Behavioural Ecology of the Southern Emu-wren (*Stipiturus malachurus*)

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Abstract

In this thesis, I describe the behavioural ecology of an Australian passerine, the Southern Emu-wren *Stipiturus malachurus* (Maluridae). The southern emu-wren is threatened in several parts of its range, and yet information on the species’ breeding biology, habitat use and mating system is lacking. These data are fundamental to effective conservation management. My research investigated the breeding behaviour and habitat ecology of a population of southern emu-wrens in Portland, Victoria, Australia, over three breeding seasons (2000/01, 2001/02 and 2002/03). I also collected data pertaining to habitat use from populations located in Anglesea and Lower Glenelg National Park (Victoria, Australia).

Southern emu-wrens commonly formed socially monogamous pair bonds, although cooperative breeding was observed for the first time in this species, where male offspring within several families delayed breeding to help raise younger siblings. Successful nests produced 1.8 fledglings on average, however, a nest had only a 56% chance of success during incubation and nestling phases. Nest failure was mainly attributed to depredation and snakes were identified as major nest predators. The slow breeding rate of the southern emu-wren is typical of a small passerine in the Southern Hemisphere. Nevertheless, adult mortality was unusually high. In one breeding season the adult population was reduced by 50%. The population recovered when individuals dispersed from the adjacent coastal heathland to fill territory vacancies. This highlights the vulnerability of populations to local catastrophe, and potential extinction if spatial separation of populations exceeds the species’ dispersal capacity.

In view of the ongoing threats facing habitats occupied by the southern emu-wren, it was important to identify the fine-scale habitat preferences of the species. Emu-wrens appeared to discriminate between habitats according to structural rather than floristic characteristics. Habitats with dense vertical foliage of shrubs, grasses and sedges/rushes between ground level and 100 cm, and dense horizontal cover of medium to tall shrubs were used most frequently. However, when availability of habitat was taken into account, habitat use was negatively correlated with the vertical density of low shrub foliage and species richness. Within habitats, emu-wrens more frequently used plant species that had a dense canopy cover (26 ± 2% of total cover, crown diameter 93 ± 5 cm), high foliage density between 50-100 cm, and average heights of around 1
Plant species in which the birds nested comprised ~14% of total canopy cover and were
densest between ground level and 50 cm. Canopy cover, vegetation height and vertical foliage
density were consistently important variables correlated with emu-wren habitat use at multiple
fine-scales.

The breeding success and survival of emu-wrens during the breeding season was closely related
to the habitat composition of territories. Prey abundance, based on total insects and preferred
nestling prey types, varied significantly across emu-wren territories according to habitat type.
Reproductive success (number of offspring fledged) was highest in territories containing a
greater proportion of tall shrubland, which had the highest insect abundance of any habitat.
Closed heathland and sedge/rushland also had high food abundance compared to other habitat
types, but higher fledging success occurred only within closed heathland, possibly because
predator density was lower in this habitat type. High snake density was associated with reduced
adult survival during the breeding season and a lower probability of nest success. In
sedge/rushland, any benefits of prey abundance may therefore be offset by a high density of
predators. Emu-wren age and size were unrelated to breeding output of pairs, suggesting that
ecological factors may swamp effects of individual quality on emu-wren fitness components.
Effective conservation management of the southern emu-wren therefore needs to consider not
only the preservation and restoration of key habitats but also joint management of predator
populations.

Biparental care appears essential to the survival of emu-wren offspring. Males contributed a
higher rate of provisioning and brought larger prey items to the nest than females. Female
provisioning rate appeared to be constrained by lengthy periods devoted to brooding nestlings.
Paternal contributions were greater for larger broods, while female effort remained constant
regardless of brood size. Southern emu-wrens are an ideal study model for exploring
evolutionary theory relating to sex-biased parental care because the species is sexually
dichromatic and these plumage differences develop when offspring are only seven days old.
There were no biases in the proportion of feeds to broods of different sex ratio or sons and
daughters, however, parents biased the size and type of prey fed to sons and daughters, feeding
sons more profitable and larger prey items in the late nestling phase. Parents may bias care
towards sons due to their higher energetic needs associated with size and plumage dimorphisms, or their tendency to become cooperative helpers, thus repaying the cost of parental investment.

To investigate the genetic mating system of the southern emu-wren, I isolated and characterised 7 hypervariable microsatellite loci from southern emu-wrens for use in paternity analyses. Extra-pair matings compromised 9% of fertilisations in this population. Several behavioural factors appear to contribute to the low frequency of EPP occurring in the southern emu-wren. High dependency on paternal care appears to constrain females to monogamy, as the risk of reduced paternal assistance would be costly to female reproductive success. Furthermore, the benefits of paternal care may far outweigh potential benefits of EPP to males and restrict time available for EPC. In the closely related fairy-wrens, helpers compensate for reductions in paternal care, thus facilitating high rates of EPP. The infrequent occurrence of cooperative breeding in southern emu-wrens may therefore account for the extreme differences in the level of EPP in the fairy-wrens and emu-wrens.
Declaration

This is to certify that

(i) the thesis comprises only my original work except where indicated in the preface,
(ii) due acknowledgement has been made in the text to all other material used,
(iii) the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Signed by _______________________________

Grainne S. Maguire

December 2005
Preface

The research reported in this thesis was conducted with approval from the Faculty of Science Animal Experimentation Ethics Sub-committee at the University of Melbourne (Register no. 00055), under Department of Natural Resources and Environment (now Department of Sustainability and Environment) permit number 10001755, and Australian Bird and Bat Banding Scheme authority number 2472. Some fieldwork was conducted with the assistance of volunteers working under my supervision. These volunteers contributed labour in the field and played no part in the analysis or interpretation of the results. In particular, volunteer assistants helped with the collection of vegetation measurements where data collection required two people for efficiency (roles of observer and recorder; Chapter 3) and with sampling of the insect fauna of the field site (Chapter 4). Volunteers also assisted with bird capture and processing by helping set-up mist-nets and recording data (Chapters 2, 3, 4, 5). Volunteers helped search territories for colour-banded birds on a daily basis and assisted with set-up of video surveillance equipment at nests (Chapters 2, 3, 4). All field assistants are mentioned in the acknowledgements section.

Development of microsatellite markers (Chapter 6) was conducted under the guidance of my supervisor and laboratory managers, who are duly acknowledged.

The thesis is a series of five papers (Chapters 2-6), preceded by a chapter of aims (Chapter 1) and concluded with a general discussion (Chapter 7). This approach has led to some repetition in the methods section. Chapter 2 is published in Australian Journal of Zoology (2004) 52, 583-604, co-authored by Raoul Mulder. Raoul provided detailed advice and feedback. Chapter 3 has been accepted for publication by Wildlife Research (September 2005), and Chapter 4, by Journal of Avian Biology (September 2005). Chapters 5 and 6 will be published with Raoul Mulder as a co-author. Raoul provided advice and feedback for these papers. I am the principal contributor to all chapters in this thesis, and the primary author on all publications arising from this thesis.
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Chapter 1

Introduction

This thesis investigates the behavioural ecology and conservation biology of the southern emu-wren *Stipiturus malachurus*, a diminutive member of the *Maluridae*. Although many other members of this family have been the subject of extensive research (Rowley and Russell 1993; Mulder *et al.* 1994; Brooker and Rowley 1995; Dunn and Cockburn 1996; Mulder 1997; Rowley and Russell 1997; Van Bael and Pruett-Jones 2000; Rowley and Russell 2002), our knowledge of emu-wren ecology and behaviour is based almost entirely on field notes taken by Fletcher almost a century ago (Fletcher 1913, 1915).

Within the Maluridae, a number of emu-wren (*Stipiturus*), grasswren (*Amytornis*) and fairy-wren (*Malurus*) species and subspecies are classified as threatened (Garnett and Crowley 2000). The primary threats to these species are habitat fragmentation and destruction. The restricted flight capabilities of these small passerines contribute to isolation of populations in a fragmented landscape, poor gene flow and an increased vulnerability to catastrophic events. Emu-wrens are particularly poor fliers, associated with their short rounded wings and long, characteristic tail of reduced structure, which appear more adaptive for scurrying through dense undergrowth (Schodde 1982).

In South Australia, draining and clearance of native swamplands and a series of major fires have severely detracted and fragmented the range of the Mount Lofty Ranges subspecies of southern emu-wren (*Stipiturus malachurus intermedius*; Littlely and Cutten 1994). This subspecies is classified as endangered, nationally (Environment Protection and Biodiversity Conservation (EPBC) Act) and in South Australia (National Parks and Wildlife South Australia (NPWSA) Act), and remaining populations face threats from continued modification of habitat, fire and introduced predators (Littlely and Cutten 1994; Garnett and Crowley 2000). Two other subspecies, the Eyre Peninsula southern emu-wren (*S. m. parimeda*) and the Dirk Hartog Island southern emu-wren (*S. m. hartogi*), are classified as vulnerable nationally (EPBC Act) due to their entire range falling within less than 100 km$^2$ (Garnett and Crowley 2000).
Conservation of threatened and endangered populations relies on a comprehensive understanding of the ecology and behaviour of a species (Beissinger 1997; Buchholz and Clemmons 1997). Understanding dispersal behaviour and habitat selection is implicit to the design of habitat reserves and wildlife corridors. Furthermore, effective population size cannot be accurately predicted without knowledge of the mating system of a species and skews in breeding sex ratio and reproductive success (Parker and Waite 1997). In cooperative breeders, for example, the number of breeders is much smaller than the size of the adult population because many individuals help at the nest rather than breed independently (Komdeur and Deerenberg 1997).

The primary aims of this thesis are to contribute information for effective conservation management of the southern emu-wren, and to explore behavioural and genetic aspects of the species’ mating system, with particular emphasis on parental care behaviour.

First I describe the breeding ecology and demographics of the southern emu-wren (Chapter 2). Cooperative breeding is widespread throughout the Maluridae, where helpers delay breeding to assist the pair with caring for offspring (Rowley and Russell 1990). Fletcher (1913, 1915) and Pickett (2000) have reported sightings of southern emu-wren family groups remaining cohesive during the breeding season and suggested that the species might also be a cooperative breeder. While the Mount Lofty Ranges southern emu-wren recovery team have collected demographic and life-history data from colour-banded populations in South Australia (Pickett 2000), these data were limited because nest monitoring was avoided to minimise disruption to the breeding of this endangered subspecies. In Chapter 2, I describe aspects of the species’ breeding behaviour that have not been previously described and provide data necessary for interpretation of later chapters.

Preservation and restoration of habitat appear to be key issues for the conservation of the southern emu-wren. Emu-wrens occupy a range of habitat types in temperate and subtropical zones within Australia (Higgins et al. 2001), however, the species’ fine-scale habitat preferences have not been explored in detail. In Chapter 3, I investigate emu-wren use of habitat and microhabitat within territories at three Victorian field sites (Portland, Anglesea and Lower
Glenelg National Park), and for the first time, characterise the species’ nesting preferences. I examine habitat use relative to availability and the composition and structure of vegetation.

Traditionally, species’ occupancy or population density have been used to infer habitat quality (Breininger et al. 1995; Garshelis 2000). However, in view of the constraints to territory selection arising from competition and limited dispersal opportunities (Fretwell and Lucas 1970; Pulliam 1988; Caughley 1994), a more informative approach to assessing habitat quality is to explore variation in the breeding success and survival of individuals in a population across habitat types (Jones 2001; Luck 2002a). In Chapter 4, I investigate variation in fitness components of emu-wren pairs related to territory quality. I use complex statistical models to determine which attributes of the territory, including vegetation characteristics, resource abundance and predator densities explain variation in reproductive success and survival of emu-wren pairs during the breeding season. Emu-wrens are predominantly insectivores, however, data on diet selectivity is lacking (Higgins et al. 2001). I therefore examine the prey content of the nestling diet using video surveillance observations and compare this to availability in the environment by sampling aerial and foliage-based insects. Individual quality can interact with, or confound the effects of territory quality (e.g. Dale and Slagsvold 1996; Bart and Earnst 1999), hence I attempt to control for this effect by including age and morphometrics of pairs in all analyses.

Parental care behaviour is closely linked with the evolution of mating systems (Wittenberger and Tilson 1980). Parents have limited resources to invest in offspring and this can come at a cost to survival and future reproduction (Trivers 1972). In birds, biparental care is usually necessary for successful rearing of offspring. However, reduced male care might be expected in environments where food is abundant, permitting females to successfully raise offspring unaided and males to increase their reproductive success through mating opportunities with other females (Davies 1992; Silver et al. 1985). In Chapter 5, I explore the contributions of the sexes to parental care. In sexually dimorphic species, allocation of care is expected to differ for the sexes based on energetic demands, differential dispersal behaviour or the perceived value of the sexes (Lessells 1998, 2002). Emu-wren offspring develop sexually dichromatic plumage seven days after hatching, providing an opportunity to explore whether parents differentiate their level of care for sons and daughters. Sex-biased investment can have important implications during seasons of
low food availability, and can be a mechanism for biasing the population sex ratio (Breitwisch 1989; Teather 1992).

The frequency of extra-pair paternity (EPP) varies considerably between avian species, with some of the highest rates recorded within the fairy-wrens (Brooker et al. 1990; Mulder et al. 1994; Karubian 2002). A number of hypotheses attempt to explain this interspecific variation including the ‘constrained female’, ‘restricted schedule’ and ‘adult survival’ hypotheses. In Chapter 6, I use microsatellite analysis of paternity to determine the genetic mating system of the southern emu-wren. Southern emu-wrens are Malurids with high levels of paternal care and low annual survival, and each of these characteristics predicts varying levels of EPP according to the major hypotheses.

I conclude this thesis by discussing the main results of my research and by highlighting deficiencies in our knowledge of the species. I also provide suggestions for future research (Chapter 7).
Breeding biology and demography of the Southern Emu-wren


**Abstract**

The breeding biology and demography of the southern emu-wren (*Stipiturus malachurus*) were studied over three breeding seasons (2000-2002) in the south-west of Victoria, Australia. The nesting biology of the species was typical of the family Maluridae: clutch size ranged from two to three eggs, the incubation period averaged 19 days, and nestlings fledged on average 14.2 days after hatching. In total, 69% of clutches successfully hatched and 67% of broods produced fledglings, with a mean of 1.8 young fledged per clutch. Males provisioned offspring at high rates, while females were exclusively responsible for incubation and brooding. Nest failure was mainly due to predation, mostly by snakes. Cooperative breeding was observed for the first time in this species, with male offspring delaying breeding to help raise younger siblings. Juveniles were capable of breeding in their first year and dispersed as far as 1.2 km away. Mortality of individuals was high and the mean duration of pair bonds was short ($5.63 \pm 0.62$ months, $n = 62$). Population numbers fell dramatically in September 2001, when almost half the adult population disappeared, which suggests that this population could be vulnerable to local extinction.

