or carbonate fraction (predominantly calcitic), and the organic fraction (predominantly proteinaceous) (Silyn-Roberts and Sharp, 1986; Burley and Vadehra, 1989). Both fractions are generally well preserved through geologic time; the organic fraction is sequestered within the calcite crystals (Miller *et al.*, 2000), and the inorganic fraction undergoes minimal recrystallization and exchange with the environment because calcite is the stable polymorph of $CaCO_3$. The inorganic fraction is presented in this study.

Emus obtain the bulk of their dietary carbon from vegetation (Davies, 1978; Dawson *et al.*, 1984). The egg-laying season occurs during the winter months (July–September) and lasts a few weeks, where eggs are laid every 2–3 days (Coddington, 1992; Blache *et al.*, 1997; Blache and Martin, 1999). Eggshell carbonate reflects the average isotopic composition of the female bird's diet over the preceding 3–5 days (Hobson, 1995). Thus, the isotopic composition of EES carbonate represents a dietary signal integrated over 3–5 days during the winter months.

Lake Eyre

The flora of the Lake Eyre region is dominated by the families of Chenopodiaceae (including saltbushes, bluebushes, bindyis), Asteraceae (including daisies) and Poaceae (grasses) (Badman *et al.*, 1991). Mimosaceae (including *Acacia* spp.) and additional forbs and herbaceous plants are also present in the Lake Eyre region. In response mainly to edaphic factors, chenopods dominate south of Lake Eyre, and grasses become increasingly abundant east and north of the lake (Badman *et al.*, 1991) where dunefields are the dominant landforms.

The Lake Eyre region is in the arid zone. Precipitation is less than 175 mm/yr, highly variable and may occur at any time of the year, although slightly more precipitation falls during the summer months (Gentilli, 1971; Tapper and Hurry, 1993; Bevan of meteorology, Australian commonwealth climate averages, eved 18 January 2004 from http://www.bom.gov.au/climate/average/tables/cw_017031.shtml). Local pastoralists have observed that winter rains seem to favour the growth of daisies and other herbaceous plants, whereas summer rains

favour the growth of grasses (Malcolm Mitchell, personal communication, 1995). Because emus lay their eggs in winter, their diet is naturally biased towards C_3 vegetation.

Objectives

The main goal of the research was to evaluate changes in relative amounts of C_4 and C_3 vegetation change at Lake Eyre, South Australia, over the last 200 years. In order to achieve this goal, we met the following objectives:

- 1) to determine the carbon isotope fractionation factor for emu eggshell, $\Delta^{13}C$, where $\Delta^{13}C = \delta^{13}C_{\text{eggshell}} - \delta^{13}C_{\text{diet}}$;
- 2) to perform an isotopic survey of the dominant plants at Lake Eyre;
- 3) to compare the modern isotopic data from Lake Eyre emu eggshell with those from the rest of the Holocene (during the relatively stable climate mode of the latest interglacial) to evaluate whether emu diets, and consequently vegetation, had changed measurably since European pastoralists settled the region.

Methods

Sample collections

The $\Delta^{13}C$ values were determined for the inorganic and organic fractions of multiple EES collected from two different farms in Idaho, between 1995 and 1998. These animals were fed primarily from commercially produced ratite food; ambient vegetation made up a small amount of the emu diet.

The dominant plants at Lake Eyre were sampled from areas around Madigan Gulf and Lake Eyre North (Figure 1) in June 1994, and in April 1997. Nine modern emu eggshell samples, all less than 30 years old, were collected from a variety of nests and private collections within 50 km (i.e., maximum range of emus during the egg laying season) of Madigan Gulf, Lake Eyre. A total of 101 emu eggshell samples greater than 200 years old were collected from sediments in Madigan Gulf and the North Harbor region of Lake Eyre (Figure 1). Sedimentary deposits from which eggshell were collected include (1) the playa-marginal aeolian units dominated by beach materials associated with regressive shorelines and components from the deflated playa floor and (2) the longitudinal dunes east of the lake (Magee *et al.*, 1995; Magee and Miller, 1998).

