DIET, MOBILITY AND SUBSISTENCE-SETTLEMENT SYSTEMS IN THE LATE HOLOCENE LOWER MURRAY RIVER BASIN OF SOUTH AUSTRALIA: TESTING MODELS OF ABORIGINAL SEASONAL MOBILITY AND SEDENTISM WITH ISOTOPIC AND ARCHAEOLOGICAL DATA

F. Donald Pate

1 College of Humanities, Arts and Social Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia

Abstract

Bone collagen stable carbon and nitrogen isotope data for archaeological human remains suggest that the territorial behaviours reported in relation to Tindale’s ethnographic research for the lower stretches of the Murray River of South Australia in the vicinity of the river mouth and adjacent coastal regions can be extended back through the late Holocene. Testing hypotheses regarding the presence of late Holocene semi-sedentary and sedentary subsistence-settlement systems along various regions of the Lower Murray and adjacent coast requires comprehensive archaeological research, including improved chronometric dating for a range of archaeological sites, demonstration of the use of a range of key plant and animal foods, and expansion of stable isotope applications to include strontium and oxygen. This paper provides an overview of the natural environment of the Lower Murray River region of South Australia, including the availability of water and a range of food resources. The importance of foods available in the vicinity of the riverine zone that could have provided reliable dietary sources is emphasised. Such ecological data regarding the abundance and availability of key plant and animal foods are fundamental to improved understandings of hunter-gatherer behavioural variability in the region.
Introduction

Aboriginal subsistence-settlement systems in the ecologically diverse Lower Murray River region of South Australia (SA) would have been influenced significantly by the distribution and abundance of water, flora and fauna (Lawrence 1968; Peterson 1976; Tindale 1981). This paper investigates the interaction of food and water resources available in the region and the exploitation of those resources by past Aboriginal populations. It provides an overview of some of the key plant and animal foods that could potentially allow more sedentary lifeways, including year-round use of base camps.

Previous research has demonstrated that sedentary and semi-sedentary settlements are possible among hunter-gatherers in areas with abundant and reliable water and food resources. Furthermore, in order to increase the reliability of food resources over longer periods of time, hunter-gatherers extended the availability of key foods by employing food preservation, storage, fire management, and technological innovations including fish weirs, nets and holding areas for eels and fish (Bettinger 1982; Builth 2002; Cohen and Armelagos 1984; Fitzhugh and Habu 2002; Gamble 2008; Hiscock 2007; Kelly 1983; Lee and DeVore 1968; Lourandos 1985; Owen 2004; Pate 1997, 1998, 2006; Pate and Owen 2014; Price and Brown 1985; Williams 1987).

The Lower Murray region was one of the most densely populated geographic areas of Australia prior to European colonisation (Clarke 1994; Mulvaney 1969:40; Radcliffe-Brown 1918:230-231; Wilson 2017). On the basis of historical and ethnographic accounts from the Lower Murray region of SA, Clarke (1994:75) reported that ‘Aboriginal descent group territories in this resource rich riverine-coastal zone, being relatively small, reflected a more sedentary life style’ (also see Peterson 1976). However, within these territories seasonal movements of habitation sites occurred in relation to harsh coastal weather and limited food sources associated with the winter months. Some non-coastal groups also practiced seasonal movements from lakes and rivers to nearby sheltered inland areas during winter (Clarke 1994; Tindale 1981).

Archaeologists have employed isotopic analyses of hunter-gatherer skeletal remains from various global regions to
test ethnographic and historical models related to seasonal mobility versus more sedentary behaviours associated with year-round use of base camps. Subsistence-settlement systems based on ethnographic and historical data cannot simply be extended to the archaeological past employing analogies. Variability in hunter-gatherer subsistence-settlement behaviours across space and time must be investigated using archaeological data. In some cases, the isotopic data contradict the ethnographic and historical models and suggest the presence of different behaviours in the past, while in other cases the isotopic data support the long-term persistence of subsistence-settlement systems (cf. Roberts et al. 2013; Sealy and van der Merwe 1986, 1988; Sealy 2006; Tafuri et al. 2017; Walker and DeNiro 1986). Oxygen isotope analyses of shells from archaeological middens and mounds have also been used to demonstrate seasonal or year-round use of coastal sites (Jew et al. 2014).

Bone collagen stable isotope data (Pate and Owen 2014) suggest that the territorial boundaries reported by Tindale (1974) for the Lower Murray and adjacent coastal regions of SA were established by the late Holocene. Stable carbon and nitrogen isotope data for coastal skeletal samples demonstrate a heavy reliance on marine-based foods and limited movement to inland riverine and terrestrial habitats (Pate et al. 2002; Owen 2004). Further research is required in order to determine the extent to which sedentary and semi-sedentary behaviours were associated with hunter-gatherer populations along the upper inland stretches of the Murray River in SA (cf. Clarke 1985a, 1985b, 1994, 1998, 2009, 2015; Hill et al. 2016; Pate 1997, 2006; Littleton 1999; Littleton and Allen 2007; Martin 2006, 2011; Westell and Wood 2014).

Stable isotope data for the inland riverine Swanport and Roonka archaeological populations near Murray Bridge and Blanchetown, SA (Figure 1), respectively, indicate that late Holocene inhabitants focused on C3-based plant an animal food sources associated with the river and adjacent plains and did not include marine foods in their diets (Pate 1998a, 1998b, 2000, 2006). Thus, marine foods from the southern coast were not
being imported to inland riverine regions and people living at Swanport and Roonka did not spend significant amounts of time in southern coastal regions where they would have had access to marine foods. However, the bone collagen stable carbon and nitrogen isotope data do allow for movement of the Swanport and Roonka inhabitants along the inland stretches of the river, as similar C₃-based plant and animal foods would be associated with these regions.

The expansion of stable isotope research to include strontium and oxygen in tooth enamel (Bentley 2006; Budd et al. 2004; Pate 2008a, 2008b) could provide more detailed information regarding restriction of hunter-gatherer movements between various geographic localities and provide data to examine hypotheses regarding semi-sedentism and mobility for both coastal and inland riverine regions. Westell and Wood (2014) and Martin (2006, 2011) argue that earth mound sites along the Lower Murray and Murray Riverine Plain were associated with repeat-use pit ovens for the intensive exploitation of wetland resources for food and fibre. They suggest that the use of reliable root/tuber foods like bulrush (Typha spp.) allowed increased levels of residency and population growth from the mid to late Holocene.

The reliable riverine water sources and diverse foods associated with the Lower Murray and adjacent mallee plain ecosystems, provided the environmental conditions for the potential establishment of long-term residential hunter-gatherer bases associated with logistical mobility to access foods and other resources in the surrounding landscapes (Binford 1980, 1982, 1983; Bettinger 1999; Habu and Fitzhugh 2002).

Pate (2006:238–239) provides an overview of the ethnographic and historical accounts relating to the socioeconomically complex Ngarrindjeri, who were organised into a number of territorial clans. The Ngarrindjeri occupied a large triangular area of coastal and riverine land stretching from just above Murray Bridge in the north to Encounter Bay in the southwest and Kingston in the southeast. This region includes the coastal Coorong, the Murray River mouth, and the Lower Murray River in the vicinity of Swanport (See Bell 1998; Berndt and Berndt 1993; Jenkin 1979; Meyer 1846; Radcliffe-Brown 1918; Salgado 1994; Taplin 1859–79, 1874; Tindale 1974; Pate et al. 2003; Wilson et al. 2012; Wilson 2017).
In addition, ethnographic and historical accounts identify a range of key plant and animal foods that were used in the resource rich Lower Murray region at the time of European contact. Coastal inhabitants had access to marine fish and shellfish, waterfowl and their eggs, marine mammals (seals, sea lions and stranded dolphins and whales), and vegetable foods like berries. Further inland, key food sources included freshwater fish, shellfish, crayfish, yabbies, turtles, waterfowl, bird eggs, possums, rats, bandicoots, wombats, snakes, lizards, bardi (or witchetty) grubs, and bulrush root (*Typha* spp.). Valued meat was obtained from larger mammals such as kangaroos, wallabies and emus (Angus 1847; Berndt and Berndt 1993:80; Clarke 1994, 2009, 2011, 2015; Pate 2006:237–238; Worsnop 1897). The availability of a range of reliable riverine foods would have provided an environment that allowed the potential development of sedentary and semi-sedentary subsistence-settlement systems.