**Introduction**

Emu-wrens (genus *Stipiturus*) and fairy-wrens (genus *Malurus*) of the family Maluridae are closely related and share several morphological traits. However, although there have been a number of long-term studies of several fairy-wren species (e.g. Rowley and Russell 1993; Mulder *et al.* 1994; Brooker and Rowley 1995; Dunn and Cockburn 1996; Mulder 1997; Rowley and Russell 1997; Van Bael and Pruett-Jones 2000; Rowley and Russell 2002), comparatively little is known about the biology of emu-wrens. Hence, it is unclear whether the emu-wrens share many of the unique behavioural traits exhibited by *Malurus* species, such as cooperative
breeding (Rowley and Russell 1990) and elaborate extra-pair courtship displays associated with a promiscuous mating system (Brooker et al. 1990; Green et al. 1995; Mulder 1997).

The emu-wrens are the smallest malurids and exhibit distinctive morphological traits. For example, the tail has only six retrices, where the individual feathers resemble those of the emu (Dromaius novaehollandiae), giving rise to the common name for the genus. Of the three Stipiturus species, the southern emu-wren (Stipiturus malachurus) has the broadest distribution (Higgins et al. 2001), and, depending which taxonomy is adopted, might be further divided into seven (Rowley and Russell 1997) or eight (Schodde and Mason 1999) subspecies. Three of these subspecies are currently listed as threatened according to IUCN Red List categories (IUCN Species Survival Commission 1994; Garnett and Crowley 2000; EPBC Act).

The southern emu-wren is a small (5-9 g) insectivorous passerine that is a sedentary resident of temperate and subtropical zones of southern and eastern mainland Australia, as well as Tasmania and several small, offshore islands (Barrett et al. 2003). It lives in typically low dense vegetation, including wet and dry heathlands, swamps, sedge/rushlands, tussock grasslands, shrublands and open forests with a heath understorey (Higgins et al. 2001). The species has limited flight capabilities because of its long, graduated tail and short, rounded wings and hence the birds rarely fly or venture from the cover of dense vegetation. As a consequence, emu-wrens are extremely difficult to observe, which probably accounts for the lack of information on their biology. Published studies of southern emu-wrens are limited to the field notes of Fletcher (1913, 1915) on the nesting behaviour of the Tasmanian subspecies (S. m. littleri), and to a series of reports describing the demographics of populations of the endangered S. m. intermedius in the Mount Lofty Ranges (Littlely et al. 1997, and reports therein; MLR Southern Emu-wren Recovery Team 1998; Pickett 2000).

I report here on a 3-year study of the breeding behaviour of colour-banded southern emu-wrens (S. m. malachurus). These data form part of a larger study of the habitat ecology, demography and mating system of this species. In this chapter I describe 1) population demographics, in particular longevity, juvenile dispersal and population sex ratios; 2) courtship, pair formation and persistence; and 3) nest characteristics, the breeding cycle and fledging success.
Methods

Study area

I studied southern emu-wrens from July 2000 to March 2003 in a network of swamps, wet-heath and adjacent coastal heathland at Portland, south-western Victoria (38°23’ S, 141°36’ E). The study site is elevated and close to cliffs bordering the Southern Ocean and hence frequently experiences strong, moist, on-shore winds. Portland has an annual rainfall of 821 mm and the highest rainfall occurs in June and August. The annual mean minimum temperature is 5° C and the mean maximum is 24° C. During the years monitored, the coldest months were from May to August and the hottest month was February (Victorian Regional Office of the Bureau of Meteorology).

The main study site was a 16 ha wetland system owned and managed by Portland Aluminium. The area was formerly a dumping site for smelter waste, but has been intensively modified and rehabilitated following the implementation in 1991 of a master plan for the management of a ‘Smelter in the Park’ concept (Brake et al. 1991). Because this area was originally a taxonomically rich stand of wet heath, a series of swamps was constructed and major replanting operations were undertaken to create a wetland system. The area now consists of a patchwork of dense wet heath, open dry heath, sedge/rushlands and swamps, interspersed with occasional stands of native trees. The dominant species within this heathland area include prickly teatree (Leptospermum continentale), scented paperbark (Melaleuca squarrosa), coast beard heath (Leucopogon parviflorus), scrub sheoak (Allocasuarina paludosa), pithy sword-sedge (Lepidosperma longitudinae), sea-rush (Juncus krausii), short purple-flag (Patersonia fragilis) and coast spear-grass (Stipa flavescens). Weeds within the area are intensively managed, with frequent chemical and mechanical eradication of outbreaks of coast wattle (Acacia longifolia var. sophorae), gorse (Ulex europaeus) and blue pea (Psoralea pinnata). This area was occupied by between 9 and 15 emu-wren pairs during the study. Emu-wrens defended territories of 0.30 to 2.86 ha (mean 0.97 ± 0.09 ha, median 0.83 ha, n = 51) year-round on the study site, although boundaries became less defined over the winter months.

In August 2002 I extended the study site to incorporate two additional areas of emu-wren habitat. The first area, referred to as ‘Burnt Hill’, was a 2 ha natural swamp at the southern end of the wetland area, which had regenerated post-fire as thick coastal scrub. This was dominated by
coast daisy (*Olearia axillaris*), seaberry saltbush (*Rhagodia condolleana*) and coast beard heath (*Leucopogon parviflorus*), with an understorey of sedges, including coast sword-sedge (*Lepidosperma gladiatum*) and native tussock grasses (*Poa labillardierei*). The area supported 2-3 emu-wren pairs during the study, occupying 1.15 ha on average. The second extension, known as ‘Dean’s Heath’, was a 4 ha area of coastal dune extending west of the smelter property, dominated by coastal heath including coast wattle, silver banksia (*Banksia marginata*), dusty miller (*Spyridium parvifolium*), winged spyridium (*Spyridium vexilliferum*) and *Correa* species. During the study this area was occupied by 6-7 emu-wren pairs inhabiting territories of 1.11 ± 0.10 ha.

**Capture and colour-marking of individuals**

I captured emu-wrens in mist-nets, either by erecting nets along regular pathways traversed within a territory, or by herding individuals towards nets. Once captured, each bird was individually marked with a numbered metal ring (Australian Bird and Bat Banding Scheme) and a unique combination of three colour bands, one above metal and two on the opposite tarsus. For each captured bird, I measured body mass (to the nearest 0.1g using a Pesola balance), tail length (longest completely developed middle retrix; to the nearest 1mm using a flat ruler), wing length (from carpal joint to flattened tip of longest primary; nearest 1mm using a blunt-ended ruler), male bib width and length (area covered with blue feathers; nearest 1mm using dial calipers), overall head length (back of head to tip of bill; nearest 0.01mm using dial calipers) and tarsus length (nearest 0.01mm using dial calipers). I recorded the sex of the individual based on sexually dichromatic plumage: males can be distinguished from females by the presence of a lavender blue bib and supercilium. I noted the presence or absence of a brood patch, cloacal protuberance and/or bent tail, as well as signs of moulting. I assessed mite load for each bird by qualitatively scoring mites from 1-10 (1 = 1-10% mite coverage of primary, 2 = 11-20% mite coverage of primary, etc) for each primary.

Juveniles develop their adult plumage within 4-6 months of fledging and are thereafter indistinguishable from adults. If an individual was captured with adult plumage in August, I estimated age as 9 months, based on a minimum assumption that the individual had fledged in November the previous breeding season (the peak fledging period). I estimated the age of any individuals arriving at the study site in February and showing signs of juvenile plumage (more
diffuse streaking, unstreaked ear coverts, duller colouration of bib, lores and supercilium, zero 
wear on primaries and retrices) as 3 months old.

**Population monitoring**

I conducted regular (4-6 days per week) census counts of the emu-wrens during each breeding 
season, from the last week in July until early March of the next year (I refer to the 2000/01 
breeding season as the 2000 season, and so on, throughout this chapter). To facilitate navigation 
and enable precise geographic recording of the location of censused individuals, I erected posts 
at 100 m intervals in a grid. Using a spot mapping area-search approach (Pyke and Recher 1984; 
Bibby et al. 1992), I monitored sites for emu-wrens following regular routes through known 
territories. The order of visits to territories was alternated daily. Morning observations began one 
hour after sunrise and extended until noon or earlier if extreme climatic conditions prevailed 
(strong winds, rain or high temperatures). I resumed area searches 3-4 hours before sunset, or 
when climatic extremes abated, and continued until nightfall.

For each emu-wren observed, I recorded the following information: time first sighted (Eastern 
standard time, EST), the group size, sex, age class and colour-band identity of birds, notes on 
behaviour, and their location using a Garmin GPS II+ unit with auto average capability and 5-10 
m spatial accuracy. I observed birds for as long as they remained visible, which, on average, was 
for 9.8 min (median 4 min, \[ n = 1773 \]). Due to the difficulty of observing emu-wrens, this 
translated to only 6.6% of observation time out of 208, 494 and 732 person-hours spent 
surveying the study sites in each of three seasons respectively.

**Longevity**

For juveniles I calculated longevity from the month of fledging to the month of the last known 
sighting of that individual. For adults I estimated age at banding and calculated longevity to the 
last month sighted. For individuals banded in the final breeding season, I made two visits in the 
following breeding season (2003) to census banded birds. I did not census the birds during each 
winter. Thus, if an individual was present at the end of one season but absent at the start of the 
next, I used the last month it was seen as the date of disappearance. My estimates of longevity 
are therefore minima.
Dispersal
I searched 52 ha of habitat surrounding the study site during the breeding season in an attempt to locate dispersing juveniles. I converted GPS readings (Australian Map Grid datum 1984) of the location of dispersing juveniles, from latitude/longitude coordinates to projected coordinates in Eastings/Northings using the program GDA Geocentric Data of Australia 1994. I then imported these converted data into ArcView GIS 3.2A (Geographic Information System by ESRI 1999, New York) with the Spatial Analyst extension. I then calculated the distance each individual had dispersed from the projected aerial image.

Nest monitoring
I found nests by following adults engaged in building or females engaged in incubation back to the nest, by flushing females from the nest during incubation, or by following adults that were feeding nestlings. In some cases I found evidence of an active nest, but the nest itself could not be found. For example, I occasionally captured females with swollen abdomens (indicating the presence of an egg about to be laid), or observed females with a bent tail (suggesting incubation), or recorded males or females with nesting material or carrying prey to an unknown location. In cases where these observations were repeated over a week or more, I recorded this as a ‘nesting attempt’ for the relevant pair. Nests were found at various stages of development, and in 67% of cases ($n = 49$), I estimated the date the first egg of the clutch was laid, by calculating backwards from the age of the nestlings or fledglings. I estimated the age of fledglings using tail length (Pickett 2000). I visited nests every 1-2 days to record clutch sizes, dates of hatching and fledging, and to band and measure nestlings when they were between 11-14 days old. Daily mortality rates were calculated following Mayfield (1961, 1975) to obtain the probability of nest success during each stage (incubation or nestling period). For all nests the date of failure was known.

During the 2000 and 2001 seasons, I carried out 90 min nest watches at each nest during the nestling period. The observer was situated out of view and within 15 m of the nest, and recorded the time of each visit and the identity of the attending bird. In 2002, I set up miniature charge-coupled device (CCD) cameras near individual nests. For nests found during the building phase, I set up cameras on the day after the last egg was laid (one day after incubation began) to
minimise disturbance to the nesting pair. For all other nests located, I installed cameras as promptly as possible. I recorded ~8 h of video at each nest per day, starting at ~0745 h.

**Nest site characteristics**

Once a nest had ceased being used, I measured the following attributes: direction the nest entrance faced (aspect) in degrees, distance from the ground to the base of the nest *in situ*, distance from the top of the nest to the height of the foliage, height of the nest plant (all to nearest cm), width of the nest plant, height of understorey species and distance from nest entrance to the outer edge of the nest plant. For analysis, I assigned the bearing of the aspect, measured in degrees, to one of four quadrants (north, south, east, west). I also measured the surrounding vegetation, including the approximate mean height of vegetation within a 2 m radius of the nest, and the distance from the nest plant to the nearest shrub, sedge/rush or grass tussock. Finally, I removed the nest and measured the following dimensions using dial calipers: outer height, width and length, entrance width and height, and depth from the inner lip of the base of the entrance.

**Statistical analysis**

I present all data as means ± standard error. Morphometric data were approximately normal. I compared variation in morphometrics for the sexes in each age class using ANOVA. I examined collinearity between adult morphological characters using Pearson correlation coefficient matrices. I calculated an index of relative body mass using the residuals of body mass against the first principal component of all body-size attributes. I used REML models to compare the morphological characters of the sexes within mixed-sex broods and between single-sex broods, using nest identity as a random effect and sex as a fixed factor. To predict success or failure of a nest based on its size and positioning, I entered all nest characteristic variables measured into a forward stepwise, logistic-regression model. I used ANOVA to compare nestling provisioning rates (feeding visits per hour) across pairs and according to sex of the attending adult.

**Results**

**Adult morphology**

The sexes showed slight but significant dimorphism in several morphometric measures; males had greater wing, tail, head-bill and tarsus lengths than females (Table 1). There were no
differences in body mass between the sexes and mite loads were equivalent. There was no relationship between weight and the principal component of body-size attributes, so that I could not calculate an index for body condition of adults ($F_{1,62} = 0.033, p = 0.857$). In females, body mass was negatively correlated with mite load (Pearson correlation coefficient $= 0.529, n = 30, p = 0.003$).

Moulting of primaries was characteristic of adults captured in February and March. I most commonly observed the gradual replacement of retrices in birds captured from December to March. Body plumage moulting was observed late in the breeding season, although a considerable number of adults exhibited crown and flank moult from October onwards.

**Social organisation and demographics**

Table 2 outlines the composition of the population at Portland over three breeding seasons, including the percentage of individuals banded per season of the total population, and the percentage of all banded birds resighted from one season to the next. In 2001, 43% ($n = 14$) of individuals not resighted were juveniles (either banded as nestlings or young fledglings) and these individuals might have dispersed from the area rather than died. Population numbers fell halfway through 2001, with 18 banded adults (75% of the adult population) disappearing during 1 month. The population recovered to 23 individuals and in the following 2002 season, I resighted 52% of banded individuals that were alive at the end of 2001. In a 1-week census in November 2003 I resighted only 37% of banded birds ($n = 13$) across all sites.

**Longevity and site fidelity**

The oldest surviving individuals were males and were 48 and 43 months old respectively (a minimum estimate as they were still alive November 2003). The oldest female was 36 months old and paired with the oldest male on site. Overall, the mean age for adults was 18.8 months (females $17.9 \pm 1.2$ months, $n = 34$; males $19.8 \pm 1.3$ months, $n = 34$). The cause of adult mortality was unknown in most cases, although in two cases leg fractures that occurred during nesting resulted in females becoming virtually immobile for ~2 months before disappearing from the site and another male was sighted missing one leg prior to disappearance. A further 22% of disappearances occurred when pairs had an active nest with eggs or nestlings ($n = 13$), an additional 32% during the breeding season ($n = 19$, of which 61% were either long-term pairs or
sighted courting or nest building just prior to disappearance), and 41% occurred during winter ($n = 25$) and thus potentially could include dispersal events. It is likely that most birds that disappeared died, because they were not located during censuses of adjacent areas of habitat. However, several individual breeders changed territories and although two females were not observed for 2 and 12 months, respectively, they reappeared at the study site. Consequently other banded birds might still have been alive outside the study area and my estimate for survival of territory holders must be considered conservative.