Isotopic analysis

EES samples, emu diets and Australian plants were prepared and analysed for isotopic composition as presented in Johnson *et al.* (1998, 1999). The carbon isotope composition of the inorganic fraction of the EES was measured at the Research School of Earth Sciences, Australian National University, using a Finnigan MAT 251 stable isotope ratio mass spectrometer (IRMS) interfaced to a Kiel carbonate device. The total organic fraction of modern EES samples and emu food was analysed in the School of Oceanography, University of Washington using a Carlo Erba elemental analyser (EA) coupled to a Finnigan Delta Plus IRMS via a combustion interface. The Australian plants were analysed at the Geophysical Laboratory, Carnegie Institution of Washington on a Finnigan MAT 252. The $\delta^{13}C$ values of replicate runs of the same plant samples were within the analytical error of the procedure ($\pm 0.2\%$). Interlaboratory comparisons were run regularly between the isotope facilities employed for this study and yielded $\delta^{13}C$ values within 0.3‰.

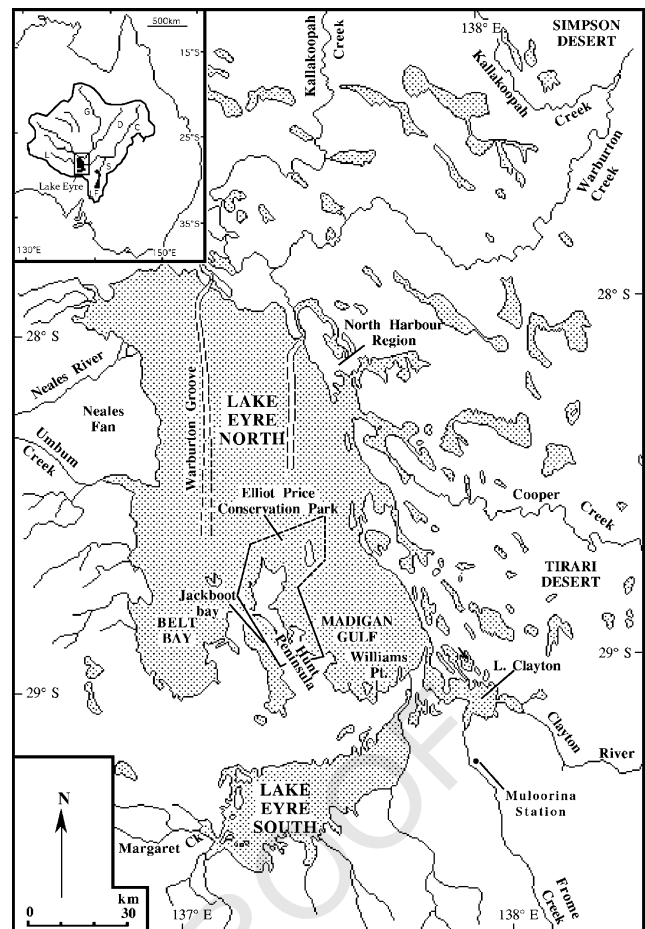


Figure 1 Map of Lake Eyre, South Australia, in the context of the Lake Eyre Basin (see inset), where the shaded regions represent playa lake floors. Emu eggshell samples were collected for isotopic analysis from southern and eastern sites around Lake Eyre North, including Madigan Gulf (Hunt Peninsula and William's Point) and the North Harbor region. Modified from Magee and Miller (1998)

Results

Chronology

AMS radiocarbon dates on EES samples younger than 20 000 years were converted to calendar years (Cal. Yr) using CALIB 4.1, Beta 1 (Stuiver *et al.*, 1998). All EES were dated independently using amino acid racemization (AAR) of D-alloisoleucine to L-isoleucine (see reviews on AAR in Johnson and Miller, 1997; Miller *et al.*, 2000). The calibration curve for AAR in EES at Lake Eyre was determined from 90 paired AAR and calibrated AMS ^{14}C dates on EES, eight luminescence dates on aeolian sand from which emu eggshell was extracted and five thermal ionization mass spectrometry (TIMS) uranium series dates on *Genyornis* eggshell (Miller *et al.*, 1999). For this paper 37 new AMS radiocarbon dates have been obtained and have been integrated into the age model (Table 1).