Archaeological research suggests that a majority of the late Holocene earth mounds concentrated along the Murray Riverine Plain of southeastern Australia were associated with the baking/steaming of carbohydrate-rich wetland plant food such as bulrush (*Typha*), club rush (*Bolboschoenus*) and water ribbons (*Triglochin*), as reported in ethnographic and historical accounts for the region (Coutts et al. 1979; Gott 1999; Martin 2006, 2011; Westell and Wood 2014). These mounds consist of ashy sediments, charcoal, baked clay heat retainers, bone, stone and shell artefacts, a range of wetland faunal remains, and occasionally intrusive human burials (Martin 2011:162–163). These ethnographic and historical records provide data to construct hypotheses about prehistoric diet and associated settlement systems in the region. A comprehensive understanding of the distribution and abundance of water and food resources in the Lower Murray will improve scientific processes involving the generation and testing of hypotheses employing archaeological data. Detailed information regarding the abundance and distribution of key plant and animal foods associated with the riverine ecosystem will provide important data to address hypotheses regarding the existence of sedentary
and semi-sedentary lifeways in the Lower Murray region during the late Holocene. Expanded archaeological research in the region will improve our understanding of Aboriginal behavioural diversity across the diverse Lower Murray ecosystems.

**Figure 1** Map showing key places referred to in the text (adapted from Pate 2006).
Murray River Ecology

The Murray River is the major tributary of the extensive Murray Darling river system of southeastern Australia. Both the Murray and the Darling rise in the higher rainfall areas of the Great Dividing Range on the eastern coast and then flow through the dry, flat lowlands to the southwest. The rivers deliver large quantities of water to these semi-arid lands. The Murray River originates in the 2228 m Kosciusko Plateau of New South Wales and flows for approximately 2600 km to the Southern Ocean southwest of Adelaide, South Australia (Gill 1973; Hills 1974; Jennings 2009; Walker et al. 1986).

The Murray is the only major river in SA. Its waters enter the state on the southeastern border, flow westerly toward the Mount Lofty Ranges and then southerly to the ocean. SA topography is generally low in relief. Approximately 50 per cent of the state is less than 150 m above sea level and over 80 per cent is less than 300 m. The Murray drops less than 22 m in its 642 km trek between the border and the ocean (Aitchison 1974).

SA is the most arid state in Australia, with 83 per cent of the land mass receiving less than 250 mm of rainfall per annum. The northeastern region of the state occurs in the arid core of the continent where mean annual rainfall is less than 125 mm (Gentilli 1971, 1972; Lee and Gaffney 1986; Williams 1979). Consequently, the Murray River, with its abundant water supplies, provided an important ecosystem for inland settlement by past Aboriginal populations.

The river morphology exhibits great variability within the state. From the state border to Overland Corner (on the river 75 km east of Roonka, Figure 1) the river meanders through a wide alluvial valley bordered by tall limestone cliffs. Below Overland Corner, the Murray has dissected the uplifted limestone Pinnaroo Block producing a steep-sided gorge topography (Twidale et al. 1978). The Lower Murray Gorge was incised during middle and late Pleistocene glacio-eustatic regressions (Twidale et al. 1978). Today, limestone cliffs tower 30–40 m above the river bottom. This deeply entrenched gorge has restricted floodwater dispersal and swamp development...
(Twidale et al. 1978). Thus, there is an abrupt transition from the surrounding semi-arid mallee eucalypt plain to the narrow alluvial river flats. The limestone cliffs decrease in height 30 km south of Blanchetown near Swan Reach, and wide alluvial flats emerge again. Numerous swamps and broad, shallow lakes occur in this coastal lacustrine zone. These conditions continue for an additional 90 km to the river mouth at Lake Alexandrina. (Brown and Stephenson 1991; Fenner 1931; Firman 1973, 1985).

The modern river morphology became established between 8000 and 6000 years ago. Ancestral rivers in the Murray Darling system dating from ca. 14,000 to 7000 BP were generally larger and straighter than their modern counterparts (Fluin et al. 2009; Hill et al. 2009; Pels 1964; Prendergast et al. 2009). The change of the Murray River to its present slower, meandering morphology resulted in increased floral and faunal productivity associated with the increased representation of shallow lagoons, billabongs, swamps, and lakes (Brown and Stephenson 1991; Gingele et al. 2007; Pardoe 1995). Lake Alexandrina at the river mouth was well-established by 7800–7600 cal yrs BP (Fluin et al. 2009).

Prior to historical interventions, like locks and dams, the water level of the Murray River was primarily affected by precipitation in the eastern highlands. An examination of sediments in a deep sea core (MDO3-2611) collected off the coast of SA (Gingele et al. 2007) identified two periods of higher river water levels and discharge at 13,500–11,500 and 9500–7500 years BP associated with higher rainfall in eastern Australia. During the period from 17,000–5000 years BP, the sedimentary signature in the core was dominated by alluvial sediments from the Murray Darling Basin (MDB).

Water derived from monsoonal rains is transported down the Darling and spring snow melt down the Murray. Waters begin to rise in the Lower Murray in the late winter through early spring. However, the arrival of floodwaters from the two sources usually does not coincide and there are two peaks during this period. When they do coincide, a large flood results and the Murray floodplain can be entirely inundated during these heavy floods. Regular flooding cannot be expected due to the unpredictability of droughts in the highlands. The river usually reaches its highest level in mid-December. In late December the water begins to recede and reaches its lowest
level during the late summer and fall (Burton 1974; Gill 1973; Johnson 1974). Water temperature ranges from 8.5° C in the winter to 25.5° C in the summer with a mean of 16.8° C (Shiel et al. 1982). Even during extended periods of drought in the highlands that significantly reduced river flow, there were reliable water supplies available in deep recesses of the river bottom (Burton 1974).

The Lower Murray region has distinct seasonal variability, as does most of SA. The summers are hot and dry with mean maximum January temperatures of 28–32° C. Winters are cool and wet with July minimum temperatures of 3–5° C. Two-thirds of the rainfall occurs from May to August as gentle showers. Scattered convectional thunderstorms are common during the summer months. The Mount Lofty Ranges create a distinct rain shadow effect. Mean annual precipitation reaches 1200 mm in the ranges east of Adelaide and decreases eastward until only 250–300 mm is received along the Murray River. There is considerable variation in precipitation from year to year, and extensive droughts lasting from two to five years are common. The inland areas experience more frequent droughts than the wetter coastal region. Evaporation exceeds precipitation during all seasons. Due to the high evaporation rates and sandy texture of the soils, standing surface water is rare and ephemeral. Water will accumulate on claypans and soaks (claypans filled with sand) for short periods following rainfall. Smaller streams on the adjacent plains originate in the better-watered upland regions. The major ephemeral streams, the Marne River and Burra Creek, drain the Mount Lofty Ranges (Aitchison 1974; Hills 1974; Nix 1981; Tisdall 1974;).