The longest occupation of a territory by any one pair was 26 months (mean 13.2 months). Individuals showed high site fidelity, although upon losing their partner, males were more likely to remain on the territory (92%, $n = 12$) whereas females were more likely to disperse (67%, $n = 12$). The mean duration that any one adult remained on site was 8.3 months. This was similar for males and females across seasons, although in 2001 disappearance of individuals tended to be biased towards females (females 4.3 months, males 6 months). Unbanded adults appeared at the study sites at all times of the year, indicating immigration of individuals from surrounding areas. The timing of disappearances for both adults and juveniles was highest within breeding seasons compared with winter, with the exception of 2003 when a high number of individuals disappeared over winter.

**Juvenile dispersal**

Individuals banded as nestlings/fledglings remained on the study site for a mean $4.3 \pm 0.7$ months ($n = 48$) and mean dispersal age was 3.8 months post-fledging. Most juveniles, that is, individuals less than one year old, arrived at the study site during November and February. Only 9 of 39 individuals banded as nestlings/fledglings dispersed and were resighted on vacant territories within the study site. However, no other banded individuals were found in the 52 ha area surrounding the study site, despite regular bimonthly searches and sightings of 89 unbanded individuals. The mean distance dispersed by those juveniles resighted was 593 m (range 300-1200 m) (Fig. 1). A further 6 juveniles (5 males) remained on the natal territory after reaching independence. Four of these males acted as helpers for one season on their natal territories, one inheriting his natal territory after the disappearance of the breeding pair. I observed another male foraging independently 2 months after fledging, but he then returned to his natal territory.
Of the juveniles that disappeared from the field site, several were observed ~2 months after fledging, foraging with their parents or siblings beyond the boundaries of the natal territory and then with siblings up to 900 m away. Either these individuals successfully dispersed beyond the surveyed area, or they died while dispersing. However, 8 juveniles that disappeared within 2 weeks of fledging most probably died. During the winter of 2003 I observed a group of juveniles that had fledged 3-6 months earlier, foraging together and moving as a cohesive unit, with individuals calling to each other. Two of these juveniles remained and established a breeding territory in this area.

Pair formation
Ten individuals banded as nestlings first formed partnerships at 4 ± 0.61 months old (minimum 2 months). Generally, juveniles that fledged early in the season (September-October) had paired by the end of the same breeding season (83%, December-February,  \( n = 6 \)) and those that fledged late in the season (January-February) were typically resighted at the beginning of the next breeding season with partners (\( n = 4 \)). Dispersing juveniles paired with other dispersing juveniles (\( n = 8 \)) more commonly than widowed adults (\( n = 2 \)). Breeding was never observed in individuals younger than 8 months old.

Of 62 pairs monitored over 3 successive years, only one partnership remained intact across all 3 seasons, whereas 5 partnerships remained stable from one season to the next. The longest pair bond was an estimated 28 months; however, I based this only on those seasons monitored. The average duration of partnerships within a season was 4.2 months, which is approximately half the length of the breeding season (2000: 5.64 ± 1.12 months, \( n = 7 \); 2001: 3.45 ± 0.54 months, \( n = 28 \); 2002: 3.50 ± 0.52 months, \( n = 27 \)). Once pairs formed, individuals appeared to show strong fidelity to their mates. When two females became injured, their male partners devoted 7 and 14 weeks of the breeding season, respectively, to feeding the females until they disappeared; one pair abandoned a nest with three 4-day-old nestlings.

Mortality was the main cause of termination of the pair bond. All 7 pairs banded in 2000 remained intact until the end of the season. During 2001, mortality rates were higher and several divorces occurred (where both members of a pair survived but changed partners), so that only 64% (\( n = 28 \)) of partnerships remained intact. Six changes in partnerships were caused by the
mortality of one member of the pair, and on a number of territories individuals lost several partners in succession. During 2002, 59% \((n = 27)\) of pairs remained stable until the end of the season. All partnerships that changed were the result of mortality and partners were typically replaced within 1-2 weeks.

I recorded eight cases of divorce. In each case, pair separation followed an unsuccessful breeding attempt. Typically, the female left the territory and the male remained \((88\%, n = 8)\), but I do not know whether she dispersed voluntarily or was evicted. Usually both members of the pair found new partners within 2 weeks, but in one case the dispersing female was without a partner for 2 months.

There were 9 cases of breeding dispersal (7 females, 1 male, and 1 pair). These were all in response to separation or mortality of a partner/pair, with individuals dispersing to another territory. The greatest distance any individual moved was 600 m over a 1 month period. In addition to these movements, several pairs shifted their territory boundaries or expanded the territory during the winter \((n = 2)\) or breeding season \((n = 3)\).

**Breeding biology**

**Cooperative breeding**

I observed cooperative breeding, in which an individual forgoes breeding to assist a breeding pair with rearing their brood (Brown 1987), in 8% of pairs at Portland \((n = 48\) pairs), occurring in 2 out of 3 seasons monitored. Helpers were always male and usually there was only one helper per nest, although I observed two male helpers at one nest. Here the second helper was identified as a son from the first brood that remained to assist with raising the second brood of the season. However, in other cases, if the helper was a son of the breeding pair, he was from a previous breeding season (at least 7 months old). Helpers contributed to feeding the young both at the nest and after fledging, and in defending the nest. Allofeeding of the breeding female by helpers was not observed. All nests with helpers successfully fledged offspring and all had the maximum clutch size of three. The reproductive output of these cooperative groups was thus relatively high compared with most of pairs. Helpers usually remained for the duration of the breeding season or until the brood reached independence. In two instances, helpers inherited the natal territory after the disappearance of both members of the breeding pair.
Courtship and copulation
I frequently observed courtship feeding of females by males during the breeding season, particularly during the months prior to nesting (21 observations, 12 pairs). I often observed the pair moving through the territory in close association, the male leading and uttering a ‘steedada’ contact call, and the female following. Males would often sing before gleaning an insect from the foliage, and offering it to the female. Prey items offered in courtship feeding were often large and included moths, grasshoppers, caterpillars and winged insects. Less commonly, females fed males (3 observations, 2 pairs). Adult females occasionally solicited feeds from males during incubation, fluttering their wings and begging with open mouths. I only observed males ‘wing fluttering’ (Rowley and Russell 1997) in the three days prior to egg laying. I observed allopreening on two occasions, where the male preened his female partner during mid-afternoon within dense cover.

I observed copulation only once, in late September at 0850 h. The female in a cooperative group was being followed closely by the dominant male and, 0.5 m behind, the helper male. The dominant male flew to the female, faced her with breast feathers puffed out and fluttered his wings. He briefly mounted the stationary female and attempted copulation, wings fluttering, after which the female flew off.

Nesting biology
I located 35 nests across three seasons (2000: \( n = 3 \), 2001: \( n = 10 \), 2002: \( n = 22 \)). Nests were extremely well concealed and built in dense sedges/rushes, grasses or shrubs. The outer shell of the nest was composed of dried grasses, stems and leaves, and other materials including fibrous roots, moss, flower petals, seed pods, dandelion fluff and synthetic fluff. These were loosely interwoven into a dome-shaped nest with a side entrance. Nests were lined with softer materials including fine grasses, flowering grass heads, feathers, dandelion fluff, sheep’s wool, rabbit fur, synthetic fluff, hairy seed pods, flower petals, soft leaves and occasionally spider silk.

Most nests faced in an easterly direction (east: \( n = 15 \); north: \( n = 7 \); south: \( n = 6 \); west: \( n = 6 \)) and 51% of nests were situated in shrubs. The most common shrub species was prickly teatree (\textit{Leptospermum continentale}, 34% of all nests). Two nests were found in gorse (\textit{Ulex europaeus}) and one nest each in hedge wattle (\textit{Acacia paradoxa}), rigid bush-pea (\textit{Pultenaea stricta}), silver
banksia (Banksia marginata) and pale turpentine bush (Beyeria lechenaultii). The remaining 49% of nests were situated in sedges/rushes, grasses and/or a groundcover species and, of these, 53% had an overhanging canopy of either prickly teatree (78%) or coast wattle (22%). The most common sedge/rush species in which nests were built were bare twig-rush (Baumea juncea), pithy sword sedge (Lepidosperma longitudinae), sea-rush (Juncus krausii), knobby club rush (Isolepis nodosa), tassel rope-rush (Hypolaena fastigiata) and coast sword sedge (Lepidosperma gladiatum). Grasses included Australian salt-grass (Distichlis distichophylla), Poa and Stipa species, as well as the introduced Yorkshire fog (Holcus lanatus).

Nests were situated at an average height of 0.3 ± 0.04 m above the ground. Average nest dimensions and nest characteristics are summarised in Table 3. Nests were built in vegetation that measured 0.9 m high by 0.9 m wide, on average. Nest openings were close to the edge of the shrub/sedge/rush. Two nests were built above 4 and 7 cm of permanent water, respectively. The distance between successive nests built by the same pair averaged 70.7 m (range 8-160 m). The mean distance between nests built by different pairs on the same territory in different years was 61.5 m (range 3-144 m). None of the nest site characteristics measured were significant predictors of nesting success/failure ($p > 0.316, n = 29$).

I observed nest building 55 times at 25 nests involving 16 different females. In 67% of these observations, only the female was observed building (17 nests), whereas in 22% of cases both members of the pair were seen building (9 nests) and in 11% the male only was observed building (5 nests). The male often accompanied the female when she carried material to the nesting site (62% of the time, $n = 37$) and perched on nearby emergent vegetation. Individuals approached the nest secretively, usually by flying into vegetation at least 10 m away from the nest site and covering the remaining distance by stealthily hopping through the undergrowth. An individual regularly followed a particular route to the nest, although the male and female commonly approached the nest from different areas of the territory. Individuals consistently left the nest using a different route. I observed nest building at all hours of the day, but most commonly in the periods 0800-1200 and 1600-1800 h. Nests took, on average, 19 ± 2 days to build ($n = 7$ nests followed from the earliest stages to completion). The first egg was laid 8 ± 1.4 days after nest completion (range 3-16 days, $n = 9$).
I found most nests at various stages of completion, 8-20 days before laying of the first egg. Three nests were abandoned during the nest-building phase (all by the same female and within days of the observer discovering the nest location) and one nest was destroyed in a storm. After nest loss during building or incubating phases, re-nesting commenced within a very short time (~2 days) and was completed within 8-20 days (mean 14.2 days). Emu-wrens recycled nesting material from old nests when rebuilding, but this was only observed for nests that were abandoned before laying ($n = 4$). Pairs that lost nests after hatching completed building of their second nest within 15 days.

Mean clutch size was $2.7 \pm 0.1$ ($n = 31$). Eggs were laid on successive days and incubation began on the day the last egg was laid. The earliest nesting attempts began mid-August and egg-laying peaked in September (Fig. 2). First clutches were asynchronous in each breeding season, spanning a mean period of 33.7 days (2000: 13/9/00-2/10/00; 2001: 16/8/01-9/10/01; 2002: 17/8/02-14/9/02). Southern emu-wrens are capable of producing more than one brood per season, but this was rare at Portland because of the high rates of nest failure and adult mortality. In 2000, three territories (one helper-assisted group and two pairs) fledged two broods successfully. No multiple broods occurred in 2001. In 2002, one pair fledged two broods of two. Second clutches were commonly laid between November and January.

**Incubation**

Only the female incubated the clutch (531 h of video recording at 10 nests). Captured males did not exhibit brood patches or the distinctive bend in the tail characteristic of incubating females. The average duration of incubation was 19 days (range 13 to 21 days; $n = 5$ nests). Females spent $25.8 \pm 0.5$ min on the nest during each incubation bout and were absent, on average, $36.8 \pm 0.9$ min before resuming incubation. The maximum period for which a nest was left unattended was 4.2 h, and the longest uninterrupted bout of incubation was 1.8 h. On average, a female spent 58.5% of daylight hours incubating, as monitored by video surveillance. Males visited the nest during the incubation period to bring prey items to the female, but only in the week prior to hatching. The visitation frequency of males ranged from once per hour to once in five hours (Fig. 3). The highest visitation rate by a male was 20 visits in 8 hours, which occurred on the day before the eggs hatched. In addition, when the female left the nest, she commonly uttered an alarm call and the male would approach her soon after with a prey item.
Eggs in the same clutch hatched within a 24 h period, 0.5-16.5 h apart, either in the early morning or late afternoon. In 17% of nests, one egg in the clutch failed to hatch (4 of 24 nests that hatched successfully). Of 31 nests in which eggs were laid, one clutch was preyed upon and 5 clutches were abandoned before hatching. In two cases of abandonment, a predator had been previously sighted near the nest. After predation, nests were typically found with the lining pulled inside out and pieces of eggshell left behind. The probability of nest survival during incubation was 0.56 (228 nest-days) and the probability that eggs survived individual loss was 0.56 (573 egg-days); therefore, overall, the probability of egg survival during incubation was 0.31.

Development of nestlings

Hatchlings were blind, pink and mostly naked, with fine grey down on the head and shoulders. On the fourth day of life, head feathers were all in pin and grey down was present down back and tail. Wing pins developed gradually, the webbing of feathers erupting during Days 7-9. Body plumage developed into grey and rufous feathering and males became distinguishable from females from Days 7-9, with bib feathers tinged white-grey compared with the rufous bib of the female. Nestlings were banded 11-14 days after hatching. They were vocal and capable of producing adult-like contact calls (‘steedada’) at this age. In all, 42% of broods were single sex (10 of 24, 55% all male) and when males from all-male broods were compared with females from all-female broods, there were no significant differences in any morphological measures, including body mass of the sexes (Table 4). However, within mixed broods, male nestlings had significantly longer tail and tarsus lengths than their female counterparts (Table 4). There was no evidence of any obvious bias in nestling sex ratios in the 3 years of the study (2000: 8M/10F; 2001: 6M/4F; 2002: 15M/17F).

Nestlings were fed and tended by both parents and by male helpers if present. In total, I collected 880 h of video-recording during the nestling period (16 nests, 14 females). Only the female brooded nestlings. In nests attended by pairs alone, male attendance rates were almost twice as high as those of females (male 7.4 ± 0.4, n = 15; female 4.9 ± 0.4 visits/hour, n = 14). When cooperative groups were considered (n = 2), the attendance rates of males and females were similar to those of pairs (male 7.2 ± 0.5, n = 2; female 4.7 ± 0.6, n = 2) and helper rates were equivalent to that of the dominant male (7.0 ± 0.6, n = 2). Overall, nests with helpers had a
higher rate of attendance, because attending adults did not reduce their rates, but received additional assistance from helpers.

Individuals fledged after a mean 14.3 days in the nest (range 10-18 days, n = 11). The average number of fledglings successfully produced per clutch was 1.8 ± 0.1, n = 36 (2000: 1.6 ± 0.2, n = 11; 2001: 1.6 ± 0.2, n = 13; 2002: 2.2 ± 0.2, n = 12). There was no evidence of any obvious bias in fledgling sex ratios in the 3 years of the study (2000: 7M/11F; 2001: 8M/6F; 2002: 13M/12F). I captured four fledging events on video. On the day before fledging, nestlings ventured from the nest for up to 23 min each time. On the day of fledging, it was common for the adult birds or helpers to visit the nest a number of times without prey, then once fledging occurred, for an adult or helper to occupy the nest, apparently to prevent the young from returning. Fledging usually occurred in the morning.