Fractionation factors

The $\Delta^{13}C$ for the inorganic and the total organic fractions of EES at each site was determined by subtracting the average $\delta^{13}C$ value of the emu diet from that of the average $\delta^{13}C$ value of the eggshell component (Table 2). The average ($\pm 1\sigma$) $\Delta^{13}C$ for the inorganic fraction of EES from the ID sites was $11.6 \pm 1.4\%$. The $\Delta^{13}C$ for the total organic fraction of EES from the ID sites was $0.8 \pm 0.9\%$. Both fractions of the EES were

Table 1 Radiocarbon results and calibrated dates for emu eggshell samples

CU ID*	¹⁴ C age	¹⁴ C std	¹⁴ C lab. ID	Calibrated dates
6877 C	11875	115	AA-10233	11852 cal. BC
6878 A	10070	90	AA-10234	9657 cal. BC
6914 C	9520	80	AA-10239	8929 cal. BC
7117 A	1405	65	AA-12611	cal. AD 653
7118 B	2985	85	AA-12612	1203 cal. BC
7120 A	7525	80	AA-12613	6350 cal. BC
7122 A	1770	60	AA-12616	cal. AD 268
7128 C	6175	75	AA-12617	5118 cal. BC
7130 A	1565	50	AA-12618	cal. AD 502
7130 B	1725	50	AA-13042	cal. AD 319
7190 A	3730	55	AA-13046	2148 cal. BC
7479 A	3585	60	AA-15138	1903 cal. BC
7214 A	11905	90	AA-15141	11875 cal. BC
6914 B	9475	75	AA-15144	8780 cal. BC
7219 E	12680	125	AA-15145	13049 cal. BC
7355 D	8175	70	AA-15408	7202 cal. BC
7511 A	7725	120	AA-15664	6610 cal. BC
7512 A	5600	80	AA-15665	4469 cal. BC
7129 B	4420	75	AA-15668	3023 cal. BC
7452 A	9635	65	AA-16397	8935 cal. BC
7605 A	11850	120	AA-17274	11842 cal. BC
7828 A	1620	50	AA-19012	cal. AD 439
7951 B	12440	90	AA-20893	12832 cal. BC
8233 D	10620	70	AA-22891	10822 cal. BC
8236 A	1145	45	AA-22892	cal. AD 882
8865 B	11750	85	AA-32850	11801 cal. BC
8873 A	350	50	AA-32852	cal. AD 1545
8874 B	320	50	AA-32853	cal. AD 1558
9507 A	1880	40	NSRL-12367	cal. AD 146
8119 A	6010	65	AA-25248	4737 cal. BC
8111 A	7240	55	AA-25249	6111 cal. BC
8000 B	10370	85	AA-20897	10343 cal. BC
9032 B	11320	75	NSRL-12362	11352 cal. BC
8230 C	11810	110	AA-25257	11826 cal. BC
8231 B	12055	75	AA-25254	12125 cal. BC
8971 A	12150	75	NSRL-12616	12246 cal. BC
8980 A	12350	55	NSRL-12617	13026 cal. BC

*University of Colorado laboratory identification number.

enriched in ¹³C relative to the diet, although only slightly for the total organic fraction.

Modern plants

There is a relatively clear division between plant-type and photosynthetic pathway as evidenced by the ^δ¹³C values of the plants (Table 3; Figure 2). All of the grasses sampled utilize the C₄ pathway, and all of the trees and herbs and most shrubs sampled utilize the C₃ pathway. The chenopods are comprised of both C₃ and C₄ plants; however, the C₃ chenopods sampled (*Enchylaena tomentosa* (ruby saltbush) and *Maireana pyramidata* (bluebush)) dominate the total biomass relative to the C₄ chenopods sampled (*Atriplex* sp. (saltbush) and *Halosarcia* sp. (samphire)). *Cyperus laevigatus* (flat-sedge) is a C₄ plant usually associated with bores, and which comprises a relatively small proportion of the total biomass. Thus, in the Lake Eyre region, the C₄ plant component is predominantly represented by grasses, and the C₃ plant component is comprised of trees, herbs and most shrubs.

The average ^δ¹³C value of the C₃ plants at Lake Eyre is $-26.8 \pm 1.8\text{‰}$ ($n = 48$), and for all C₄ plants, including 20 different grasses, is $-13.8 \pm 0.8\text{‰}$ ($n = 23$) (Figure 2). Isotopic variability between plant morphological parts (e.g., leaves, seeds and flowers) is greater for the C₃ plants than for the C₄ grasses for any given year (Table 3).