Historical accounts describe a riverine environment rich in subsistence resources at the time of European exploration in the 1830s and 1840s (Angus 1847; Clarke 2002, 2003, 2009, 2011; Eyre 1845; Lawrence 1968; Pate 2006; Sturt 1833). The river with its associated floodplain, swamps, lagoons, creeks and flats, and adjacent mallee plains provided diverse habitats which supported a wide range of floral and faunal species. The river bank and floodplain supported stands of river red gums (Eucalyptus camaldulensis). Bulrushes (Typha spp.), rushes and
sedges (*Juncus, Bolboschoenus* [formerly *Scirpus*], *Cyperus* spp.), and reeds (*Phragmites communis*) were associated with adjacent swampy areas. This aquatic environment would have provided various edible roots, waterfowl, fish, turtles, frogs, molluscs, and crustaceans. The densely wooded flats back from the floodplain were covered with river box (*E. largiflorens*), coolibah (*E. microtheca*), black oak (*Casuarina cristata*), false sandalwood (*Myoporum platycarpum*), lignum (*Muehlenbeckia cunninghamii*), shrubs, and perennial grasses. Various fleshy fruits, seeds, tubers, greens, insects, and small game (possums, koalas, rodents) would be available. Lagoons and creeks were found adjacent to these savanna woodlands. Sand flats were stabilised by native pines (*Callitris* spp.) and perennial tussock grasses (Angus 1847; Clarke 2002, 2003, 2009, 2011; Eyre 1845; Lawrence 1968; Pate 2006; Sturt 1833).

The adjacent mallee plains were vegetated by various dwarf eucalypts (2–12 m in height), including oil mallee (*E. oleosa*), bull mallee (*E. beariana*), blue mallee (*E. polybroctea*), white mallee (*E. dumosa*), and slender mallee (*E. calycogona*), saltbush (*Atriplex, Rhagodia* spp.), bluebush (*Maireana* spp.), mulga (*Acacia* spp.), and grasses (*Danthonia, Stipa, Triodia* spp.). Larger game (kangaroos, wallabies, emus), birds, reptiles (snakes and lizards), and various plant foods could be found on the mallee plains. The plains extend hundreds of kilometres into Victoria toward the east and are bordered by the Mount Lofty Ranges to the west (Bowler and Magee 1978; Cleland 1966; Laut et al. 1977; Leigh and Costin 1974; Paton 1983).

Pollen evidence from swamp and lake core sediments in southeastern Australia indicates that the period from 50,000 to 10,000 years BP was significantly drier than the Holocene (Dodson 1974, 1975, 1977; Hope 1984; Kershaw 1981). The shift from a dry Late Pleistocene to wetter Holocene in the region is supported by a range of palaeoclimatic data (Dodson 1989; Johnson et al. 1999; Magee et al. 2004).

Dodson (1975) provides an overview of climate and vegetation changes for southeastern South Australia on the basis of pollen data. The driest period was from 26,000 to 11,000 BP. An open eucalypt woodland with heath understorey was present between 50,000 and 26,000 BP. During the following period of peak aridity, a more open vegetation dominated by grasses and herbs (*Poaceae* and *Asteraceae*) with scattered eucalypts and
heath had expanded to produce a more diverse vegetal mosaic. This mosaic was replaced by the modern eucalypt woodland with heath and savanna understoreys around 10,000 BP. The presence of eucalypts throughout this period suggests that the mean annual minimum temperature for the region was above 10°C and the mean annual rainfall was greater than 200–250 mm.

According to pollen evidence from Lake Leake and Wyrie Swamp in southeastern South Australia (Dodson 1974, 1977), the climate of the Holocene has been relatively stable. A slightly wetter period occurred between 6900 and 5000 BP. From 5000 to 2000 BP conditions became drier, a wetter period returned from 2000 to 1300 BP, and from 1300 BP to the present it has been relatively dry again (Dodson 1974, 1977). Climatic data suggest that the Holocene floral and faunal distributions of the Lower Murray would have resembled those reported at the time of European contact during the dry periods, whereas the wetter periods may have allowed expansion of plant and animal species and a relatively richer subsistence base.

Recent palaeoenvironmental research (Fletcher and Moreno 2012; Gliganic et al. 2014; Moy et al. 2002; Petherick et al. 2013) suggests that there were substantial changes in the pattern and spatial distribution of western-driven rainfall in the Southern Hemisphere after 6000–5000 years BP in association with increased variability in the El Niño Southern Oscillation (ENSO). In some regions, variations in these large-scale atmospheric systems would have resulted in warmer, drier periods associated with increased ENSO activity followed by cooler, wetter phases. However, pollen data from Australia and the Pacific islands indicate little climate change during the Holocene (Pickett et al. 2004; Wanner et al. 2008). Gliganic et al. (2014) employed dated shoreline lake sediments, lacustrine shells and speleothems to examine the impact of these large-scale atmospheric variations on regional palaeoenvironments in southern central Australia. Elevated lake levels in the Flinders Ranges of South Australia associated with increased rainfall are identified for the periods 5800–5200, 4500, 3500–2700 and 1000 years BP. They argue that these late Holocene periods of
increased precipitation would have increased the reliability of resources for regional human populations during a time of reduced winter rainfall (Gliganic et al. 2014).

Thus a range of palaeoenvironmental evidence suggest that Aboriginal people living along the Lower Murray River would have had access to a rich riverine ecosystem during at least the last 7000 years. In contrast, the abundance and reliability of plant and animal food resources associated with the adjacent semi-arid mallee plains would have fluctuated during the late Holocene in relation to alternating cooler, humid and warmer, drier climatic phases related to variations in ENSO activity.

The perennial water supply which originates in the eastern highlands created a unique habitat within the semi-arid plains region that would have provided a large, permanent water source for Aboriginal populations. According to historic accounts, the Lower Murray was one of the most densely settled Aboriginal areas of Australia, along with the northern, eastern and southern coastal regions where rainfall was highest.

In this district the natives were very numerous, their encampments being scattered along the narrow strip of ground between the limestone cliffs and the water’s edge: there they find plenty of food from the fish, mussels, crayfish, bullrush root and other products of this larger river.

(Angas 1847:58)

The greater availability and reliability of food and water resources in these areas supported larger populations. Eyre (1845) estimated an Aboriginal population of three to four persons per mile of river in the Moorunde region, 11 km south of Roonka. He noted that settlement sizes changed from season to season according to the abundance of food. During the summer, the river flooded and increased the habitat size of mussels, crayfish and fish. Summer camps were quite large and consisted of simple brush windbreaks on the banks of the river. Eyre (1845) had encountered Aboriginal congregations of up to 600 individuals. In the winter, the populations dispersed into smaller camps consisting of solid log huts covered with grass and vegetation or rockshelters in response to the cold, wet weather. Sturt (1833) also encountered Aboriginal groups exceeding 100 persons as he travelled southward along the Lower Murray. On
the basis of the observations of Taplin (1879), Radcliffe-Brown (1918:230) estimated that the Aboriginal population in the Lower Murray was between 1800 and 6000 people, at a density of between 1–3.2 individuals per square kilometre prior to the European introduced smallpox epidemics (Clarke 1994:57–60; Humphries 2007).

A higher degree of sedentism associated with long-term residential bases or year-round occupation of residential base camps would be possible in the resource rich regions of the Lower Murray environment (Owen 2004; Pate 2000, 2006; Pate and Owen 2014). However, some mobility may have been necessary due to the scheduling and seasonality involved with floral and faunal procurement (Binford 1980; Flannery 1968; Poiner 1976) and the distribution of food resources and stone tool raw materials across the landscape. Stratified archaeological sites such as rockshelters and mounds accompanied by cemeteries could be related to increased sedentism and use of long-term residential base sites, but such year-round use of residential base sites must be demonstrated employing a range of archaeological data.