Once the young fledged, they remained immobile and well hidden in cover, with the tending adults coming back and forth to the one location to provide food. Fledglings became mobile 8-12 days after leaving the nest. At first their flight was clumsy, landings awkward, and they were unable to cross large, open spaces. Fledglings were encouraged to follow tending adults, who produced a variety of calls outside their normal repertoire (‘tchluck’, ‘cluck’). There was no evidence of brood division by parents or helpers after fledging. By Day 25 post-fledging, juveniles were still being fed by adults, yet were developing adult-like plumage, which made them indistinguishable from their parents. By Day 35 post-fledging, juveniles could be distinguished only by the lack of wear on their feathers and a more heavily striated crown. From this age, juveniles were gradually observed more frequently foraging independently on the natal territory. By Day 50, they were entirely nutritionally independent, but would still associate with parents and helpers on occasion.

Adult birds defended young on numerous occasions by circling the observer, producing alarm calls and shepherding young into dense cover. The adult male often increased his visibility, approaching the observer and then flying away from the hidden young, singing atop vegetation and apparently trying to lead the observer out of the area. He would then fall silent and stealthily return, in a series of short flights, close to the ground, often in a large circle. The rodent-run
distraction display (Rowley 1962; Harrison and Parker 1965) was observed on 7 occasions; 5 performances by adult males (4 individuals), 1 by a male helper and 1 by an adult female.

Estimating age of juveniles
When I considered all morphological measures, head-bill length was the best predictor of age (in days) of juveniles ($r^2 = 0.81, F_{1,40} = 173.242, p < 0.001$; logarithmic curve regression: headbill = $\log_{10}(12.69 + 3.45*/$days old)). Tail length was also a good predictor of juvenile age ($r^2 = 0.71, F_{1,42} = 98.599, p < 0.001$; linear regression: tail = $6.91 + 1.07*/$days old).

Breeding success
Table 5 summarises the breeding success of pairs at Portland over three breeding seasons. Thirty-five nests were found in total, of which 31 had eggs and 24 hatched successfully (although in 4 cases, one egg did not hatch). Of those that hatched successfully, 16 broods produced fledglings (42% of eggs produced fledglings, $n=83$), although in 5 of these nests, one chick did not survive to fledging. In two cases where one of the brood died within the nest, the dead nestling was removed from the nest by the adult male or female and discarded nearby. In another case, the dead nestling attracted ants to the nest, causing the surviving young to fledge prematurely. Three nests ($n = 31$ nests) were abandoned after the eggs hatched. One was abandoned 4 days after hatching when the adult female injured her leg. Another female abandoned two successive broods to starvation after losing two consecutive adult male partners (on the day of hatching and 5 days after hatching). The probability of nest survival during the nestling period (274 nest-days), and nestling survival to fledging (683 nestling-days), was 0.56. Overall, the probability of egg and nestling survival from the start of incubation to fledging was 0.29.

Only two potential nest parasites were present in the study site at Portland: Horsfield’s bronze-cuckoo *Chrysococcyx basalis* and the pallid cuckoo *Chrysococcyx basalis*. A single emu-wren nest was parasitized by a Horsfield’s bronze-cuckoo throughout the duration of this study. I found the nest 4 days after the cuckoo had hatched, with the original clutch of two eggs found at the base of the nest shrub. The cuckoo was successfully raised and fledged after ~16 days. On average, the cuckoo chick was visited $20.7 \pm 2.2$ times per hour (90 min nest watches). This is
approximately double the average visitation rate at a normal nest (90 min nest watches: 8.6 ± 1.1 visits per hour, \( n = 7 \)) (Fig. 4).

I identified snakes as nest predators at three nests. One nest with two 5-day-old young was visited by a common copperhead (*Austrelaps superbus*). I observed the snake with its head in the nest, devouring the young (yet leaving behind an unhatched egg) while the adult female was being banded nearby. Two nests were preyed upon by tiger snakes (*Notechis scutatus*) (captured on video). In each case the clutch had been visited by a tiger snake a few weeks earlier, yet the eggs had been left unharmed. It is not clear whether the same individual snakes returned, but broods were subsequently raided by tiger snakes 6 and 8 days, respectively, after hatching. I found another nest intact and empty 9 days after hatching (when young could not yet have fledged), which a snake might also have depredated. I captured on video predation by a feral cat at one nest. This nest was already damaged by strong winds, increasing its conspicuousness, and the nestlings were extremely vocal. At another nest, a cat pounced at the adults while they were collecting prey items for their brood. The adult male produced an alarm call and followed the cat from the territory as it fled from the observer, whereas the adult female coaxed the young from the nest, resulting in a premature fledging.

I often recorded evidence of a breeding attempt within a territory without finding the active nest. In 2000, I found only 20% of suspected nests (\( n = 15 \)), compared with 48% in 2001 (\( n = 21 \)) and 81% in 2002 (\( n = 27 \)). Suspected nests included cases where individuals were seen carrying nesting material, but the nest was never found and there was no evidence that it was successful (\( n = 5 \)); where adult birds were observed carrying prey and behaving secretively, but the nest was not found and fledglings were never observed, suggesting nest failure (\( n = 3 \)); or where dependent young were found on territories where no nest had been found (\( n = 20 \)). Taking into account attempts where nests were not found, an estimated 57% of nests successfully produced fledglings (\( n = 63 \)). This estimate is biased toward successful nests because observations of nest-building or incubation were rare and more likely to be missed than the appearance of fledglings on a territory.
Discussion

Mating system

The closest taxonomic relatives of the emu-wrens (*Stipiturus*) are the well studied fairy-wrens (*Malurus*), which are facultative cooperative breeders exhibiting extremely high rates of extra-pair paternity (Brooker *et al.* 1990; Mulder *et al.* 1994; Karubian 2002). In previous studies of the southern emu-wren (Fletcher 1913, 1915; Pickett 2000), cooperative breeding has never been observed. In this study, cooperative breeding in southern emu-wrens was facultative and appeared to be relatively uncommon. Cooperative groups were more likely to produce a second brood (this study and unpublished data from another population), and had higher reproductive success than pairs in terms of the proportion of successful nesting attempts and number of fledglings produced. However, sample sizes were small. The frequency of cooperative breeding changed across years and did not appear related to habitat saturation or a shortage of mates (‘ecological constraints’ hypothesis: Emlen 1982, 1984). Territory turnover was frequent because of high mortality rates, and hence territories and mates were not in limited supply. Furthermore, individuals were capable of pairing 2 months after fledging, and successfully breeding only 8 months post-fledging. A higher frequency of cooperative breeding occurs in a population of *S. m. malachurus* in Anglesea, Victoria (38% of 8 territories in 10 ha; unpublished data). This population experienced low mortality rates and ultimately fewer territory vacancies, which could suggest limited breeding opportunities. While the causes of cooperative breeding in emu-wrens remain unclear, it appears to occur less commonly in southern-emu wrens than it does in the fairy-wrens.

Fairy-wrens have evolved a number of traits in association with their highly promiscuous mating system, which are seemingly absent in the southern emu-wren. Firstly, emu-wren males did not develop cloacal protuberances such as those described for a number of *Malurus* species (Tuttle *et al.* 1996; Mulder and Cockburn 1993). Such enlarged cloacal protuberances are typical of species with intense sperm competition, and their absence in southern emu-wrens suggests that levels of sperm competition are lower in this genus. Secondly, I never observed extra-pair copulations or extra-pair courtship displays such as those performed by *Malurus* involving the presentation of a flower petal (Bradley and Bradley 1958; Rowley 1991; Mulder 1997). Male emu-wrens were occasionally observed in neighbouring territories, but always in the company of
their mate, and typically while foraging. This would suggest that extra-pair paternity might occur at lower frequencies in the southern emu-wren (see Chapter 7).

**Sexual selection**

Southern emu-wren juveniles develop directly into adult plumage, with sexes clearly distinguishable in the nest; this is a unique pattern of plumage development within the Malurinae. However, early plumage maturation does not necessarily imply early sexual maturation, because breeding has never been observed for individuals younger than 8 months after fledging. An exploration of hormonal levels and testis development of juveniles in southern emu-wrens might clarify this issue. Perhaps early plumage development facilitates juvenile acquisition of territories. Unlike fairy-wrens, species of *Stipituris* do not moult into an eclipse plumage during the non-breeding season. The timing of the moult depends on age and individual quality in *M. cyaneus* (Mulder and Magrath 1994; Dunn and Cockburn 1999), but little is known about how body condition and morphology vary with age in the southern emu-wren.

The larger body size of male emu-wrens could be an indicator of sexual selection pressure. Sexual size dimorphism is classically a sexually-selected trait (e.g. Hedrick and Temeles 1989; Andersson 1994; Owens and Hartley 1998). It has been suggested that extreme tail lengths, and the handicap they produce on lengthy flight, might be an indicator of individual quality (Møller et al. 1998; Balmford et al. 2000). The reduced structure of the retrices is thought to be an adaptation to living in dense habitats. Here flight becomes less necessary so that the demands on the tail to function as a rudder and brake in flight are lessened, and the webbing of the tail-feathers becomes skeletonized, reducing both the potential for damage and the costs of preening (Schodde 1982). However, this does not explain the extreme length of the tail, which makes up 69% of total body length, compared with an average of 50% in fairy-wrens (Higgins et al. 2001). Within the Portland population, tail length was extremely variable among males and females, but males had significantly longer tails than females overall.

**Pair formation and mate-fidelity**

Long-term pair bonding and a low likelihood of divorce appear common in malurids (Rowley and Russell 1990, 1993, 2002). In Portland, longevity of emu-wren pair bonds was determined mainly by mortality. Paired individuals that survived generally maintained long-term, socially
monogamous pair bonds. Divorce usually followed breeding failure (cf. ‘incompatibility’ hypothesis, Rowley 1983; ‘better option’ hypothesis, Davies 1989; Ens et al. 1993; but see Choudhury 1995), but it is unknown whether the pair breakdown was mutual or initiated by one individual. The costs of divorce appeared negligible, because both individuals typically found partners soon after and often increased their reproductive success in new partnerships.

*Breeding behaviour*

Breeding takes place in Portland at a time of year when insects are usually abundant (Bryant 1975; Pyke 1984; Cucco and Malacarne 1996), a pattern similar to that observed in other insectivorous passerines (e.g. Magrath 1999; Magrath et al. 2003). However, laying dates were asynchronous, which suggests that additional factors might explain variation across pairs in the timing of laying. These factors might include age, previous breeding experience or differences in territory quality (Perrins 1970). The probability of producing a second brood was higher when the first clutch was initiated early, and the presence of cooperative helpers reduced the interval between the first and subsequent clutches. Production of a second brood did not influence pair survival, although data are limited due to the rarity of multiple broods. Overall, the length of the breeding season was typical for a passerine inhabiting southern, non-arid Australia (Woinarski 1989).

Contrary to past reports (Fletcher 1913, 1915; Hutton 1991), I observed both the male and female building nests. The female alone incubated the clutch, as reported by Fletcher (1913), although Hutton (1991) reported that the male relieved the female on rare occasions in captivity. Both incubation and nestling periods were ~4 days longer than for the Tasmanian subspecies (Fletcher 1915). In Portland, a mean of 1.8 young successfully fledged per clutch, similar to 1.7 juveniles fledging per clutch in the Mount Lofty Ranges (Pickett 2000). Population sex ratios were close to parity in all years. However, male biases have been reported in other populations of southern emu-wrens (Pickett 2000), as well as in nesting records and museum specimens (Schodde 1982). Production of a greater number of male fledglings may vary with ecological conditions, and may be related to the disproportionate costs of raising sons and daughters (see Chapter 5) or the tendency for males to exhibit higher philopatry than females.
Southern emu-wrens are potential hosts to a number of brood parasites (Brooker and Brooker 1989), but nest parasitism was extremely rare in Portland. One pair successfully raised a Horsfield's bronze-cuckoo nestling, but both the hosts and the parasite disappeared shortly thereafter. The observed higher provisioning rates and loud vocalisations of the cuckoo throughout the nestling and fledging period suggest the energetic costs and predation risks are higher than for raising emu-wren nestlings. Nest failure was more commonly caused by predation, with snakes identified as the major predators. Failure of nests seemed unrelated to nest placement or concealment, and it is likely, therefore, that predators (snakes and feral cats) used scent and auditory cues to detect nests. I found several nests torn apart with fragments of egg shell remaining; this is characteristic of a range of potential predators present within the study area, including water rats (*Hydromys chrysogaster*), bush rats (*Rattus fuscipes*), red foxes (*Vulpes vulpes*) and avian predators such as the forest raven (*Corvus tasmaticus*).

The breeding success of this population of southern emu-wrens was similar to that reported for other small Australian passerines (Woinarski 1985; Yom-Tov 1987; Rowley and Russell 1991). Passerines living in the Southern Hemisphere are characterised by small clutches, multiple nesting attempts, high levels of nest predation, extended parental care and high adult survival (Russell 2000). This slow reproductive rate and long breeding season are considered to be either an adaptation to a favourable and stable, temperate climate (Woinarski 1985) or a strategy to overcome high rates of nest predation (Martin 1993). However, when mortality rates are high, the slow reproductive rates of many Australian species may retard population recovery and increase the risk of a population becoming endangered. The breeding success of the Portland population is similar to that exhibited by populations of the endangered *S. m. intermedius* (Pickett 2000), but lower than that reported for the Tasmanian subspecies (85%, *n*=26; Fletcher 1915). Although this variation could arise from a number of spatial and temporal factors (e.g. Rowley and Russell 1993; Dowling 2003), it could be cause for concern if mortality continues to exceed fecundity at Portland.

*Implications for population decline*

Mortality of individuals at Portland was high and adults often remained on a territory for less than the full duration of the breeding season. Although several individuals survived to over three years old, this was rare, especially for females. Most adult disappearances occurred when the
pair was nesting, suggesting that emu-wrens might be particularly vulnerable to predation during this time, or suffer from deterioration of health or exhaustion. Densities of natural and introduced predators appear high at Portland and constitute an apparently significant threat to emu-wren numbers. Densities of snakes, based on sighting frequencies, were higher at Portland (0.62 sightings per visit, \( n = 270 \)) than at other surveyed sites (Anglesea: 0.05 sightings per visit, \( n = 40 \), Lower Glenelg National Park: 0.09 sightings per visit, \( n = 11 \)). The recent local extinctions of a number of small mammals (e.g. heath mouse (\textit{Pseudomys shortridgei}), swamp antechinus (\textit{Antechinus minimus})) and a decline in the number of frogs within the area (e.g. growling grass frog (\textit{Litoria raniformis})) (Coulson \textit{et al.} 1999; Ellen Mitchell, pers. comm.) may further contribute to a greater vulnerability of emu-wrens to predation by snakes, because of the presumably reduced availability of alternative prey.