Table 2 Carbon isotope and C/N values of the inorganic and organic fractions of EES and emu food collected from two emu farms in Idaho

Sample ID/location	Inorganic fraction	Organic fraction	
	^δ ¹³ C	^δ ¹³ C	C/N
<i>Kooskia, ID</i>			
BC 1242 (EES #1)	-9.6	-20.3 ± 0.3 ($n = 2$)	4.1
BC 1243 (EES #2)	-8.9	-19.7 ± 0.1 ($n = 2$)	3.9
BC 1244 (EES #3)	-9.4	-20.0 ± 0.3 ($n = 2$)	3.8
BC 1245 (EES #4)	-10.3	-20.5 ± 0.5 ($n = 2$)	3.9
Avg EES	-9.6 ± 0.6 ($n = 4$)	-20.1 ± 0.4 ($n = 4$)	3.9 ± 0.1 ($n = 4$)
BC 1246 (Emu Food)		-20.2 ± 0.9 ($n = 3$)	22.6 ± 1.4 ($n = 3$)
$\Delta^{13}\text{C}$, Kooskia	10.6	0.1	
<i>Buhl, ID</i>			
BC 1388 (EES #1)	-8.3	-20.2	3.8
BC 1389 (EES #2)	-9.1	-20.1	3.9
BC 1390 (EES #3)	-9.7	-20.2	3.9
Avg EES	-9.0 ± 0.7 ($n = 3$)	-20.2 ± 0.2 ($n = 3$)	3.9 ± 0.0 ($n = 3$)
BC 1391 (Emu Food)		-21.6 ± 0.8 ($n = 2$)	16.5 ± 2.4 ($n = 2$)
$\Delta^{13}\text{C}$, Buhl	12.6	1.4	
Average $\Delta^{13}\text{C}$	11.6 ± 1.4 ($n = 2$)	0.8 ± 0.9 ($n = 2$)	

Replicate runs on individual samples are represented by mean ^δ¹³C values ($\pm 1\sigma$) and the number of analyses performed (n). The final $\Delta^{13}\text{C}$ was determined by averaging the fractionation factors at the two farms.

In C₃ plants, the average ^δ¹³C values of seeds and flowers are $\sim 2\text{‰}$ enriched in ¹³C relative to their corresponding plant leaves; however, there is no significant difference between the isotopic composition of C₄ grass flowers/seeds and C₄ leaves. Because emus selectively feed on the seeds, fruits and flowers of plants (Davies, 1978; Dawson *et al.*, 1984), the isotopic differences between plant tissues may be important in assessing the emu diets between individual years using the mass balance calculations presented in Equation (1).

Isotopic and vegetation trends through the Holocene

We use the isotopic record of EES between 200 and 11 500 years old (hereafter referred to as pre-modern Holocene) as a baseline by which to evaluate whether changes in vegetation have occurred since pastoralists have occupied the Lake Eyre region. This time period encompasses the relatively stable climate state of the current interglacial, and is reflected by consistent carbon isotope values, where the average ^δ¹³C value is $-10.0 \pm 1.7\text{‰}$ ($n = 72$) (Figure 3). This is in contrast to the modern EES samples, where the average ^δ¹³C value is $-13.4 \pm 1.5\text{‰}$ ($n = 9$) (Figure 3). The range in isotopic values for any specific time period is between 4 and 6‰, and captures the interannual variability of foraging behaviour and vegetation in emu diets.

In order to compare isotopic trends spanning the entire Holocene, it is necessary to account for the isotopic depletion of atmospheric CO₂ that has occurred as a result of the accelerated oxidation of fossil fuels. Since the onset of the industrial revolution, atmospheric CO₂ has become depleted in ^δ¹³C by 1 to 1.5‰ relative to the rest of the Holocene (Marino and McElroy, 1991), which should also be reflected in the isotopic composition of EES. Applying an isotopic correction

Table 3 The $\delta^{13}\text{C}$ values of the leaves, flowers and seeds of the dominant plants at Madigan Gulf, Lake Eyre