An examination of the seasonal availability of plant and animal foods provides one means to address the temporal association of hunter-gatherers with various archaeological sites (Bailey 1983; Jochim 2012; Kelly 1983; Rocek and Bar-Yosef 1998; Rossignol and Wandsnider 1992). Physical anthropology and stable isotope analyses provide powerful methods that can supplement conventional archaeological data to examine variability in pre-contact Aboriginal diet, health, settlement patterns and landscape use in the Lower Murray River Basin (Katzenberg 2000; Larsen 2003; Pate 1997, 2000, 2017; Pate and Owen 2014; Pate and Schoeninger 1993).
The Riverine Ecosystem

Soils and Terrestrial Vegetation
The soils and vegetation of the riverine zone are more uniform when compared to the adjacent mallee plain because they are less dependent on local rainfall. There is an abrupt vegetation transition from the semi-arid mallee to the better-watered, more fertile black silts of the river floodplain. The open mallee woodland with its sclerophyllous-chenopodiaceous shrub understorey is replaced by densely wooded flats and a savanna understorey. The river banks are covered with bulrushes, rushes, and sedges (Leigh and Costin 1974; Specht 1972).

Canopy composition changes with reduced soil fertility and water availability away from the river front. River red gums (E. camaldulensis) are dominant along the river’s edge and are replaced by river box (E. largiflorens) on the flats adjacent to the floodplain. Eucalypts in these better-watered areas reach 30 m in height and have a foliage protective cover of 10–30 per cent. Coolibah (E. microtheca), false sandalwood (Myoporum platyteam), black oak (Casuarina cristata), dry-land tea tree (Melaleuca lanceolata), sand pine (Callitris spp.), and mulga (Acacia spp.) are the dominant species in the low woodlands of the drier peripheries. These trees are 5–10 m tall and have a foliage protective cover of less than 10 percent. The drought-resistant understorey expands as the canopy thins out (Specht 1972).

The savanna understorey is dominated by tussocks of perennial kangaroo grass (Themeda triandra), wallaby grass (Danthonia spp.), and spear grass (Stipa spp.). In the drier areas away from the river, the tops of these grasses become dormant and wither and die in response to the hot, dry summer conditions. They achieve their maximum growth during the late spring following winter rainfall (Gott 1982; Specht 1972).

Orchids (Orchidaceae), liliaceous plants (Liliaceae and Hypoxidaceae), and yam daisies (Microseris lanceolata) are other dry-land plants that are widespread on the banks adjacent to the river. These plants sprout green leaves from underground rhizomes in the cooler days of autumn and use starch stored in roots, tubers, corms, or bulbs until they can grow vegetatively with winter rainfall. Flowers occur in spring and the plants
continue growth until water becomes limiting in the summer. During summer dormancy, the plants are reduced to their underground parts again (Gott 1982; Specht 1972).

Shrubs, including golden wattle (Acacia pycantha), kangaroo thorn (A. paradoxa), daisy (Olearia spp.), hopbush (Dodonaea viscosa), and native box (Bursaria spinosa), are sparse, but will expand with repeated firing. Onion weed (Asphodelus fistulosus), onion grass (Romulea spp.), and other annuals invade the understory in the spring after rainfall (Gott 1982; Specht 1972).

Wetland plants occur in dense stands in locations with permanent water or in areas that are seasonally flooded by the river. Dominant representatives include bulrushes (Typha spp.), rushes (Cyperaceae) and waterribbons (Triglochin procerum). These plants propagate from rhizomes in addition to producing numerous small seeds in the spring. Maximum growth occurs during the hot summer. The river also floods during this period and increases the area which will sustain growth. In the late summer and early autumn, the tops of the plants die in response to reduced temperature and recession of floodwaters (Gott 1982; Specht 1972).

**Terrestrial Fauna**

A number of small mammals are associated with the riverine habitat. The nocturnal herbivorous phalangers are adapted to an arboreal life. This family includes possums (Trichosurus vulpecula, Pseudocheirus peregrinus) and the koala (Phascolarctus cinereus). These small mammals nest in the hollows of trees and feed upon tender shoots and leaves, flowers, nectar and fleshy fruits. The koala's highly specialised diet is restricted to the leaves of Eucalyptus spp. (Barrett 1955; Jones 1969; Ride 1970).
Aquatic Flora and Fauna
The freshwater biome includes two main ecosystem types: running waters or lotic habitats (streams and rivers) and standing waters or lentic habitats (lakes, ponds, swamps, marshes). Swamps and marshes are some of the most productive habitats on earth (Simmons 1979). Most of the flora and fauna are concentrated in the shallow littoral zone. Rooted plants, such as cattails (*Typha* spp.), lilies (*Nymphaea* spp.) and pondweeds (*Potamogeton* spp.), and small floating plants, such as duckweeds (*Lemna, Wolffia* spp.), are the dominant producers. Consumers include worms, insects, crustaceans, and molluscs. Waterfowl, fish, turtles, and amphibians move in and out of the littoral zone. Phytoplankton become the dominant producers in the open-water zone. Algae and dinoflagellates are concentrated near the surface. Zooplankton include copepods and cladocerans. Fish and fish-eating birds are the dominant larger animals. Bottom dwellers include worms, insects, and mussels (Simmons 1979; Williams 1981a, 1983).

The combined effects of annual discharge values, erratic changes in water level, drought, and the aridity of the surrounding mallee have produced a depauperate fauna in the Murray Darling system. Twelve families, 18 genera, and 19 species of fish occur in the Murray Darling, whereas 13 families, 52 species, and over 260 species are found in the Mississippi-Missouri system. Lack of speciation is also evident in the Murray Darling waterfowl, mammal, and invertebrate fauna. Riverine species have all adapted to the widely fluctuating water levels and associated changes in productivity (Keast 1981a; Smith 1978; Williams 1981b).

The riverine fauna is dominated by invertebrates consisting primarily of arthropods, e.g., insects, crustaceans and their allies. The macro-invertebrate fauna is very limited due to the unstable nature of the river bottom (Williams 1981a, 1983). Two species of mussels (Mollusca) *Velesunio ambiguus* and *Alathyria jacksoni* and several crustaceans, including the freshwater shrimp (*Paratya australiensis*), river prawns (*Macrobrachium*) and crayfish (*Cherax* spp. and *Eusastacus armatus*), occur in the Lower Murray (Williams 1981a, 1983).
Insects
Larvae of the large rain moth *Trictena atripalpis* (bardi grubs) escape dry seasons and droughts in moist underground burrows at the bases of eucalyptus trees along the river. Each moth will lay thousands of eggs at the base of large river red gum trees (*E. camaldulensis*). When the grubs hatch they burrow into the soil and feed on the tree roots. Following rainfall, the moths emerge from the burrows and disperse (Common 1990). These large populations of bardi grubs would have provided a reliable food source for hunter-gatherers (See Grehan 1989; Tindale 1966; Yen 2012; Yen et al. 2017).

Fish
Although the Murray Darling fish species diversity is low, the river supports a large number of important food species, including catfish, perch, cod, and blackfish (Clarke 2002). The Murray cod (*Maccullochella macquariensis*) is the largest freshwater fish in Australia and can reach lengths of up to 1.8 m and weights of up to 113 kg. The average specimen weighs 10 kg. Golden perch (*Plectroplites ambiguus*) weigh up to 4 kg and average 1.4 to 1.8 kg. Breeding in many of these larger species is triggered by increasing spring water levels and rising water temperature. During these periods, both habitat size and food supply are expanded. Increased plankton and detritus input and greater aquatic plant and insect productivity provide this additional food (Barrett 1955; Frith 1974; Keast 1981b; McDowall 1996). Adult golden perch and silver perch (*Bidyanus bidyanus*) migrate upstream for distances up to 1000 km after spawning, whereas Murray cod and freshwater catfish (*Tandanus tandanus*) are relatively sedentary (Reynolds 1983). Radio-tracked Murray cod in the Murray River have migrated up to 120 km upstream to spawn before returning to exactly the same river channel from which they departed (Todd and Koehn 2009).
The control of river flow by locks has had a detrimental effect on the distribution and abundance of fish. Floodwater control has decreased habitat size and reduced breeding opportunities. Winter flows have been reduced and late summer/autumn levels increased. *Macquaria australasica, Maccullochella mitchelli* and *Gadopsis marmoratus* are seriously threatened, while *T. tandanus, P. ambiguus*, and *M. macquariensis* numbers have been drastically reduced (Frith 1974; Shiel et al. 1982).