In September 2001, population numbers rapidly declined. One possible explanation for this population crash was a shortage of critical resources such as food. I did not measure the abundance of emu-wren prey during 2001; however, climatic conditions in the months prior to September were similar to those in previous years at Portland (Victorian Regional Office of the Bureau of Meteorology). August 2001 experienced higher than usual rainfall (2000: 14.6 mm; 2001: 39 mm; 2002: 16.6 mm), and September 2001, higher than average maximum temperatures (2000: 14.8°C; 2001: 17.1°C; 2002: 15.4°C). Given the well established positive correlation between temperature and insect abundance (e.g. Bryant 1975; Pyke 1984; Cucco and Malacarne 1996), it seems unlikely that resources were lower than usual in that month. A more likely possibility is that the crash resulted from high levels of predation on adult birds. The sudden population decline coincided with the laying of fox baits across the study site and increased sightings of feral cats in the area (Kevin Saunders and Ron Jeffries, pers. comm.). This was the first year in which the frequency of fox baiting was increased from biannually to three times per year; this apparently resulted in more effective reductions in fox numbers (Kevin Saunders, pers. comm.). This may in turn have led to enhanced survival of feral cats, by reducing competition and predation pressure, as has been found for other populations (Risbey \textit{et al.} 1999, 2000; Read and Bowen 2001). Feral cats are known to be more significant predators of small passerines than foxes (Risbey \textit{et al.} 1999; Read and Bowen 2001) and video monitoring at Portland has shown that they prey on southern emu-wrens. Degradation of habitat probably further contributes to the predation of southern emu-wrens within the area (as for the Eurasian
treecreeper (*Certhia familiaris*): Huhta et al. 2004). Each year, Portland Aluminium land managers remove large tracts of weed species across smelter property and in some areas this creates large unvegetated patches.

When the population crashed in 2001, replenishment of population numbers occurred through local immigration of unbanded individuals from surrounding ‘source’ populations. Territory vacancies that arose through mortality were filled rapidly. It is not known how far individuals can disperse, but with limited capabilities for long-distance flight over non-vegetated areas, habitat connectivity presumably plays a key role in sustaining the population at Portland, where juveniles were found up to 1.2 km away from natal territories. In the Mount Lofty Ranges the fate of dispersing juveniles remains unknown, but three adults have dispersed distances of 2.5 km (Pickett 2000), and one individual dispersed 1.8 km after translocation (Marcus Pickett, pers. comm.). Given such limited dispersal capabilities, this species may be quite vulnerable to local extinction, especially in isolated habitat fragments. In the Mount Lofty Ranges, populations are small and highly fragmented and in many cases, have declined to non-viable states (Littlele et al. 1997; MLR Southern Emu-wren recovery team 1998; Pickett 2000). With greater isolation of small populations, emigration and immigration become imbalanced (Dale 2001). Dispersing individuals must traverse greater distances, thereby increasing exposure to predation and in many cases, only encountering unsuitable tracts of habitat, leading to further losses (Dale 2001). The effects of inbreeding on small isolated populations remain poorly understood. However, incestuous pairings (e.g. mother/son) have been documented in the Mount Lofty Ranges (Pickett 2000). Despite similarities between mortality rates of the endangered subspecies (Pickett 2000) and the ‘secure’ subspecies at Portland, differences in the recruitment rates of local-born individuals to the adult population (Mount Lofty Ranges 60% $n=30$; Portland 26% $n=39$) suggest that dispersal is the key to population viability at Portland.

Within the Passeriformes, members of the Maluridae and Acanthizidae have the highest number of species listed as endangered or threatened in Australia (Garnett and Crowley 2000). These threatened species are commonly at risk from habitat fragmentation or destruction, and, because they are often habitat specialists, are more vulnerable to habitat alteration from modified fire regimes or intense grazing. Furthermore, many of these species are incapable of prolonged flight (e.g. bristlebird (*Dasyornis*), grasswren (*Amytornis*) and emu-wren (*Stipiturus*) species) and have
limited dispersal in highly fragmented landscapes. The status of *S. m. malachurus* in Victoria is currently ‘secure’ (Garnett and Crowley 2000; DSE *Advisory List of Threatened Vertebrate Fauna in Victoria* 2003) and the species is considered one of the most common birds in dense treeless coastal heaths in southern Victoria (Richard Loyn, pers. comm.). Nevertheless, emu-wren habitats face ongoing threats from fragmentation and clearance for agriculture and tourism, and invasion by native and introduced weeds (e.g. *Acacia longifolia var. sophorae*, *Ulex europaeus*, *Chrysanthemoides monilifera*). The present study highlights how suddenly population crashes can occur. In isolated patches the probability of recolonisation may be low. Without sustained conservation and rehabilitation of key habitats, local extinctions of emu-wren populations, as a result of stochastic events, seem probable.
Table 1. Comparative morphology of adult male and female southern emu-wrens at Portland. Values are means ± standard error. (*, \(p < 0.05\); **, \(p < 0.01\); ***, \(p < 0.001\)).

<table>
<thead>
<tr>
<th></th>
<th>Female ((n = 34))</th>
<th>Male ((n = 33))</th>
<th>d.f.</th>
<th>F</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass (g)</td>
<td>7.3 ± 0.1</td>
<td>7.3 ± 0.1</td>
<td>66</td>
<td>0.03</td>
<td>0.865</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>17.92 ± 0.10</td>
<td>18.59 ± 0.10</td>
<td>67</td>
<td>20.22</td>
<td>&lt; 0.001***</td>
</tr>
<tr>
<td>Head bill length (mm)</td>
<td>26.04 ± 0.13</td>
<td>26.91 ± 0.11</td>
<td>67</td>
<td>27.19</td>
<td>&lt; 0.001***</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>41.4 ± 0.3</td>
<td>42.8 ± 0.2</td>
<td>67</td>
<td>33.08</td>
<td>&lt; 0.001***</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>103.0 ± 1.3</td>
<td>109.4 ± 1.4</td>
<td>67</td>
<td>10.91</td>
<td>0.002**</td>
</tr>
<tr>
<td>Mite load</td>
<td>14.9 ± 2</td>
<td>16.3 ± 1.9</td>
<td>60</td>
<td>0.67</td>
<td>0.415</td>
</tr>
<tr>
<td>Bib area (length x width mm)</td>
<td>316.6 ± 12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Composition of the southern emu-wren population at Portland study sites (Main, Dean’s Heath ‘DH’, Burnt Hill ‘BH’) for three successive breeding seasons (2000-2002).

<table>
<thead>
<tr>
<th>Season</th>
<th>Site</th>
<th>Adults (m:f)</th>
<th>Juveniles (m:f)</th>
<th>% banded</th>
<th>% resighted</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>Main</td>
<td>16:13</td>
<td>8:12</td>
<td>69</td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>Main</td>
<td>12:12</td>
<td>9:5</td>
<td>76</td>
<td>59</td>
</tr>
<tr>
<td>2002</td>
<td>Main</td>
<td>9:8</td>
<td>5:9</td>
<td>90</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>DH</td>
<td>9:6</td>
<td>6:4</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>BH</td>
<td>1:1</td>
<td>5:3</td>
<td>70</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Dimensions and placement of nests (n=35) by southern emu-wrens at Portland.

<table>
<thead>
<tr>
<th>Category</th>
<th>Mean ± s.e.</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest dimensions (mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outer length</td>
<td>112.6 ± 2.5</td>
<td>84.5</td>
<td>139.7</td>
</tr>
<tr>
<td>Outer width</td>
<td>71.6 ± 1.4</td>
<td>57.6</td>
<td>87.7</td>
</tr>
<tr>
<td>Outer height</td>
<td>104.3 ± 2.9</td>
<td>63.7</td>
<td>134.1</td>
</tr>
<tr>
<td>Inner depth</td>
<td>42.8 ± 1.8</td>
<td>28.5</td>
<td>78</td>
</tr>
<tr>
<td>Entrance width</td>
<td>40.3 ± 1.2</td>
<td>25.7</td>
<td>50.7</td>
</tr>
<tr>
<td>Entrance height</td>
<td>42.7 ± 1.2</td>
<td>28.8</td>
<td>51.3</td>
</tr>
<tr>
<td>Position of nest (cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance of nest base from ground</td>
<td>28.5 ± 3.6</td>
<td>0</td>
<td>94.5</td>
</tr>
<tr>
<td>Distance of nest from top of shrub/tussock</td>
<td>54.9 ± 4.5</td>
<td>24</td>
<td>119</td>
</tr>
<tr>
<td>Height of understorey grasses/sedges/rushes</td>
<td>81.0 ± 5.3</td>
<td>36</td>
<td>174</td>
</tr>
<tr>
<td>Height of nest shrub/sedge/rush</td>
<td>84.3 ± 5.0</td>
<td>49</td>
<td>172</td>
</tr>
<tr>
<td>Crown of nest shrub/sedge/rush</td>
<td>88.1 ± 7.5</td>
<td>30</td>
<td>215</td>
</tr>
<tr>
<td>Distance from edge of shrub/sedge/rush</td>
<td>37.5 ± 3.2</td>
<td>14</td>
<td>90</td>
</tr>
<tr>
<td>Surrounding vegetation (cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average height of surrounding vegetation</td>
<td>93.3 ± 4.1</td>
<td>59.1</td>
<td>156.9</td>
</tr>
<tr>
<td>Height of tallest vegetation</td>
<td>176.6 ± 6.1</td>
<td>102</td>
<td>235</td>
</tr>
<tr>
<td>Height of shortest vegetation</td>
<td>34.5 ± 3.6</td>
<td>3</td>
<td>99</td>
</tr>
<tr>
<td>Distance to nearest cover</td>
<td>43.9 ± 5.3</td>
<td>5</td>
<td>173</td>
</tr>
</tbody>
</table>
Table 4. Comparative morphology of southern emu-wren nestlings measured 11-14 days after hatching (3 days before fledging) at Portland. Results of REML GLM are provided for comparison of male and female nestlings between single-sex broods and within mixed broods. Values are overall means ± standard error. (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th></th>
<th>Male (n=15)</th>
<th>Female (n=12)</th>
<th>Between broods (n=9)</th>
<th>Within broods (n=10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight (g)</td>
<td>6.0 ± 0.3</td>
<td>5.6 ± 0.3</td>
<td>( \chi^2 = 0.01, p = 0.939 )</td>
<td>( \chi^2 = 0.11, p=0.743 )</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>18.07 ± 0.20</td>
<td>17.27 ± 0.46</td>
<td>( \chi^2 = 0.00, p = 0.963 )</td>
<td>( \chi^2 = 7.55, p = 0.006** )</td>
</tr>
<tr>
<td>Head-bill length (mm)</td>
<td>21.14 ± 0.23</td>
<td>20.77 ± 0.30</td>
<td>( \chi^2 = 0.91, p = 0.340 )</td>
<td>( \chi^2 = 3.65, p = 0.056 )</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>27.2 ± 0.8</td>
<td>25.3 ± 1.1</td>
<td>( \chi^2 = 1.40, p = 0.236 )</td>
<td>( \chi^2 = 0.18, p = 0.673 )</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>12.4 ± 0.7</td>
<td>11.2 ± 0.9</td>
<td>( \chi^2 = 1.23, p = 0.267 )</td>
<td>( \chi^2 = 3.97, p = 0.046* )</td>
</tr>
</tbody>
</table>

Table 5. Summary of the fate of all emu-wren nests found at Portland over three consecutive breeding seasons (2000-2002).

<table>
<thead>
<tr>
<th></th>
<th>2000 season</th>
<th>2001 season</th>
<th>2002 season</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nests found</td>
<td>3 (2 pairs)</td>
<td>10 (9 pairs)</td>
<td>22 (17 pairs)</td>
<td>35 (28 pairs)</td>
</tr>
<tr>
<td>Nests abandoned</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Nests parasitised</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Clutches hatched</td>
<td>3</td>
<td>5</td>
<td>16</td>
<td>24</td>
</tr>
<tr>
<td>Eggs</td>
<td>9</td>
<td>26</td>
<td>48</td>
<td>83 (31 nests)</td>
</tr>
<tr>
<td>Nestlings</td>
<td>8</td>
<td>12</td>
<td>40</td>
<td>60 (24 nests)</td>
</tr>
<tr>
<td>Fledglings</td>
<td>7</td>
<td>8</td>
<td>20</td>
<td>35 (16 nests)</td>
</tr>
</tbody>
</table>
Fig. 1. Dispersal of nine southern emu-wren juveniles (M: male, F: female) at Portland for the three seasons monitored (2000-2002). Arrowheads denote direction of dispersal and shapes represent territories at Portland.
Fig. 2. Seasonal distribution of emu-wren clutch initiation across all Portland study sites and years. First clutches and replacement clutches are grouped separately from clutches laid after the successful production of at least one fledgling.
Fig. 3. The mean number of feeding visits by males at six nests during the incubation phase (in the 7 days before hatching) at Portland (2001-02).
Fig. 4. Mean number of visits per hour by attending adult southern emu-wrens at seven nests observed using standard 90 min continuous sampling. Pole 17 nest was parasitised by a Horsfield’s bronze-cuckoo.
Fine-scale habitat use in the southern emu-wren (*Stipiturus malachurus*)

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**Abstract**

Fine-scale variation in habitat structure and composition is likely to influence habitat use by avian species with limited flight capabilities. I investigated proportional use of available habitat and microhabitat by the southern emu-wren (*Stipiturus malachurus*), a threatened, flight-limited passerine, at three sites in Victoria, in relation to vegetation structure and composition. Emu-wrens appeared to discriminate between habitats with regard to structural rather than floristic characteristics. Habitats with dense vertical foliage of shrubs, grasses and sedges/rushes between ground level and 100 cm, and dense horizontal cover of medium to tall shrubs were used most frequently. However, when availability of habitat was taken into account, habitat use was negatively correlated with the vertical density of low shrub foliage and species richness. Within habitats, emu-wrens more frequently used plant species that had a dense canopy cover (26 ± 2% of total cover, crown diameter 93 ± 5 cm), high foliage density between 50-100 cm, and average heights of around 1 m. Plant species in which the birds nested comprised ~14% of total canopy cover and were densest between ground level and 50 cm. Canopy cover, vegetation height and vertical foliage density were consistently important variables correlated with emu-wren habitat use at multiple fine-scales. This study provides valuable information for conservation management of the species, in particular, the restoration of degraded habitats.

**Introduction**

The long-term impacts of habitat change in Australia are becoming evident by the increasing number of bird species with threatened or endangered status (Garnett and Crowley 2000). The species most at risk appear to be those restricted to fragmented environments in land systems dominated by agriculture or urban expansion, or in habitats susceptible to climate change (Woinarski 1999). Nevertheless, changes to fine-scale characteristics of habitat associated with
altered fire regimes, grazing or invasions by weeds also have the potential to reduce habitat suitability, particularly for habitat specialists (e.g. Ford et al. 2001; DeGraaf and Yamaski 2003; Maron and Lill 2005).

Ideally, management of habitat for threatened species should be based on evaluation of habitat suitability at multiple scales (Wiens et al. 1987; Luck 2002b). However, for species with highly fragmented habitat ranges or limited dispersal opportunities, occupancy of habitats can be constrained by accessibility, so that a comparison of used and unused sites may not be possible (site attribute study design, Garshelis 2000). Use-availability studies (Garshelis 2000), which examine the proportion of time an animal spends in a particular habitat relative to its availability (typically within the territory/home range; e.g. Morris et al. 2001; Hastie et al. 2003), may be more informative in such cases.