Genus	Species	Leaves	Flowers	Seeds	Coll. year
Grasses					
<i>Aristida</i>	<i>holathera</i>	-12.9 ± 0.6 ($n = 2$)			1997
<i>Astrelba</i>	<i>pectinata</i>	-13.8	-12.7		1997
<i>Cenchrus</i>	<i>ciliaris</i>	-13.1			1994
<i>Chloris</i>	<i>pectinata</i>	-13.4	-12.8		1997
<i>Dactyloctenium</i>	<i>radulans</i>	-15.4	-13.6		1997
<i>Distichlis</i>	spp.	-14.4			1994
<i>Enneapogon</i>	<i>avenaceus</i>	-14.3	-12.8		1997
<i>Enneapogon</i>	<i>cylindricus</i>	-13.2 ± 0.1 ($n = 2$)			1994
<i>Enneapogon</i>	<i>dielsii</i>	-13.7 ± 0.5 ($n = 2$)	-13.1		1997
<i>Enneapogon</i>	<i>polyphyllus</i>	-13.9 ± 0.1 ($n = 2$)			1994
<i>Eragrostis</i>	<i>setifolia</i>	-14.4	-13.4		1997
<i>Gymnoschoenus</i>	<i>sphaerocephalus</i>	-14.5	-14.0		1997
<i>Iseilema</i>	spp.	-13.3	-12.6		1997
<i>Panicum</i>	<i>decompositum</i>	-13.7	-13.5		1997
<i>Paracfarum</i>	<i>novae-hollandiae</i>	-12.8 ± 0.1 ($n = 2$)			1997
<i>Sporobolus</i>	spp.	-14.3	-13.4		1997
<i>Tragus</i>	<i>australiense</i>	-15.4	-13.7		1997
<i>Trianthema</i>	<i>triquetra</i>	-14.3			1994
<i>Triraphus</i>	<i>mollis</i>	-14.2	-14.0		1997
<i>Zygodloa</i>	<i>paradoxa</i>	-13.4			1997
Trees, shrubs and forbs/Herbs					
<i>Abutilon</i>	<i>malvacaea</i>	-27.6	-24.3		1997
<i>Acacia</i>	<i>aneura</i>	-25.6 ± 1.5 ($n = 4$)			1994
<i>Acacia</i>	<i>estrophiolata</i>	-25.2			1994
<i>Acacia</i>	<i>ligulata</i>	-25.4 ± 1.5 ($n = 5$)	-22.0 ± 0.2 ($n = 2$)	-23.4 ± 0.7 ($n = 2$)	1994
<i>Acacia</i>	<i>murryana</i>	-29.5			1994
<i>Acacia</i>	<i>salicina</i>	-28.4	-28.4		1997
<i>Acacia</i>	spp.	-24.6			1994
<i>Acacia</i>	<i>tetragonophylla</i>	-24.8 ± 0.5 ($n = 3$)	-21.5		1994
<i>Amaranthes</i>	<i>ptilotus</i>	-29.3	-26.1		1997
<i>Brachisome</i>	<i>ciliaris</i>	-28.8			1994
<i>Brachisome</i>	<i>ciliaris</i>	-31.6	-30.3		1997
<i>Callitris</i>	<i>columellaris</i>	-26.1			1994
<i>Calotis</i>	<i>latiuscula</i>	-25.9			1994
<i>Calotis</i>	spp.	-29.0			1994
<i>Chielathes</i>	<i>lasiophylla</i>	-28.9			1994
<i>Citrullus</i>	<i>lanatus</i>	-27.3	-23.9 ± 0.1 ($n = 2$)		1994
<i>Clenolaena</i>	spp.	-28.9			1994
Asteraceae*		-29.0	-22.9		1997
<i>Cyperus</i>	<i>gymnocaulos</i>	-22.8			1994
<i>Cyperus</i>	<i>laevigatus</i>	-12.17			1994
<i>Eremophila</i>	<i>freelingia</i>	-23.5			1994
<i>Eremophila</i>	<i>longifolia</i>	-25.9			1994
<i>Eriocaulan</i>	<i>carscrii</i>	-26.6			1994
<i>Erodium</i>	spp.	-27.4			1994
<i>Eucalyptus</i>	<i>camaldulensis</i>	-26.2 ± 1.9 ($n = 4$)			1994
<i>Frankenia</i>	<i>foliosa</i>		-26.4		1994
<i>Frankenia</i>	spp.		-24.8		1997
Goodeniaceae*		-29.1		-26.5	1997
<i>Hakea</i>	<i>suberea</i>	-26.8	-26.4		1994
<i>Haloragis</i>	spp.			-27.2	1997
<i>Ixiolaena</i>	spp.	-29.5	-23.9		1997
<i>Jasminum</i>	<i>didyrium</i>	-26.1			1994
<i>Lotus</i>	<i>cruentus</i>	-26.4			1997
<i>Lysiana</i>	<i>exocarpi</i>	-27.9 ± 0.7 ($n = 2$)			1994
<i>Nicotiana</i>	<i>velutina</i>	-25.27			1994
<i>Nitraria</i>	<i>billardieri</i>	-25.7			1997
<i>Phragmites</i>	<i>australis</i>	-25.56			1994
<i>Pittosporum</i>	<i>phylliraeoides</i>	-25.68	-25.2 ± 0.1 ($n = 2$)		1994
<i>Psoralea</i>	<i>australasia</i>	-27.8	-24.8		1997
<i>Psoralea</i>	<i>cinera</i>	-25.0	-23.3		1997
<i>Ptilotus</i>	<i>obovatus</i>	-26.8	-24.3		1997
<i>Santalum</i>	<i>lanceolatum</i>	-27.1		-24.9	1997
<i>Senna</i>	<i>artenesioides</i>	-25.5			1997
<i>Senna</i>	<i>artemescriides</i>	-25.6 ± 2.0 ($n = 2$)			1994
<i>Swainsona</i>	<i>bushittii</i>	-27.3 ± 0.7 ($n = 2$)			1997
<i>Vitadinnia</i>	spp.		-27.1		1997