**Waterfowl**  
The Murray Darling is the most important waterfowl breeding area in Australia. Twelve of the 19 species of Australian ducks, geese and swans are common inhabitants of the river system, and two northern tropical species, the grass-whistle duck (*Dendrocygna eytoni*) and water-whistle duck (*D. arcuata*), are occasional visitors. These birds feed on aquatic plants, invertebrates and small fish (Frith 1982). Waterfowl provided a key food source for Aboriginal people inhabiting the Lower Murray region (Clarke 2016).  

Waterfowl behaviour is also keyed to changes in river level and food abundance. Species that inhabit shallow, temporary waters (*Malacorhynchus membranaeus, Anas gibberifrons*) are highly nomadic. Breeding occurs in response to rising water levels and increased food supplies, but as soon as the floods recede the habitat can no longer support the entire local population and some migrate to better-watered coastal plains and estuaries. The remaining waterfowl species occupy the more permanent deeper swamps and lakes. They are sedentary or migrate regularly between local swamps and lakes. Shorebirds include plovers, dotterels, stilts, avocets, pratincole, gulls, and terns (Frith 1974, 1982; Pizzey 2013).

**Reptiles**  
Three species of turtle inhabit the Lower Murray, the Australian snake-necked turtle (*Chelodina longicollis*), broad-shelled long-necked turtle (*C. expansa*), and Murray short-necked turtle (*Emydura macquari*). In Australia, freshwater turtles are referred to as ‘tortoises’ to distinguish them from the larger marine forms. Freshwater turtles (‘tortoises’) are found in the river and associated streams, lagoons, and swamps. Adults feed...
on fish, molluscs, crustaceans, frogs, tadpoles and aquatic insects (Cogger 2014; Goode 1967; Worrell 1970).

*E. macquari* and *C. longicollis* go ashore frequently to bask in the sun, but *C. expansa* only leaves the water to lay eggs. From 10–15 elongated, brittle-shelled eggs are laid in nests excavated in moist soils. The eggs are buried and left unattended to hatch with the heat of the sun. *C. longicollus* and *E. macquari* nest in early summer and eggs hatch in late summer or early fall, whereas *C. expansa* lays eggs in fall which overwinter and hatch the following spring. The young emerge fully developed and immediately enter the water to feed on insect larvae. *C. expansa* adults are the largest freshwater turtles in Australia. They achieve carapace lengths up to 50 cm and weights over 5.5 kg. *C. longicollis* and *E. macquari* reach carapace lengths of 25 cm and 30 cm, respectively (Cogger 2014; Goode 1967; Worrell 1970).

Ectothermic reptiles are extremely sensitive to temperature changes (Heatwole and Taylor 1987). Turtles enter a state of winter dormancy (brumation) in response to cold temperature. *C. longicollis* retreats to moist earthen burrows on the shore, while *C. expansa* and *E. macquari* burrow underwater in bottom mud or in adjacent banks.

A wide variety of predators pose a threat to turtles at all stages of their life cycle (Goode 1967). Eggs are eaten by possums, snakes, lizards, water rats, and dingoes. Juveniles are consumed by waterfowl and snakes, and adults by hawks, eagles, waterfowl, water rats and dingoes.

**Amphibians**

Frogs were the only amphibians found in the pre-European Lower Murray environment. Urodeles and caecilians (newts and salamanders) and toads (Bufonidae) did not occur in the native Australian fauna. Most frog species are nocturnal and terrestrial, but the genus *Litoria* also contains arboreal members. All adults are carnivorous and will eat anything they are able to catch, kill and swallow. Insects and small rodents are common constituents of the diet. Adult size ranges from 13.8 mm in *Ranidella deserticola* to 104.2 mm in *Litoria caerulea* (McFarland et al. 1979; Tyler 1978; Tyler et al. 1981).
Water loss is a major problem faced by amphibians due to the permeability of their skin. Moist microhabitats are required to regain water lost by evaporation and for the successful development of eggs and larvae. Many terrestrial forms (Neobatrachus, Cyclorana spp.) burrow to locate moisture, while others (Limnodynastes spp.) are restricted to permanent water sources. Most Australian frogs are opportunistic breeders that use ephemeral waters for reproduction. L. rubella completes larval development in as few as 14–15 days following fall and winter rainfall, whereas species occupying permanent waters may require up to 5 months. Riverine species breed year-round or in the late winter and spring in response to rising river levels and increased food supplies. Many terrestrial frogs remain dormant in burrows or other moist microhabitats during the hot, dry summer (McFarland et al. 1979; Tyler 1978; Tyler et al. 1981).

**Mammals**

Aquatic mammals include the platypus (Omithorkynchus anatinus) and water rat (Hydromys chrysogaster). These animals shelter in burrows excavated in the banks of the river and associated creeks and lagoons. The diurnal platypus feeds on mussels, freshwater shrimp, insects, and worms at dawn and towards dusk. Much of its time is spent in the deep burrow, which may extend up to 30 m from the water’s edge. The female lays two to three soft-shelled eggs in a nest concealed in the burrow. The platypus remains in its burrow in hibernation during winter (Barrett 1955; Jones 1969; Morcombe 1968). The highly specialised water rat is unique to Australia. It feeds on crayfish, mussels, small fish, insects and aquatic plants. The nocturnal animal is extremely shy. Adults reach lengths of over 50 cm (Barrett 1955; Jones 1969).

**Molluscs**

Freshwater mussels are sessile bivalve filter feeders. They inhabit rivers, streams, lagoons, and billabongs in waters of less than 10 m depth. Murray River species burrow in fine alluvial silts or attach to large submerged dead trees. These shallow habitats expose them to great temperature variations and frequent desiccation (Burky 1983; Russell-Hunter 1983; Seed 1983; Smith 1978).
Hibernation in muddy bottom sediments occurs in response to cold winter temperatures. *Velesunio ambiguus* becomes inactive at water temperatures below $12^\circ\text{C}$ (Hoffmann 1983; Millington and Walker 1983; Walker 1981a, 1981b). Mussels also aestivate in mucus cocoons with falling late summer/autumn river levels and the summer drying of terrestrial habitats. Adults can survive in these cocoons for years. Larger specimens survive up to 30 per cent longer than smaller ones due to slower desiccation rates associated with lower surface area/volume ratios (Dudgeon 1982; Morton 1979; Williams 1983).

Great variations in mussel population size occur with fluctuating habitat size and food supplies. Large numbers of eggs are produced in the spring as habitat area is increased by rising river levels and winter rainfall. The glochidial larvae attach to and are dispersed by fish hosts (Burky 1983). *Velesunio ambiguus* adults from the main river stream reach lengths up to 94 mm and heights to 55 mm. Lagoon forms are smaller and more flattened (Cotton 1961; Millington and Walker 1983).