Here, I adopt the latter approach in a study of the southern emu-wren (*Stipiturus malachurus*), a highly sedentary Australian passerine that is strongly adapted to densely vegetated habitats. These habitats include wet and dry heathlands, low *Eucalyptus* scrublands and woodlands, the swampy margins of wetlands and sedge/rushlands (Loyn 1985; Higgins et al. 2001). Emu-wrens have poor flight capabilities associated with their long tails of reduced structure and short rounded wings, and consequently disperse short distances (Pickett 2000; Maguire and Mulder 2004; Chapter 2). At the landscape scale, habitat fragmentation and isolation have had a major impact on the persistence of emu-wren sub-populations (see Littlely and Cutten 1994), particularly within South Australia, where the Mount Lofty Ranges subspecies of southern emu-wren is classified as endangered (according to national, EPBC Act, and state, NPWSA, legislation). In the only study investigating emu-wren habitat characteristics to date, Wilson and Paton (2004; see also Wilson 2000) showed that habitat patches that were unoccupied by emu-wrens in the Mount Lofty Ranges had similar characteristics to those occupied throughout South Australia, and attributed the absence of emu-wrens to the inaccessibility of patches.

In Victoria, despite the disappearance of emu-wrens from highly populated areas (Ashby 1926; Austin 1956; Serventy 1982), the species is classed as secure (Garnett and Crowley 2000; DSE Advisory List of Threatened Vertebrate Fauna in Victoria 2003). Most remaining habitat occurs within coastal reserves (Barrett et al. 2003). Nevertheless, coastal habitats are susceptible to
changes in structure and composition related to senescence, altered fire regimes and weed invasions (Russell and Parsons 1978; Specht 1981a; Carr et al. 1992; McMahon et al. 1994). Variation in the vegetation characteristics of habitats is likely to influence habitat quality including prey availability, protection from predators, and availability of nesting sites (Kolowski and Woolf 2002).

The aim of this study was to investigate whether emu-wrens use habitats disproportionately in relation to availability, vegetation composition and structure, given the wide range of habitat types available to the southern emu-wren in Victoria. I compared emu-wren habitat use within three Victorian sites (Anglesea, Portland and Lower Glenelg National Park) at several fine scales: (i) habitat types within territories and (ii) individual plant species within territories, including (iii) a separate analysis of plants specifically used for nesting.

Methods
Study Sites
This research was carried out over a three-year period. From July 2000 to March 2003, I collected information on habitat structural complexity and emu-wren habitat use at three sites in western Victoria (Anglesea, Lower Glenelg National Park and Portland; Fig. 1).

At Anglesea (38°25′ S, 144°09′ E), I monitored 10 ha of undisturbed coastal heath within the Mary D. White Heathland Reserve in the Lorne-Angahook State Park, inhabited by six emu-wren pairs/cooperative groups. This site is on a hillside with a southwesterly slope and experiences a mean annual rainfall of 923 mm, a mean minimum temperature of 6°C in July and a mean maximum of 23°C in January (Victorian Regional Office of the Bureau of Meteorology). The reserve is dominated by shrub species, especially prickly teatree (Leptospermum continentale) and dusty miller (Spyridium parvifolium), with scattered stands of Otway grey gum (Eucalyptus goniocalyx) and coast wattle (Acacia longifolia var. sophorae).

At Lower Glenelg National Park (38°08′ S, 141°20′ E), I monitored a 6 ha area within the ‘Kentbruck Heathland’, inhabited by four emu-wren pairs whose territories incorporated all available habitat within the designated study area. This natural dry heathland is approximately 15 km inland and is dominated by dense shrub cover and dispersed stands of soap mallee
(Eucalyptus diversifolia). The area has a mean annual rainfall of 835 mm, a mean minimum temperature of 6° C in July and a mean maximum of 24° C in February (Victorian Regional Office of the Bureau of Meteorology).

At Portland (38°23’ S, 141°36’ E), I monitored three sites along the coastline bordering the Southern Ocean. These were arbitrarily defined with some emu-wren population interchange occurring between sites. Each varied in plant species composition and management history. All Portland sites frequently experienced strong, moist on-shore winds, and had an annual rainfall of 821 mm, a mean minimum temperature of 5° C in July and a mean maximum of 24° C in January (Victorian Regional Office of the Bureau of Meteorology). The first site was a 16 ha wetland system owned and managed by Portland Aluminium. This area was formerly a dumping site for smelter waste, but was later intensively modified and rehabilitated (Brake et al. 1991). Originally a taxonomically-rich stand of wet heath, this area now consists of a patchwork of vegetation communities including open and closed dry heath, tall shrubland, sedge/rushlands and swamps, and occasional stands of coast wattle, brown stringybark (Eucalyptus baxteri) and myrtle wattle (Acacia myrtifolia). Weeds within the area are intensively managed, with frequent chemical and mechanical eradication of outbreaks of coast wattle (A. longifolia var. sophorae), gorse (Ulex europaeus) and blue pea (Psoralea pinnata) occurring across the site. During the study, the area was occupied by between 9 and 15 emu-wren pairs. Occurring immediately south of this area, the second Portland site (‘Burnt Hill’) covered 2 ha of natural swampland and thick coastal shrubland that regenerated following a fire in 1997. This area supported between two and three emu-wren pairs. The third site extended west of the smelter property, within ‘Dean’s Heath’, which is cooperatively managed by Portland Aluminium and the Victorian Department of Sustainability and Environment. The area is within a broad swale and has undergone intensive management for the control of coast wattle, including a prescribed burn in 1993 followed by hydro-axing (McMahon et al. 1994). This 4 ha coastal heathland is dominated by regenerating coast wattle, native flowering shrubs and occasional thickets of drooping she-oak (Allocasuarina verticillata) and was occupied by 6-7 emu-wren pairs/cooperative groups during the study period.
Habitat Use

In South-western Victoria, the emu-wren breeding season extends from late July to early March (Maguire and Mulder 2004; Chapter 2). At each site, I regularly surveyed colour-banded emu-wrens during the breeding season. Monitoring the movements of emu-wrens during the non-breeding season was not possible due to reduced calling frequencies and adverse sighting conditions. I visited Anglesea three days per month during the 2000 breeding season ($n = 195$ sightings) and Lower Glenelg one day per month during the 2002 breeding season ($n = 38$ sightings). I monitored the emu-wren population at Portland more frequently: for 4-6 days per week during the 2000-2002 breeding seasons (wetland: $n = 991$; Burnt Hill: $n = 51$; Dean’s Heath: $n = 217$ sightings). All sites were monitored at similar times of day and across a similar range of weather conditions.

To facilitate navigation and enable precise geographic recording of the location of marked individuals, I erected posts at 50 m intervals in a grid at each site. A team of two to three observers was trained to search the study site and record sightings of emu-wrens. Observers monitored sites using a spot-mapping area search approach (Pyke and Recher 1984; Bibby et al. 1992), following regular paths that were spaced approximately 15 m apart so that habitats across sites were surveyed with equal intensity. The starting location of area searches was alternated daily. Morning observations began one hour after sunrise and extended until noon, and observations were then resumed 3-4 hours before sunset and continued until dusk. Observers recorded only one sighting per territory (of one individual or both members of the pair simultaneously) per session to maintain independence of samples. The observer moved slowly and quietly through the territory. Southern emu-wrens were detected when vocalising (68%), flying or hopping through vegetation (24%), incidentally spotted while stationary and silent (1%), or flushed from vegetation (7%). Typically when emu-wrens were detected audibly, they were singing nearby in emergent vegetation or song was heard from a distance and the observer travelled in the direction of the sound and waited until the individual was observed (43%). In other cases, alarm calls were given when the observer passed close to an individual (20%), territorial calls were emitted from within vegetation (5%), or quiet calls such as ‘tchluck’ (associated with family groups) or ‘steedada’ (associated with foraging) were heard (32%). The majority of emu-wren behaviours are accompanied by vocalisations during the breeding season.
For each emu-wren observed, the following variables were recorded: date, time (EST), colour-band identity or sex and age class (‘adult’ or ‘juvenile’), description of behaviour, plant species occupied and location (using a Garmin GPS II+ unit with auto average capability and 5-10 m spatial accuracy). When nests were found, the plant species in which the birds nested were identified and recorded. Thirty-seven nests were found during the study and these were located across all available habitat used by emu-wrens. No nests were found at Lower Glenelg, so I was unable to investigate nest-site selection at that site.

I determined the territory size of each pair per season by plotting all GPS fixes (45 ± 4 fixes per territory per season) on to either an aerial image in ArcView 3.2A (GIS by Environmental Systems Research Institute Inc. 1999) or a detailed hand-drawn grid map of the area. I determined territory boundaries using the Minimum Convex Polygon technique (Mohr 1947; Hooge and Eichenlaub 1997), and further refined these using the locations of observed territorial disputes, which occurred regularly between neighbouring groups. I mapped vegetation at each field-site through on-site surveys using the classification system of Specht et al. (1995), which differentiates vegetation communities based on the percentage of foliage projective cover of the tallest stratum, and the height and/or growth form of the tallest stratum. I transferred GPS data points of habitat boundaries onto available aerial images of the Portland area in ArcView (using the chlorophyll colour-tones of the image to further delineate vegetation zones) and onto detailed maps of the Anglesea and Lower Glenelg sites. I then estimated the area of each vegetation type available per territory per season, and across the entire site to the nearest whole percentage. I was then able to calculate the total number of sightings per vegetation type, per territory per season.

Vegetation Surveys
At each site, vegetation surveys were carried out in the season corresponding to monitoring of emu-wren habitat use. Within each vegetation community, I randomly selected a central point for a sampling plot by choosing coordinates from a random number table, then marked this with a permanent wooden stake. I rejected coordinates if they occurred on the edge of a vegetation community and took a new set of random numbers instead. At Anglesea, I established a total of
ten plots: three in closed heath, three in heath, two in low *Eucalyptus* with a heathy understorey, and two in low closed heath. At Lower Glenelg National Park, I established four plots, each in closed heath. At Portland, I established 26 plots; eight in closed heath, five in heath, two in open heath, two in closed sedge/rushland, two in sedge/rushland, two in grassland, three in tall shrubland, one in mature coast wattle, and one in very low closed forest. At each designated study site, emu-wrens incorporated all available vegetation within territories, with three exceptions: low closed heath occurring on the top of Anglesea slopes, and short grassland and mature stands of coast wattle occurring on the boundaries of the Portland sites. Each emu-wren territory included at least two distinct vegetation types, and the distribution of plots across sites resulted in the measurement of at least one vegetation type per territory. Emu-wrens appeared to use habitat across the entire territory and were observed in every sampling plot with the exception of three plots (one in short grassland and two in low closed heath) where use was recorded as zero.

I used two methods for assessing structural complexity of habitats: the line-intercept method (Tansley and Chipp 1926; Canfield 1941), which gives a horizontal profile of canopy cover, and the point-centred quarter method (PCQ: Goodall 1952; Wilson and Paton 2004), which gives a vertical profile of cover. Within each sampling plot, I established four 20 m line-transects (randomly selected from a possible 40 m) running north, south, east and west and beginning five metres out from the central stake. This length of transect is considered optimal for measuring cover within dense shrub and heathland environments (Kent and Coker 1992) and is similar to the average distance an emu-wren displaced per sighting (18.7 ± 1.8 m). I also randomly chose a point along each line-transect as the centre of a circular quadrat with a 5 m radius.

Canopy cover is defined as the total area occupied by the vertical projections of the crown or canopy of an individual plant, including gaps between foliage less than 10 cm (Greig-Smith 1957; Daubenmire 1968). Following the ‘line-intercept’ protocol of Canfield (1941), I measured the starting and finishing point (to the nearest cm) of each species whose canopy fell in the vertical plane below and above the transect line and was cut by this line. I also measured the height of each individual of each plant species, and its density, by counting the number of stems or bunches of culms of each plant, excluding non-tussock grasses and stoloniferous or rhizomatous plant forms where individuals cannot be distinguished. It should be noted that
density estimates provide a measure of plant community dominance in terms of the individual numbers of each species, but do not reflect contribution to total plant biomass (Kent and Coker 1992). I also categorised each species according to its growth form: tree for a woody plant usually with a single stem; shrub for a woody plant with many stems arising at or near the base; low shrub for one with maximum adult growth to 70 cm; herb for any non-sclerophyllous plant, commonly less than 60 cm high; and bare ground, grasses, ferns and sedges/rushes (Specht et al. 1995).

Adapting the PCQ methodology of Wilson and Paton (2004), I divided circular quadrats into quarters along each major compass bearing (north, south, east and west), taking vertical profiles of the vegetation foliage density at every half metre (41 sampling points). Vertical profiles were recorded according to presence/absence using a 2 m metal cylindrical rod of 5 mm diameter, which was lowered into the vegetation. The rod had markings at every 10 cm, so that within each section, the presence of each species touching the rod was noted. I did not record the total number of vegetation contacts per vertical profile, but assumed that species with a greater proportion of vegetation contacts per vertical profile were more vertically dense compared to those with few contacts.

Statistical Analyses
All data were checked for normality and homogeneity of variance, and transformed where necessary using log or arcsine transformations. For data collected using the line-intercept method, I calculated the total canopy cover of each species as a proportion of each 20 m transect, and the mean crown diameter of individual plants of a species, by dividing the total canopy cover of that species by plant density, for each line. For data collected using the PCQ method, the cover of each species was taken as the proportion of points at which a species was present. Variation between sampling points within plots was not significant ($p > 0.05$), suggesting that spatial variation in habitat structure and composition was negligible within habitats. Thus, mean values were calculated for each plot.

A number of electivity indices exist for relating habitat use to habitat availability (Lechowicz 1982). I used Vanderploeg and Scavia’s (1979a, 1979b) $E^*$ index: $E^*_{i} = [W_i - (1/n)]/[W_i + (1/n)]$, where $W_i = (r_i/p_i)/(\Sigma r_i/p_i)$, $n$ is the number of kinds of habitat, $r_i$ is the proportion of use, and $p_i$
is the proportion of habitat in the environment. This is a relativised electivity index (with values between plus and minus one) which takes into account preference for a particular habitat as a function of its availability and the abundance of other habitats present. The E* index includes a measure of the deviation from random use that makes comparison of electivities from diverse sites meaningful (Lechowicz 1982). Habitat use by emu-wrens was calculated as the proportion of sightings per habitat type for each pair, per territory per season. I used restricted maximum-likelihood (REML) analysis to investigate whether emu-wren habitat use was correlated with ‘habitat type’, controlling for repeated sampling of pairs by expressing ‘pair identity’ as a random effect. To determine whether certain habitats were being used consistently more (or less) than the availability of those habitats, I used electivity as the dependent variable.

To ascertain which structural characteristics of vegetation within habitat categories explain variation in emu-wren habitat use, I used hierarchical partitioning with 12 explanatory variables against 1) proportion of emu-wren use, and 2) electivity values. Hierarchical partitioning has an advantage over multivariate linear regression, because it avoids the problems of collinearity by measuring the increase in $r^2$ in relation to all possible combinations of variables (MacNally 2000, 2002). For data collected from PCQ measures, I carried out hierarchical partitioning using two different sets of explanatory variables: 1) mean cover estimates for each growth form, species number and mean vegetation contacts per height range, and 2) mean vegetation contacts per growth form per height range.