(continued)

Table 3 (continued)

Genus	Species	Leaves	Flowers	Seeds	Coll. year
<i>Wurnbea</i>	spp.	-25.8			1994
Chenopods					
<i>Atriplex</i>	spp.	-12.9			1994
<i>Enchylaena</i>	<i>tomentosa</i>	-25.2			1994
<i>Halosarcia</i>	spp.	-14.8			1994
<i>Marieana</i>	<i>pyramidata</i>	-27.3			1994

Plants were collected in 1994 and 1997 and were identified to the species level as often as possible; however, two samples could only be identified to the Family level (those marked with an *). Average values ($\pm 1\sigma$) are presented when multiple samples of the same species were analysed.

of 1‰ to the modern EES samples (where the corrected values are more enriched in ^{13}C than uncorrected values) allows for comparisons to be made across the entire data set.

The modern corrected EES values are significantly depleted in ^{13}C relative to the pre-modern Holocene EES (unpaired *t*-test; $t = 4.0$, $df = 79$, $p < 0.0001$), where the average $\delta^{13}\text{C}$ value of the corrected modern EES is $-12.4 \pm 1.5\text{‰}$ ($n = 9$). This isotopic shift represents a change in vegetation and emu diets that is more rapid and more significant than any other that occurred during the entire Holocene prior to pastoralist expansion into Lake Eyre.

The relative percent age of C_3 and C_4 vegetation consumed by emus is derived from Equation (1), where the $\Delta^{13}\text{C}$ for EES carbonate is 11.6‰ and the average $\delta^{13}\text{C}$ values of the EES are used. For the pre-modern Holocene calculations, the $\delta^{13}\text{C}$ values of C_4 and C_3 plants are assumed to be -13‰ and -26‰ , respectively, and reflect a pre-industrial atmospheric CO_2 composition that is enriched by 1‰ relative to present and incorporated into the plant tissue. For the modern calculations, the average $\delta^{13}\text{C}$ values of C_4 and C_3 plants are -14 and -27‰ , respectively.

Between 200 and 11 500 years ago, emu diets were consistently comprised of $\sim 65\%$ C_3 plants and $\sim 35\%$ C_4 grasses. During the Holocene, climate was relatively stable, although Lake Eyre carried a shallow permanent lake in the early Holocene whereas it received only intermittent floodings in the late Holocene (Magee and Miller, 1998). These intermittent fillings of Lake Eyre presumably resulted from higher varia-

bility in interannual rainfall associated with the strengthening of the El Niño Southern Oscillation (ENSO) phenomenon during the late Holocene (Rodbell *et al.*, 1999). Nevertheless, emus were able to adjust their diets to these Holocene shifts in climate and provide a relatively stable picture of ambient vegetation.