**Crustaceans**

Shrimp are simply smaller genera of prawns. The maximum length of the freshwater shrimp *Parataya australiensis* is 25 mm, while river prawns (*Macrobrachium* spp.) grow to 178 mm and weigh up to 400 g. The SA freshwater forms inhabit inland rivers and other permanent waters. They are active at warm water temperatures. Optimum growth occurs at 28–30° C in *M. rosenbergii*. Their diet includes detritus, smaller crustaceans, molluscs, polychaetes, and other invertebrates (Hale 1927–1929; Neal and Maris 1985).

Females carry from less than 100 to over 100,000 eggs on their pleopods for three to five months. In *M. rosenbergii*, the planktonic larvae wash downstream to estuarine waters where they mature within four months. The juveniles will only survive in brackish waters with salinities from 12–16 ppt. Adults migrate upstream to fresher waters (Neal and Maris 1985; Provenzano 1985; Vernberg and Vernberg 1983).
Freshwater crayfish are quite common throughout inland Australia. They occupy the shallow waters of billabongs, creeks, lagoons, and rivers (Frost 1975). Crayfish are omnivorous. Adults eat large quantities of aquatic vegetation. They are grazers in addition to taking phytoplankton and detritus with filtratory setae. Animal foods include smaller crustaceans, molluscs, fish, annelids, arthropods, and zooplankton. The young feed on plankton and detritus. Feeding generally occurs during the early morning and evenings. Fish are the primary predators (Cobb and Wang 1985; Grahame 1983; Mills and McCloud 1983).

The yabbie (*Cherax destructor*) is a warm water species that is extremely well-adapted to the dynamic Lower Murray environment. It is active at water temperatures above 16° C in the spring, summer, and early autumn. By possessing combined characteristics of both R- and K-reproductive strategies (Pianka 2011; Sastry 1983; Stearns 1977, 1980) yabbies can rapidly increase population numbers and colonise new habitats created by spring floodwaters and winter rains. They breed throughout their active period, produce large numbers of young, provide parental care, mature early, and exhibit rapid growth rates.

From 300–400 eggs are carried on the female pleopods from October to March, and eggs hatch in about six weeks at 20°C. The young are born alive and cling to the mother until they reach 3 mm in length. This initial parental care results in very high survival rates when compared to the pelagic larvae of marine crustaceans (Provenzano 1985). Young are independent within 41–90 days of spawning, depending on water temperature. The optimum temperature for growth is between 20-25° C. Most young yabbies reach 10 cm in length within two years of hatching. Adults reach total lengths of 20 cm and weigh up to 200 g. Edible meat comprises about 25 per cent of this total weight. Life span is about three years (Faragher 1983; Frost 1975; Mills and McCloud, 1983; Provenzano 1985).

As water temperature drops below 16° C in the late autumn and winter, yabbies retreat to underwater burrows and enter a state of dormancy. Most burrows are occupied by April. They also become dormant in response to drought. As ephemeral water holes dry out in the hot summer, the crayfish enter a sealed burrow and follow the retreating water table. Tunnels may extend over 3 m deep. Aestivation will continue until water
returns to the overlying ground. Dormant yabbies have been discovered beneath lake beds which have been dry for up to eight years, although yabbies attempt to avoid summer dormancy by migrating to more stable habitats following winter rainfall (Frost 1975).

The Murray River lobster (*Euastacus armatus*) is a cold water species active at temperatures in the 5–10° C range. It is much more K-oriented than *C. destructor*. A single mating occurs in late autumn and each female produces up to 400 eggs. Development is similar to that of *C. destructor*, but greater time is involved. At these colder temperatures eggs do not hatch until four months after spawning. Adults reach 50 cm total length and weigh up to 2.5 kg. Unlike *C. destructor*, this crayfish has a small tail-body ratio. Summer dormancy takes place in mud burrows in the river banks (Frost 1975).

**Riverine Trophic Structure**

The primary limiting factors affecting the abundance and distribution of aquatic flora and fauna in the Lower Murray are fluctuating river level and water temperature. Flood waters bring inputs of nutrients, plankton and detritus, and increase habitat size for both flora and fauna. The activity-breeding cycles of crustaceans, molluscs, turtles, mammals and some fish are keyed to changes in water temperature.

Because large aquatic plants are scarce, phytoplankton and detritus are the major sources of primary productivity. In addition, wetland plants provide abundant supplies of small seeds during the spring and early summer. Insects are the dominant riverine herbivores. Omnivores include crustaceans, molluscs, fish, and waterfowl. The platypus, river rat, and turtles are primarily carnivorous (Walker et al. 1986).

In relation to Aboriginal food supply, animals are most abundant in the spring and early summer when the river level is rising and water temperatures are warm. In the winter, the crayfish *Cherax destructor*, shrimp, mussels, turtles, mammals (platypus, river rat) and some insects become dormant, and fish and waterfowl numbers are greatly reduced in response to cold
water temperatures, low river levels, and reduced food supplies. The cold-adapted crayfish *Eusastacus armatus* is most abundant during these periods (Walker et al. 1986).

Due to the erratic discharge values of the Murray River that existed prior to historical water management practices, the magnitude of these seasonal changes in floral and faunal distribution and abundance would have been less predictable. Furthermore, major non-seasonal droughts in the eastern highlands have disrupted the regular cycle in the past and reduced the lower reaches of the river to a series of waterholes (Frith and Sawer 1974; Walker et al. 1986).

**The Mallee Ecosystem**

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**Vegetation**
The major part of the mallee occurs between the 200 and 450 mm annual isohyets. The canopy of the mallee open scrub consists of small trees and tall shrubs dominated by *Eucalyptus* spp. Mallee eucalypts are sclerophyllous evergreen perennials which sprout from subsurface lignotubers. They have deep tap roots and shallow extensive lateral root systems. The diverse sclerophyll heathland understorey contains over 130 plant genera (Beadle 1981; Specht 1972, 1979, 1981a, 1981b; Williams 1979).

The amount and seasonality of rainfall has a great effect on the availability of mallee plant foods. Regular autumn and winter rainfall produces lush periods of vegetation growth during which both perennial and annual plant foods are abundant. Groundwater reserves accumulated during the rainy season allow plants to remain productive during the annual summer drought. However, plant foods are greatly reduced if the regular rainfall does not arrive. During these dry periods only the stems, leaves, roots, fruits and seeds of drought-resistant plants are available (Cloudsley-Thompson and Chadwick 1964; Mayhew 1968).
Fauna

Birds
Species density surveys (Foulkes and Gillen 2000; Pianka and Schall 1981; Simpson 1973a, 1973b) indicate that birds are by far the most diverse vertebrate class inhabiting the mallee region. Foulkes and Gillen (2000) provide an overview of the maximum total number of species recorded from various past surveys. Birds (257 spp.) are followed by reptiles (75 spp.), mammals (66 spp.), and amphibians (four spp). Mobility allows birds to successfully exploit patchy distributions of food and water. Nectar, flowers, pollen, fleshy fruits, seeds, and insects are primary sources of food. Abundant nectar-producing plants provide a concentrated high energy source in an otherwise marginal environment (Recher 1981). Numerous species of passerine birds feed primarily on nectar. The Meliphagidae (honey-eaters) contribute greatly to the high species diversity in the mallee.

Many of these small birds conserve preformed and metabolic water and do not need to drink. Water conservation, combined with an ability to tolerate high body temperatures, allow these birds to remain active during the heat of the day (Dawson 1981; Keast 1981a, 1981b; Kikkawa et al. 1979). Since many birds are nomadic they opportunistically enter the mallee for food and then return to better-watered surrounding areas, such as the riverine and coastal zones. The emu (Dromaius novaehollandiae) only enters the mallee following winter rainfall and is active during the evening and cooler parts of the day. Others, including the territorial mound-building mallee fowl (Leipoa ocellata) and bustard or plains turkey (Ardeotis australis), are resident species. Additional game birds inhabiting the mallee include quails, pigeons and doves (Barrett 1955; Pizzey 2013; Kikkawa et al. 1979).
Reptiles

Reptiles are well-adapted to arid regions. Several characteristics, including a thick skin with few dermal glands, excretion of concentrated uric acid, nocturnal activity, and the use of burrows during the hottest period of the day, minimise water loss to the environment. The almost exclusive carnivorous diet, including insects, frogs, birds and small mammals, provides an appreciable percentage of the reptilian water requirement. Additional water is obtained by opportunistic drinking and from metabolic sources. Breeding usually occurs in the spring following winter rainfall when a greater quantity of higher quality food is available (Mayhew 1968).