The results of my habitat analyses depend on several assumptions: 1) that habitats are discrete units, 2) that the study species perceives boundaries between habitat types, and 3) that there is no conflict between the investigator’s and species’ classification of a habitat type (Garshelis 2000; Kristan 2003). Because it is possible that one of these assumptions might be violated, I explored emu-wren use of plant species, regardless of the habitat type they occurred in, relative to their structural characteristics. Within a given plant species, there was minimal variation in the height (standard error confidence interval 6.7 - 7.9 cm) and horizontal cover of individual plants (standard error confidence interval 11.9 - 14.3 cm). I used REML analysis to model the variance in plant use associated with structural characteristics and interactions with species/growth form. I set the terms ‘plot’ nested within ‘site’ as random effects, which accounts for an unbalanced data set (Patterson and Thompson 1971; Searle 1987). Within each territory I calculated the frequency
of emu-wren observations in each plant species as a proportion of all observations made in that territory. These proportional values had a Poisson distribution, and hence mixed modelling with a logarithm link and a fixed dispersion of one (to avoid inflated $p$-values arising from under-dispersion of the variance) was used. It proved necessary to reduce potential explanatory variables. Average density ($r^2 = 0.54$, $t = 30.14$, d.f. = 782, $p < 0.001$) and average crown diameter ($r^2 = 0.45$, $t = 25.23$, d.f. = 778, $p < 0.001$), measured by the line-intercept method, were each highly correlated with average total canopy cover, and were therefore excluded from analyses. Average and maximum heights of plants were also highly correlated ($r^2 = 0.95$, $t = 121.96$, d.f. = 806, $p < 0.001$). Fixed factors included in the final model were species or growth form, mean cover, mean height, and interactions. For data collected using the PCQ method, I separated the proportion of contacts into five height ranges (0-50 cm, 51-100 cm, 101-150 cm, 151-200 cm, 201-300 cm). Height ranges were chosen to reflect layering of vegetation; the lowest layer averaged 41 ± 0.4 cm high and the layer above 82 ± 0.8 cm. Mean vegetation contacts in these height ranges were included as fixed factors in a separate model.

To assess the characteristics of plants in which the birds nested, each plant species was given a value that corresponded to how frequently it was used for nested (0 = never, 1 = once or twice, or 2 = three times or more), treating data from Anglesea and Portland sites separately. Two separate logistic regressions were carried out: a) plant species never used for nesting versus those used for nesting on at least one occasion, and b) plant species in which nests were rarely built (ranked 0 or 1) versus those frequently used for nesting (ranked 2). Explanatory variables included mean cover and height of plants, frequency per site (representative of availability) and the mean number of vegetation contacts between ground level to 50 cm, and 51 to 100 cm.

Results

**Structural and floristic characteristics of emu-wren habitat**

A total of 136 individual plant species were recorded in vegetation surveys conducted at five sites in three locations: Anglesea, 41 spp.; Lower Glenelg, 39 spp.; Portland: wetland, 84 spp.; Burnt Hill, 28 spp.; Dean’s Heath, 53 spp. Each site differed floristically in plant species contributing most to the canopy cover (Table 1). Vegetation in each site was diverse and consisted of a mixture of shrubs interspersed with long, dense or tussock-forming grasses and/or sedges/rushes. Only three species were common to all habitats: silver banksia (Banksia
marginata), tassel rope-rush (Hypolaena fastigiata) and Austral bracken (Pteridium esculentum). The most widespread tree species were Acacia longifolia and Eucalyptus species with a dense, stunted growth form. Prickly teatree (Leptospermum continentale) was the dominant shrub species in three of the five sites occupied by southern emu-wrens. The Lower Glenelg site was the most distinctive floristically.

Table 2 outlines the proportion of habitat types available at each site, and the mean proportion occurring within each emu-wren territory. Comparison of the proportion of emu-wren sightings within territories revealed significant differences between habitats ($\chi^2 = 43.54$, d.f. = 7, $p < 0.001$). Emu-wrens were sighted most frequently in closed heath, low closed Eucalyptus woodland and coastal shrubland, and least frequently in grassland, stands of coast wattle and sedge/rushland. However, comparison of the electivity values for 48 emu-wren pairs revealed no significant relationship with habitat type ($\chi^2 = 11.67$, d.f. = 7, $p = 0.112$).

When structural characteristics of habitats were considered instead of broad habitat categories, proportional habitat use varied significantly according to shrub cover ($r^2 = 28.86$, $Z$ score = 1.89, $n = 36$, $p < 0.05$; 91 ± 10% shrub cover in habitats with > 50% of sightings). However, cover and height of vegetation within habitats, as measured by the line-intercept technique, did not explain variation in electivity ($p > 0.05$). Low shrub cover, as estimated by the PCQ method, significantly explained the observed variation in proportional habitat use by emu-wrens ($r^2 = -14.62$, $Z$ score = 2.06, $n = 36$, $p < 0.05$; 14 ± 4% low shrub cover in habitats with > 50% of sightings), and mean species number was significantly negatively correlated with electivity ($r^2 = -29.96$, $Z$ score = 3.36, $n = 36$, $p < 0.05$; Fig. 2). Mean species number was positively correlated with the mean number of herb (Pearson correlation coefficient = 0.606, $n = 31$, $p < 0.001$) and low shrub species (Pearson correlation coefficient = 0.556, $n = 31$, $p = 0.001$). Furthermore, habitat types with the greatest number of species were typically very low woodland (15.2 ± 1.3 spp.) and low closed heathland (14.5 ± 0.5 spp.), compared to fewer species in closed sedge/rushland (4.8 ± 2.6 spp.), tall shrubland (10 ± 0.4 spp.) and heathland (10.5 ± 0.6 spp.).

The total vegetation contacts in each height range did not significantly explain proportional use or electivity ($p > 0.05$). Instead, when each growth form was considered separately, the vertical foliage density of shrubs and sedges/rushes between 0-100 cm (Fig. 3), and grasses between 51-
100 cm, significantly explained variation in emu-wren habitat use (Table 3a). Low shrub vertical foliage density between 0-50 cm was negatively correlated with electivity (Table 3b; Fig. 4).

**Frequency of plant use by emu-wrens**

Use of plants by emu-wrens was positively correlated with average contribution to total canopy cover ($\chi^2 = 188.02$, d.f. = 1, $n = 810$, $p < 0.001$; plants used > 20% comprised $26 \pm 2.2\%$ total canopy cover with an average crown diameter of $93.2 \pm 4.9$ cm) and the average height of plants ($\chi^2 = 169.87$, d.f. = 1, $n = 810$, $p < 0.001$; plants used > 20% had an average height of $93.7 \pm 4.6$ cm and maximum height of $131.9 \pm 5.8$ cm). There were no significant interactions between species identity and mean cover or height ($p > 0.05$). However, when interactions with growth form were incorporated into the models, average height and growth form interacted significantly ($\chi^2 = 20.83$, d.f. = 8, $n = 810$, $p = 0.008$). Use of trees declined with increasing height, while use of shrubs and sedges was positively related to height. Use of low shrubs was consistently low regardless of variation in their height. Canopy cover and growth form, and three way interactions were non-significant ($p > 0.05$).

When vertical measures of habitat complexity were analysed, use of plants by emu-wrens was once again positively correlated with average contribution to total canopy cover ($\chi^2 = 29.23$, d.f. = 1, $n = 597$, $p < 0.001$), as well as the interaction between growth form and vertical foliage density within 51-100 cm ($\chi^2 = 18.47$, d.f. = 8, $n = 597$, $p = 0.018$). Low shrubs, herbs and ferns were used infrequently by emu-wrens regardless of vertical foliage density, while use of trees, shrubs and sedges increased with greater vertical foliage density. All other terms and interactions were non-significant ($p > 0.05$).

**Plants chosen for nesting**

The most common shrub species in which the birds nested was prickly teatree (*Leptospermum continentale*, 34% of all nests), while two nests were found in gorse (*Ulex europaeus*) and one nest each in hedge wattle (*Acacia paradoxa*), rigid bush-pea (*Pultenaea stricta*), silver banksia (*Banksia marginata*) and pale turpentine bush (*Beyeria lechenaultii*). The remaining 49% of nests were situated in sedges/rushes, grasses and/or a groundcover species, and of these, 53% had an overhanging canopy of either prickly teatree (78%) or coast wattle in an early regeneration phase (22%). The sedge/rush species in which most nests were built were bare twig-
rush (*Baumea juncea*), pithy sword sedge (*Lepidosperma longitudinae*), sea-rush (*Juncus krausii*), knobby club-rush (*Isolepis nodosa*), tassel rope-rush (*Hypolaena fastigiata*) and coast sword sedge (*Lepidosperma gladiatum*). Grasses included Australian salt-grass (*Distichlis distichophylla*), *Poa* and *Stipa* species, as well as the introduced Yorkshire fog (*Holcus lanatus*).

The probability of a plant species being used for nesting was significantly correlated with canopy cover (12.6 ± 6.5 vs. 7.2 ± 10.5% cover, 62.7 ± 6.4 vs. 58.9 ± 10.4 cm crown diameter) and the number of vegetation contacts between ground level and 50 cm high (2.1 ± 5.7 vs. 1.8 ± 8.9 vegetation contacts; Table 4a). When the attributes of species commonly used for nesting were compared to those never or rarely used for nesting, the mean number of vegetation contacts between ground level and 50 cm (2.2 ± 6.3 vs. 1.9 ± 6.9 vegetation contacts) contributed to more of the observed variation than average cover (14.4 ± 7.1 vs. 9 ± 8.2% cover, 66 ± 6.8 vs. 59.2 ± 8.2 cm crown diameter; Table 4b).

**Discussion**

*Structural characteristics of emu-wren habitat*

Competition and restricted dispersal opportunities may prevent access to high quality habitats and can thus constrain avian habitat selection, leading to occupancy of poorer quality habitats (Fretwell and Lucas 1970; Pulliam 1988; Caughley 1994). Wilson and Paton (2004) suggested that the broad structural range of habitats occupied by emu-wrens in South Australia reflects the availability of habitat, rather than preferences of individual birds, particularly considering the recent history of human-induced change in the landscape. In Victoria, I found that emu-wrens used certain habitat types disproportionately, appearing to prefer closed heathland, low closed *Eucalyptus* woodland and coastal shrubland, and using grassland, sedge/rushland and stands of mature coast wattle less frequently. Elsewhere (Chapter 4) I have reported strong correlations between habitat type and abundance of preferred nestling prey types and density of elapid predators. Accordingly, emu-wrens experienced variable breeding success and survival associated with these factors. Tall shrubland and closed heathland had the highest abundance of preferred prey types, while sedge/rushland also had abundant prey but harbored high densities of snakes. Therefore, it would appear that emu-wren habitat use corresponds with the ‘quality’ of habitat as classified by prey availability and risk of predation (Chapter 4).
For the purpose of habitat rehabilitation, it is important to identify the vegetation characteristics that differentiate habitat types and relate these directly to disproportionate use. Emu-wren habitat use was closely related to the horizontal cover and vertical foliage density of medium to tall shrubs between ground level and one metre above ground level. Shrubs offer sturdy and dense cover and are a major foraging substrate of emu-wrens. Most shrubs in the study sites flower in spring and summer and provide an abundance of pollinating aerial insects, especially Lepidopterans, which are a major food source for southern emu-wren nestlings (Chapter 4). Nevertheless, the contribution of low shrubs to total canopy cover was associated with less frequent habitat use by emu-wrens. Low-growing shrubs may impose greater restrictions to movement and offer less protective cover than taller growing shrubs. This contrasts with the habitat preferences of the Mallee Emu-wren (Stipiturus mallee), which occupies habitats with a high density of low shrubs (40-70 cm high), for example Leucopogon and Hibbertia (Mercer 1998). This may be due to a lower availability of other suitable growth forms within the mallee understorey, or relate to differences in the behaviour of the two species.

In addition to the importance of shrubbery, emu-wrens most frequently used habitats with dense vertical foliage of sedges/rushes between 0-100 cm, and grasses between 51-100 cm. Few grass species contributed to the upper 51-100 cm canopy and these were typically tussock-forming grass species. Considering the limited use of flight by emu-wrens and their foraging habits, preferences for shrubs, taller tussock-like grasses and sedges/rushes that comprise most of the vegetative cover within the understorey are not surprising.

When emu-wren use of habitats was standardised according to habitat availability, preferences for given habitat types were no longer apparent. Nevertheless, direct comparison of the structural characteristics of habitats to the ‘electivity’ index, revealed total species number and the vertical foliage density of low shrubs between ground level and 50 cm as significant explanatory variables. Low shrubs again dominated foliage cover within habitats that were used infrequently, but this is the first time that the diversity of species present in habitats has been identified as important for emu-wrens. Habitats with high species richness were used less frequently than habitats with fewer species; these were typically low closed heathland and very low woodland habitats. This relationship may be inter-related with the structural differences of those habitats rather than floristics (e.g. Rotenberry 1985), particularly because species rich habitats had greater...
numbers of low shrub and herb species present - growth forms that have low structural suitability for emu-wrens.

McLellan (1986) argued that observed use is a better indicator of habitat selection than use relative to availability. He reasoned that an animal familiar with its own territory knows the availability and location of resources, so that an animal’s location at any given moment represents selection. However, infrequent use of a habitat may occur for widely varying reasons: access may be limited, it may be possible to extract resources in a short amount of time, or the habitat may be of little value (Garshelis 2000). Regardless of whether use in relation to availability or proportional use is calculated, my results seem to be consistent. Floristic composition appears to be of lower importance than the structure of habitats (see also Wilson and Paton 2004), and while these habitats are extremely dense and limit the movement of most birds and animals, the southern emu-wren appears to be highly adapted to these habitat characteristics.

*Frequency of plant use by emu-wrens*

Plant use was also unrelated to species identity, thus emu-wrens do not appear to differentiate floristically between species. This may account for the variation in species composition of sites occupied by emu-wrens throughout Victoria and South Australia (Wilson and Paton 2004). Instead, the structural characteristics of plants influenced how often they were used. The plants most frequently used contributed greatly to total canopy cover and hence were readily available. Nevertheless, use also depended on plant height, with emu-wrens preferring plants with average heights to 1 m and maximum heights to 1.5 m. Furthermore, emu-wrens discriminated between heights of plants within each category of growth form. They were observed more frequently in tall shrubs (and these were not necessarily the most available), whereas there was a negative relationship between tree height and use by emu-wrens. Shorter specimens of *Acacia* and *Eucalyptus* trees are typically more dense towards the base and therefore would offer more protective cover for emu-wrens when foraging. At Dean’s Heath, branches and grasses were used for foraging or protective cover as frequently as shrubbery and sedges/rushes at other sites in Portland, because these were within the preferred height range. Canopy height has previously been found to be a simple and reliable estimator of habitat use by avian insectivores, even if it is unlikely that birds respond solely to this factor (Gilmore 1985).
In many tree and shrub species, the vertical structure of the plant can change with maturity, as numerous slender stems are replaced by fewer stems of increasing girth (Specht 1981b). Therefore, the results obtained from the PCQ method offer an alternative measure of vegetation density that can account for variation in plants of different ages that horizontal profiles may overlook. According to vertical profile data, the density of foliage in the height range of 50 to 100 cm was most critical in determining frequency of use of plants by emu-wrens. This is a narrower range than that associated with proportional use of habitat types and that found by Wilson and Paton (2004) in their comparison of habitats occupied by emu-wrens in South Australia and Kangaroo Island, suggesting finer scale selection of microhabitat.