The pre-modern Holocene results are in contrast to the nine samples collected from the same region within the last 30 years that strongly reflect a dominance of C_3 plant uptake ($\sim 85\%$) and reduction in C_4 grass biomass ($\sim 15\%$). The sample sizes are sufficiently large to conclude that the observed differences in eggshell $\delta^{13}\text{C}$ values represent significant changes in the vegetation consumed by the egg-laying birds between 200 years ago and the present-day relative to the rest of the Holocene.

Discussion

The isotopic shifts that have occurred at Lake Eyre suggest a loss of $\sim 20\%$ of C_4 relative to C_3 plant biomass after pastoralists expanded into Lake Eyre. The dietary shift reflects a change in available food supply to the emus in response to either an effective reduction in C_4 vegetation biomass, or an increase in palatable C_3 vegetation.

Strong evidence exists for expansion of C_3 shrubs following pastoralist settlement of semi-arid western NSW and South Australia in the 1890s (summarized in Noble, 1997). A series of good seasons during the 1870s and early 1880s and the increased use of artesian waters for watering stock in the arid zone increased the numbers of both exotic (e.g., sheep, cattle, rabbits) and indigenous (e.g., kangaroo) animals on the

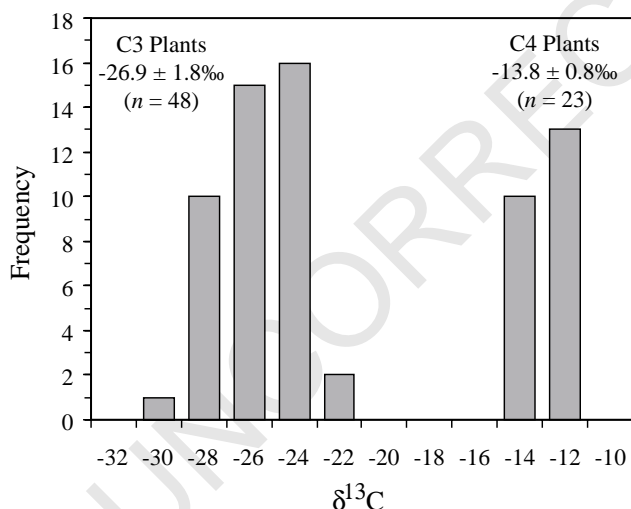


Figure 2 Frequency versus $\delta^{13}\text{C}$ values of dominant plants sampled at Madigan Gulf. One value was plotted for each plant; all $\delta^{13}\text{C}$ values are those of the leaves, except for four C_3 plants, where only the flowers were measured. Averages ($\pm 1\sigma$) were determined for the C_3 plants (trees, shrubs, forbs/herbaceous plants and chenopods) and for the C_4 plants (grasses, flat-sedge and chenopods)

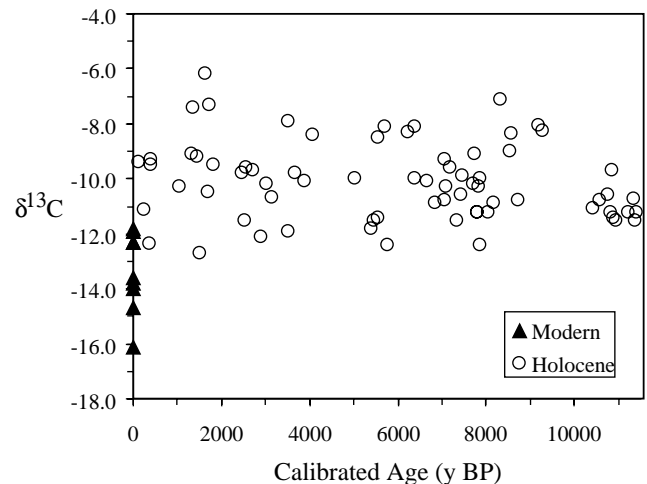


Figure 3 The $\delta^{13}\text{C}$ values of Holocene emu eggshell, Lake Eyre, South Australia. Modern samples represent samples collected over the last 30 years, and Holocene samples represent samples that are between 200 and 11 500 years old

land. In the late 1890s several years of drought following many years of excessive grazing pressure resulted in a near complete loss of palatable vegetation for sheep and cattle. The surface vegetation loss resulted in enhanced soil erosion and decreased fires and, in semi-arid western NSW, an increase in C_3 woody shrubs relative to grasses (Noble, 1997).