Fat storage allows reptiles to reduce activity or remain dormant in their burrows during colder months or periods of food shortage. Such daily and seasonal metabolic inactivity allows reptiles to capitalise on limited and unpredictable food supplies. It is a major factor contributing to their relative success over mammals and birds in the arid interior of Australia (Mayhew 1968; Pianka 2011).

Lizards and snakes are the dominant reptilian groups of the mallee. Rawlinson's (1966) literature review of reptiles recorded in the Victorian mallee reports 73 species representing 34 genera and nine families. These include 45 species of lizards and 25 species of snakes.

Microhabitat specialisation and variability in times of activity have contributed to the great lizard diversity. Many species are restricted to sandridges, sandplain-\textit{Triodia} or shrub-\textit{Acacia} habitats. A large number are nocturnal. Nocturnal lizards include geckos, pygopodids, and skinks. Most agamids and varanids are diurnal. The majority of lizards in regions with Mediterranean climates breed only during the spring when insects become abundant (Barrett 1955; Mayhew 1968; Pianka 1981).
The elapids are the most common snakes of the mallee. Snakes have a relatively limited heat tolerance and consequently most arid-land snakes are nocturnal. Days are spent in burrows, hollow logs or cool riverine habitats. Their diet includes rodents, frogs, lizards, birds, bird eggs, other snakes, insects, and additional small invertebrates. Snakes are capable of going without food for periods of six to twelve months without any serious consequences. Breeding occurs in the spring and autumn (Barrett 1955; Mayhew 1968; Pianka 1981).

**Mammals**

Small rodents are the dominant mammal group of the mallee. Mallee rodents include rats, mice, rat-kangaroos, and bandicoots. The burrowing rodent-like wombats (*Lasiorhinus latifrons*) are also common (Cloudsley-Thompson and Chadwick 1964; Jones 1969; Lee et al. 1981; Ride 1970).

Nocturnal activity, combined with the use of burrows and nests during the heat of the day and/or daily torpor, allows rodents to evade arid-land conditions and reduce evaporative water loss. Evaporative water loss is a critical problem due to their small size and large surface area/volume ratio. Most of their water is obtained from food and metabolic sources. Many rodents enter a prolonged state of dormancy or aestivation during the annual summer droughts. Aestivation is similar to winter hibernation, but it occurs in response to extended periods of heat and aridity rather than cold (Bartholomew and Dawson 1968; Cloudsley-Thompson and Chadwick 1964; Lee et al. 1981).

Rodent populations and territorial ranges were drastically reduced by the 1890–1920s due to competition with introduced European species (Lee et al. 1981). Rabbits (*Oryctolaquus cuniculus*) and house mice (*Mus musculus*) competed for burrow space and food, while foxes (*Vulpes vulpes*), dogs (*Canis familiaris*) and cats (*Felis catus*) increased predation pressures (Keast 1981b; Lee et al. 1981). Other nocturnal burrowers include the echidna or spiny anteater (*Echidna aculeatus*) and the numbat or marsupial anteater (*Myrmecobius fasciatus*). These mammals feed on a variety of small insects, including ants and termites.
Large herbivores are represented by the family Macropodidae, which includes kangaroos and wallabies (Dawson 1995; Hume 1982; Main and Barker 1981). The lower metabolic rates and ruminant-like digestion of kangaroos allow an efficient use of poor quality fibrous vegetation (Janis 1976; Tyndale-Biscoe 2005).

During drought periods small 2.5 kg hare-wallabies (*Lagorchestes* spp.) can survive on the open mallee using water obtained directly from vegetation (preformed water) and via metabolic oxidation (metabolic water), whereas kangaroos over 25 kg must move toward areas where free water is available (Main and Barker 1981). Large kangaroos move toward the Murray River in the summer and then return to the mallee and arid grasslands following winter rainfall (Archer 1984a; Frith and Calaby 1969).

Distributions of macropods are also related to habitat and diet. The major proportion of the diet consists of grasses. Grasses are supplemented with herbs. The red kangaroo (*Macropus rufus*) occupies open plains and remains highly mobile during the rainy season in search of newly sprouted grasses and ephemeral dicots which have greater water and protein contents. Red kangaroos occur on the arid grasslands bordering the mallee. Grey kangaroos (*Macropus fuliginosus*) rarely venture beyond the dense mallee scrub and wooded areas adjacent to the Murray River. They consume greater quantities of grass than red kangaroos and are less selective. The grey kangaroo remains closer to the river during drought periods, while red kangaroos move toward the river front from the arid grasslands (Frith and Calaby 1969; Jones 1969; Newsome 1965a, 1965b; Tyndale-Biscoe 2005).

Solitary macropods include the euro (*Macropus robustus*) and wallabies. Euros and rock wallabies (*Petrogale* spp.) seek shade in rocky outcrops, gullies, and beneath mulga (*Acacia aneura*). Euros do not normally venture further than a 1 km radius of their shelters. They feed on lower quality perennial grasses such as spinifex. Other wallabies are widespread throughout all inland woodland and desert communities (Frith and Calaby 1969; Jones 1969; Newsome 1965a, 1965b; Tyndale-Biscoe 2005).
The native carnivorous mammals that have inhabited the SA mallee region are confined to two families, the Dasyuridae and the Thylacinidae. The Tasmanian devil (*Sacrophilus harrisii*) and the native cats (*Dasyurus* spp.) are included in the Dasyuridae, and the dog-like Tasmanian wolf or thylacine (*Thylacinus cynocephalus*) is the only member of the family Thylacinidae. All of these carnivores were nocturnal.

The Tasmanian devil and Tasmanian wolf are no longer present on the mainland. Mainland extinction in southeast Australia probably dates back no more than a century. The Tasmanian devil survived in Western Australia until 430±160 BP and in the Northern Territory until at least 3120±100 BP. Mainland evidence for the Tasmanian wolf comes from the Kimberley region at 0±80 BP and the southwest at 3090±90 BP (Archer 1981). Native cats still survive today, but their populations and ranges have been reduced substantially (Archer 1981; Barrett 1955).

Competition associated with the introduction of the dingo (*Canis familiaris dingo*) between 4000 and 3000 BP may have been responsible for the mainland extinction of the thylacine and the Tasmanian devil since these native vertebrate fauna survived in Tasmania in the absence of the dingo. Competition with dingoes and European introduced dogs (*Canis familiaris*), red foxes (*Vulpes vulpes*) and cats (*Felis catus*), accompanied by reductions in rodent populations, led to Tasmanian devil and native cat declines (Archer 1984b; Gollan 1984; Johnson and Wroe 2003; Oskarsson et al. 2011). Native cats were also killed by farmers because of their incessant raids on hen houses (Archer 1981; Barrett 1955; Jones 1969).
Aboriginal Subsistence-Settlement Systems in the Lower Murray Environment

The palaeoenvironmental data indicate that there has been little change in the climate and vegetation of southeastern Australia during the last 10,000 years. Major vegetation changes are confined to the period following European colonisation. The modern productive Murray River system was established by 7000 BP. Therefore, Aboriginal populations living along the Lower Murray River experienced a similar natural environment throughout the past 7000–8000 years (Fluin et al. 2009; Hill et al. 2009). Coastal groups near the mouth of the Murray River would have had a greater access to marine resources following sea-level stabilisation at 6000 BP (Lampert and Hughes 1974; Perlman 1980).