We surmise a similar scenario at Lake Eyre, where a combination of overgrazing (by introduced and native animals) and drought reduced the C_4 grass carrying capacity. This, in turn, led to loss of nutrients via increased soil erosion, a decrease in fuel load and consequently fire frequency, and an expansion of shrubs relative to grasses in the region. In the case of the arid zone, C_3 chenopod and woody shrubs expanded relative to C_4 grasses. (C_4 chenopods (e.g., *Atriplex* sp.) make up a small percentage of the total biomass, thus, we attribute the shift in vegetation to a loss of C_4 grasses relative to C_3 chenopods).

It is also possible that the isotope data represent an unchanged C_4 biomass and an increase in C_3 plant consumption over the last 200 years. Perhaps a particularly palatable C_3 species was introduced to Lake Eyre and became a significant component of emu diets, for example. Pending evidence supporting this scenario, and given the land-use history of the area, we favour the following explanation: loss of C_4 grasses relative to C_3 vegetation as a result of a combination of overgrazing, drought and change in fire frequency.

It is important to recognize that the most compelling case for pastoralist alteration of Lake Eyre vegetation does not lie in any one specific mechanism proposed herein. Instead, it is the timing, magnitude and rate of recent isotopic change that implicates European activities as a probable cause for the vegetation change.

The magnitude of the recent change is far greater than any that occurred during the Holocene. Similar conclusions have also been drawn for several sites in southeastern Australia (Dodson and Mooney, 2002). European impact on Australian ecosystems was extensive and far-reaching, leaving no area of the continent untouched.

The recent vegetation change at Lake Eyre approximates that which occurred during the last glacial maximum (LGM) (Johnson *et al.*, 1999), the period of time between 15 000 and 28 000 years ago, when climate was extremely arid (Wasson, 1986; Magee *et al.*, 1995; Croke *et al.*, 1996; Magee and Miller, 1998) and 8–10°C cooler than present (Miller *et al.*, 1997). The rate of vegetation change over the last 200 years is one to two orders of magnitude greater than that of the LGM. It took decades of pastoralist activity to affect the recent change and it took thousands of years of shifting global climate to affect the LGM vegetation change.

Clearly, this recent major shift in the environment has occurred at an unprecedented rate following pastoralist colonization, and has almost certainly had profound impacts on mammalian extinctions and biodiversity, for example. Questions remain as to the long-term impacts of this vegetation change on the dependent fauna and on climate–vegetation feedback mechanisms.

Conclusions

Evidence compiled globally suggests that the Holocene has been characterized by only modest climate variability. Our time series of stable carbon isotope data from emu eggshell indicate that from 11 500 until at least 200 years ago, emu diets were relatively consistent and reflect variable rainfall patterns but no significant trend in climate. However, within the past 200 years

there was a major change in ecosystems in the vicinity of Lake Eyre, which has resulted in a loss of approximately 20% of C_4 grass relative to C_3 plant biomass.

We do not have an adequate time series within the last 200 years to evaluate the exact date of this vegetation conversion. However, the vegetation change is most probably due to the introduction of pastoral stock and/or rabbits or expansion of kangaroos into the region, coupled with periods of drought and a shift in fire regime. Matching detailed historical records of stock introductions and rabbit arrival to a more complete time series of eggshell isotopic analyses covering the same time period might resolve the relative importance of pastoral animals and rabbits in this process.

The conditions of the pastoral leases of the semi-arid and arid zones of Australia have improved significantly over the last 100 years with improved stock carrying–capacity guidelines (summarized in Noble, 1997). The modern emu eggshell isotope data represent vegetation composition of the last 30 years, and consequently may already reflect partial recovery of the vegetation at Lake Eyre. Isotopic analysis of a more complete time series of animals (i.e., emus, rabbits, sheep, cattle) spanning the last 200 years will help determine the extent to which pastoralists affected the arid zone and the degree to which it has recovered over the last 100+ years.

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