Consequently, modern ecological data can complement archaeological and historical records by providing estimates of the floral and faunal resources available to Aboriginal riverine populations during the majority of the Holocene. Although available at different seasons, the employment of a range of plant foods from the riverine and mallee ecosystems would provide year-round access to fruits and seeds (Clarke 1985b, 1994, 2015). Plant storage organs (tubers, roots, bulbs), aquatic plants, and naturally desiccated fruits, such as *Santalum* and *Solanum* spp., would remain available during periods of drought (Clarke 1985a, 2015; Gott 1982, 1999; Martin 2011; Westell and Wood 2014). However, many drought-escaping seeds and greens from the mallee habitat would not be available (Specht 1972, 1981b; Pate 1986).

Storage could be used to extend the availability of dried fruits and seeds. Techniques for the drying of plants were employed in the Lower Murray. In relation to basketmaking, rushes were sun dried or placed in a heated oven and then bundled up and stored for future use (Clarke 2015:234). Fruits of *Kunzea pomifera* were dried in the form of cakes (Tindale 1981:1879).

Faunal variety ensured that animal foods were also available throughout the year. Furthermore, buried turtle and mallee hen eggs and dormant crayfish and mussels could be obtained by digging. Various meats could be preserved by drying and then stored for future use. According to Clarke (1994:165–
fishing techniques employed in the Lower Murray region ranged from netting, spear fishing and trapping, to opportunistic harvesting and storage (Eyre 1845; Krefft 1862–1865; Tindale 1930–1952). Ethnographic accounts indicate that fish were stored in small dams, pounds or mud pools (Clarke 1994:169; Sturt 1833, Vol 2:165). In addition, the availability of fish was extended via drying on racks (Berndt and Berndt 1951:29). Bird eggs (e.g., emu, waterfowl) and freshwater mussels were stored for months by burying them in damp soil (Clarke 1994; Simpson and Blackwood 1973;). Non-local droughts that reduced river flow would have had the greatest impact on faunal abundance. Many animals, including waterfowl, fish and turtles, could migrate to better-watered areas during these stressful periods. On the other hand, local droughts resulted in increased faunal densities near the river.

If human behaviour is viewed as an adaptive response to specific environmental conditions, then pre-contact Aboriginal population size in the Lower Murray should be limited by the period of greatest resource stress. Unpredictable extended droughts that reduced both riverine and mallee resources would have provided the ultimate test of survival skills. Food storage would provide an important mechanism to sustain populations during extended periods of drought, but if food reserves were depleted, alternative strategies would be required. Access to more reliable food sources in the resource-rich Murray River mouth and nearby coastal regions would provide inland riverine populations with a means to reduce the risks associated with extended droughts.

If Aboriginal groups inhabiting the Lower Murray were to obtain non-local resources with the least amount of opposition and effort, some form of social ties would be required in these areas. Exogamous marriage between regions as practiced in the marginal desert habitats of Australia would be one mechanism to facilitate such relations (Berndt and Berndt 1993; Stanner 1965; Strehlow 1965; Yengoyan 1968, 1976). Individuals socialised in one area would carry the essential resource procurement knowledge of their homelands to their spouse’s people. Trade networks would provide access to other
resources that were not equally available to all populations, such as stone, marine and riverine shell, ochre, and local foods (McBryde 1984; McCarthy 1939). Alternatively, the use of food storage, fish traps, and other technological means to increase the reliability of local foods (intensification) could be employed to reduce the dependence on neighbouring groups and favour more closed social relations associated with territoriality (Clarke 1994; Lourandos 1985, 1988, 1993, 1997).

Historical Aboriginal population numbers were reduced substantially by introduced European diseases and violent confrontations with settlers. Smallpox spread rapidly along the coasts and down the river valleys (Butlin 1993; Campbell 2002). The first smallpox outbreak among Aboriginal populations occurred in Sydney in 1789, within one year of the establishment of the colony. It was again reported along the Murray River at Swan Hill in the early 1800s (Stirling 1911). The disease was common among Aboriginal groups of the Murray Darling between 1830 and 1845 (Sturt 1833; Stirling 1911; Clarke 1994).

Disputes over trespassing and the hunting of livestock resulted in numerous Aboriginal deaths. Many Aboriginal people were either poisoned or shot on sight (Eyre 1845, II; Smith 1880). Burke et al. (2016) provide a detailed overview of historical accounts of frontier violence in the western Central Murray between 1830 and 1841 with a focus on five ‘hot spots’ where repeated evidence of conflict occurred. This research investigated the significant increase in violent conflict associated with the opening of the Overland Stock Route between Sydney and Adelaide in 1838. Campbell (1939) estimated that the Aboriginal population of southeastern South Australia declined by 50 per cent every five years from 1840 through 1900.

Consequently, historic and ethnographic accounts of Aboriginal behaviour most likely do not accurately portray pre-contact lifestyles. Rapid population reductions and environmental degradation could completely disrupt former social relations and produce new adaptive requirements and opportunities. The remnants of former Aboriginal groups would be faced with the challenges of survival under a vastly different set of conditions than those experienced by their predecessors. Access to food and blanket rations, medical assistance, alcohol, and employment resulted in concentrations of large numbers of
Aboriginal people from various groups around European missions, government posts, homesteads, and population centres (Foster 2000; Foster et al. 2001; Rowley 1971). Eyre (1845, II: 445) stated that only 150 of the 600 to 800 Aboriginal people who frequented Adelaide were of local origin.

**Conclusions**

Access to reliable water and the wide range of plant and animal foods available in the Lower Murray riverine and adjacent mallee ecosystems provides environmental data to generate hypotheses about past variability in hunter-gatherer subsistence-settlement systems in the region. Ethnographic and historical data relating to diet and landscape use in various regions of the Lower Murray can contribute to model building and hypothesis testing. However, models relating to pre-contact seasonal mobility or increased sedentism associated with long-term use of residential bases must be tested employing a range of archaeological and environmental data in order to assess the validity of their application across space and time.

In relation to support for hypotheses regarding the presence of semi-sedentary or sedentary hunter-gatherer lifeways along the Lower Murray during the late Holocene, archaeological research must establish multiple lines of independent evidence that suggest the long-term use of base camps associated with particular riverine landscapes or territories. Collaborative research projects involving archaeologists and various Aboriginal communities in the region will be essential to the successful achievement of these goals.

In order to test these hypotheses across the Lower Murray region, improved data associated with the following areas is required:
Expanded excavation and chronometric dating for a range of site types, including rockshelters, middens, mounds and cemeteries to demonstrate long-term use particular archaeological sites (cf. Littleton et al. 2017; Pate et al. 1998, 2003; Wilson et al. 2012);

Comprehensive and systematic analyses of faunal and floral remains and artefacts associated with various archaeological sites to demonstrate past use of a range of key animal and plant foods;

Expanded analyses of earth mounds to provide archaeological and environmental evidence to support ethnographic models regarding the processing and use of a range of key plant and animal foods, including faunal analyses and residue analyses (chemical, phytolith) of grindstones to establish association with plants like *Typha* spp.;

Expanded stable isotope baseline values in bone and teeth for a range of animals associated with different diets and habitats;

Expanded stable isotope data base in bone and teeth for human remains associated with a range of cemetery and other burial sites across different habitats to demonstrate long-term ties to particular sites and regions, i.e., presence of base camps or territories; and

Comprehensive and systematic employment of physical anthropology associated with a range of cemetery and other burial sites across different habitats.

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