Overall, canopy cover and vegetation height and vertical foliage density appear to be key determinants of emu-wren habitat preferences, evident from analyses of habitat use at multiple fine-scales. The diverse habitat types occupied by emu-wrens appear to be similar in terms of the structural characteristics of their understories (see also Wilson and Paton 2004). Nevertheless, fine-scale differences in this structure explain variation in the use of these habitats.

Plants chosen for nesting
Emu-wrens nested in plants that had dense crowns (and thus dominated total canopy cover), and were densely branched between ground level and 50 cm. Because emu-wrens place their nests at 30 cm above ground level on average (Maguire and Mulder 2004; Chapter 2), it appears that they select vegetation that offers adequate concealment and structural support for the nest within that height range. Structural characteristics of the nesting plant do not, however, influence the success of nests (e.g., plant height and crown, and location of the nest within a plant: Maguire and Mulder 2004; Chapter 2). Similarly, in several studies of avian nest-site selection, microhabitat was important in selection of nesting sites, particularly for thermal properties, but unimportant in terms of predicting nesting success (Nguyen et al. 2003; Mezquida 2004). Most emu-wren nests failed due to predation by ground-dwelling predators including snakes and cats (Maguire and Mulder 2004; Chapter 2). These predators might not discriminate among nest sites (Tomialojc 1978; Osborne and Osborne 1980).
Habitat management implications and future research directions

Emu-wren habitat use appears to be strongly dependent on habitat structure and within Victoria, the main threats to habitat structure appear to arise from weed invasions and senescence of heathlands related to a lower frequency of fire (Russell and Parsons 1978; Specht 1981a; Carr et al. 1992). Within the Portland area, native heathlands are gradually being replaced by monocultures of coast wattle (McMahon et al. 1994). Regenerating coast wattle is structurally suitable for emu-wrens but in the long-term, mature plants are unsuitable, with foliage concentrated in the upper canopy rather than between ground level and 1 m. Removal of stands of weeds or individual weed plants from heathlands creates large open spaces and fragments habitats, further reducing suitability of habitat for emu-wrens. For weed control to be effective, post-management must include habitat restoration. Shrubs, sedges/rushes and tussock-forming grasses growing to heights of 1.5 m and with an average crown diameter close to 1 m should be planted in cleared areas, or to fill gaps in the understorey (bare ground/short grass coverage should not exceed ~20% of total canopy cover). Trees are less important components of habitat and high numbers of low-growing shrubs (maximum heights of 70 cm) should be avoided, as these detract from habitat suitability.

While the findings of this study highlight characteristics of habitat important to emu-wrens at a fine-scale, these may differ from those operating at the geographical scale (Luck 2002b). Studies at a landscape scale are required so as to account for variation arising from factors including local competition for habitat, landscape fragmentation and the spatial configuration of habitats (Wiens 1989).

The difficulties involved in studying secretive or rare species may account for the lack of data on habitat use for birds such as the southern emu-wren. For rare bird species, singing posts or locations are often used as the central point for habitat measurement plots (Ferrier 1985; Gibson et al. 2004). It may be misleading to assume that habitat used for one behaviour is representative of the habitat used for other behaviours (especially if some behaviours are more conspicuous in certain habitats). This study of emu-wrens used visual and auditory cues to detect the location of individuals within territories. The majority of emu-wren behaviours are accompanied by vocalisations (Hutton 1991; Maguire and Mulder 2004; Chapter 2), so that even when visibility was reduced, locations could be pinpointed through audio cues. The disadvantage of this
approach is that this study was limited to collection of field data during the breeding season because emu-wrens become less vocal during winter. Emu-wren habitat use may vary between winter and spring/summer in response to changes in prey availability associated with seasonal flowering (e.g. Pyke 1984) or the relaxation of territory boundaries over winter (Schodde 1982). Development of miniaturised radio-transmitters may enable more detailed studies of emu-wren habitat use in the future.
Table 1. The eight plant species contributing most to total canopy cover at five sites occupied by southern emu-wrens in this study. Numbers in parenthesis are the mean total percentage canopy cover obtained by the line-intercept and point-centred quarter (PCQ) methods.

<table>
<thead>
<tr>
<th>Anglesea</th>
<th>Lower Glenelg</th>
<th>Portland – Burnt Hill</th>
<th>Portland – Dean’s Heath</th>
<th>Portland - wetland</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leptospermum continentale</em> (48)</td>
<td><em>Melaleuca squarrosa</em> (43)</td>
<td><em>Lepidosperma gladiatum</em> (63)</td>
<td><em>Beyeria lechenaultii</em> (38)</td>
<td><em>Pteridium esculentum</em> (30)</td>
</tr>
<tr>
<td><em>Hypolaena fastigiata</em> (28)</td>
<td><em>Dillwynia glaberrima</em> (28)</td>
<td><em>Lomandra longifolia</em> (35)</td>
<td><em>Banksia marginata</em> (27)</td>
<td><em>Baumea juncea</em> (23)</td>
</tr>
<tr>
<td><em>Gahnia trifida</em> (26)</td>
<td><em>Xanthorrhoea australis</em> (24)</td>
<td><em>Poa labillardieri</em></td>
<td><em>Spyridium parvifolium</em></td>
<td><em>Acaena novae-zelandiae</em> (21)</td>
</tr>
<tr>
<td><em>Leptospermum myrsinoides</em> (25)</td>
<td><em>Baumea juncea</em></td>
<td><em>Acacia longifolia</em> (34)</td>
<td><em>Baumea juncea</em> (23)</td>
<td><em>Patersonia fragilis</em> (19)</td>
</tr>
<tr>
<td><em>Stipa</em> spp. (18)</td>
<td><em>Hakea rostrata</em> (24)</td>
<td><em>Distichlis distichophylla</em> (33)</td>
<td><em>Pteridium esculentum</em> (22)</td>
<td><em>Stipa</em> spp. (18)</td>
</tr>
</tbody>
</table>
Table 2. Proportional availability of habitats at each study site occupied by southern emu-wrens, and in parentheses, average proportional availability of habitat types within emu-wren territories. Defining characteristics of habitat are based on average cover and height of dominant growth forms according to Specht et al. (1995).

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Defining characteristics</th>
<th>Anglesea (10 ha)</th>
<th>Lower Glenelg (6 ha)</th>
<th>Ptdl – wetland (16 ha)</th>
<th>Ptdl - Burnt Hill (2 ha)</th>
<th>Ptdl - Deans Heath (4 ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed heath</td>
<td>&gt; 70% shrub cvr</td>
<td>0.27 (0.28)</td>
<td>0.67 (0.77)</td>
<td>0.12 (0.38)</td>
<td>0.50 (0.47)</td>
<td></td>
</tr>
<tr>
<td>Heath</td>
<td>30-70% shrub cvr</td>
<td>0.36 (0.40)</td>
<td>0.24 (0.48)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low closed heath</td>
<td>&gt; 70% shrub cvr, ht ~ 0.25m</td>
<td>0.11 (0.02)</td>
<td>0.04 (0.01)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucalyptus w/ heath understorey</td>
<td>&gt; 70% tree cvr, ht &lt; 5 m</td>
<td>0.19 (0.28)</td>
<td>0.29 (0.23)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coast wattle (A. longifolia) stand</td>
<td>&gt; 70% tree cvr</td>
<td>0.06 (0.19)</td>
<td>0.22 (0.16)</td>
<td>0.31 (0.28)</td>
<td>0.38 (0.50)</td>
<td></td>
</tr>
<tr>
<td>Very low closed forest</td>
<td>&gt; 70% mixed tree cvr, ht &lt; 5 m</td>
<td>0.02 (0.17)</td>
<td>0.02 (0.17)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheoak (A. verticillata) stand</td>
<td>&gt; 70% sheoak cvr</td>
<td>0.01 (0)</td>
<td>0.05 (0.37)</td>
<td>0.53 (0.49)</td>
<td>0.09 (0.07)</td>
<td></td>
</tr>
<tr>
<td>Tall shrubland</td>
<td>30-40% shrub cvr, ht &gt; 1.5 m</td>
<td>0.18 (0.25)</td>
<td>0.16 (0.37)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Closed sedge/rushland</td>
<td>&gt; 70% sedge/rush cvr</td>
<td>0.11 (0.27)</td>
<td>0.03 (0.04)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sedge/rushland</td>
<td>30-70% sedge/rush cvr</td>
<td>0.06 (0.04)</td>
<td>0.06 (0.04)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grassland</td>
<td>&gt; 70% grass cvr</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Hierarchical partitioning output for the response variables a) proportion of emu-wren use and b) electivity, using 12 explanatory variables representing the average vegetation contacts for each growth form per height range present, as measured by the point-centred quarter (PCQ) technique ($n = 36$). An asterisk denotes a significant result at the 95% confidence interval.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>a) Proportion of use</th>
<th>b) Electivity index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r^2$</td>
<td>Z score</td>
</tr>
<tr>
<td>Herb 0-50</td>
<td>3.481</td>
<td>0.90</td>
</tr>
<tr>
<td>Herb 51-100</td>
<td>3.000</td>
<td>0.75</td>
</tr>
<tr>
<td>Low shrub 0-50</td>
<td>13.145</td>
<td>0.74</td>
</tr>
<tr>
<td>Sedge 0-50</td>
<td>13.497</td>
<td>2.08 *</td>
</tr>
<tr>
<td>Sedge 51-100</td>
<td>8.125</td>
<td>1.70 *</td>
</tr>
<tr>
<td>Grass 0-50</td>
<td>7.540</td>
<td>1.24</td>
</tr>
<tr>
<td>Grass 51-100</td>
<td>8.173</td>
<td>2.54 *</td>
</tr>
<tr>
<td>Shrub 0-50</td>
<td>15.868</td>
<td>2.54 *</td>
</tr>
<tr>
<td>Shrub 51-100</td>
<td>17.021</td>
<td>2.73 *</td>
</tr>
<tr>
<td>Shrub 101-150</td>
<td>4.164</td>
<td>-0.01</td>
</tr>
<tr>
<td>Tree 51-100</td>
<td>3.407</td>
<td>0.79</td>
</tr>
<tr>
<td>Tree 101-150</td>
<td>2.578</td>
<td>0.67</td>
</tr>
</tbody>
</table>
Table 4. REML logistic models predicting a) the probability of a plant species being used for nesting by emu-wrens compared to those never chosen for nesting and b) the probability of a plant species being frequently used for nesting by emu-wrens compared to those never or rarely chosen for nesting. (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Fixed factors</th>
<th>a) nest vs. non-nest</th>
<th></th>
<th>b) rarely vs. frequently</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( \chi^2 ) (d.f. = 1)</td>
<td>( p )</td>
<td></td>
<td>( \chi^2 ) (d.f. = 1)</td>
<td>( p )</td>
</tr>
<tr>
<td>Average cover</td>
<td>8.32</td>
<td>0.004**</td>
<td>5.70</td>
<td>0.017 *</td>
</tr>
<tr>
<td>0-50 cm height range</td>
<td>6.07</td>
<td>0.014*</td>
<td>8.90</td>
<td>0.003 **</td>
</tr>
<tr>
<td>51-100 cm height range</td>
<td>0.12</td>
<td>0.729</td>
<td>0.21</td>
<td>0.651</td>
</tr>
<tr>
<td>Average height</td>
<td>0.44</td>
<td>0.507</td>
<td>0.16</td>
<td>0.688</td>
</tr>
<tr>
<td>Species frequency per site</td>
<td>0.07</td>
<td>0.785</td>
<td>0.12</td>
<td>0.725</td>
</tr>
<tr>
<td>Random factor = site</td>
<td>Variance component = 0.162</td>
<td>s.e. = 0.317</td>
<td>Variance component = 0.303</td>
<td>s.e. = 0.649</td>
</tr>
</tbody>
</table>
Fig. 1. Map of field sites in Victoria, Australia, where measurements of habitat structure and habitat use by emu-wrens were carried out (Lower Glenelg, Portland and Anglesea). Outlines of emu-wren territories are provided for each site (bolded lines represent roads).
**Fig. 2.** Electivity values (emu-wren habitat use relative to habitat availability) according to the mean number of plant species present within habitats. Positive electivity values indicate high use relative to availability and negative values, high availability but less use by emu-wrens.
Fig. 3. Proportion of habitat use by emu-wrens in relation to the vertical foliage density of shrubs and sedges between ground level to 50 cm, and 51 cm to 100 cm.
Fig. 4. Electivity values (emu-wren habitat use relative to habitat availability) according to the vertical foliage density of low shrubs between ground level and 50 cm. Positive electivity values indicate high use relative to availability and negative values, high availability but less use by emu-wrens.
Chapter 4

Territory quality, survival and reproductive success in Southern Emu-wrens


**Abstract**

Multi-factor analyses of territory quality in relation to fitness components of adults are rare, especially in non-migratory species. I studied the influence of multiple attributes of territory quality (habitat type and the abundance of food and predators) on the reproductive success and survival of a threatened Australian passerine, the Southern Emu-wren (*Stipiturus malachurus*). The abundance of frequently-selected prey types (lepidoptera, diptera, hemiptera and larvae) varied significantly across territories according to habitat type. Reproductive success (number of offspring fledged) was highest in territories containing a greater proportion of tall shrubland, which had the highest insect abundance of any habitat. Closed heathland and sedge/rushland also had high food abundance compared to other habitat types, but higher fledging success occurred only within closed heathland, possibly because predator density was lower in this habitat type. High snake density was associated with reduced adult survival during the breeding season and a lower probability of nest success. In sedge/rushland, any benefits of prey abundance may therefore be offset by a high density of predators. Emu-wren age and size were unrelated to breeding output of pairs, suggesting that ecological factors may swamp effects of individual quality on emu-wren fitness components. Preservation of tall shrubland and closed heathland habitats appear to be of key conservation priority for emu-wrens.

**Introduction**

At high population densities, competition and restricted dispersal opportunities may prevent access to high quality areas and can thus constrain avian territory selection (Fretwell and Lucas 1970; Pulliam 1988; Caughley 1994). Often, individuals are forced to occupy poor quality habitats at a cost to their fitness (Zimmerman 1971). Habitat fragmentation and isolation intensify these constraints, particularly for birds with poor flight or short dispersal distances.
Traditionally, studies assessing territory quality have correlated attributes of the territory with species presence/absence data, estimates of population density or measures of disproportionate habitat use (Breininger et al. 1995; Garshelis 2000). However, birds may be forced to occupy sub-optimal habitats, so that a more meaningful approach may be to link the average fitness experienced by individuals in a population with attributes of the territory or habitat (Jones 2001; Luck 2002a; Lambrechts et al. 2004).

Most studies that have correlated reproductive success or survival of birds with territory quality have done so for polygynous and migratory species (e.g. Leonard and Picman 1988; Bensch and Hasselquist 1991; Pärt 2001a). Very few have focused on monogamous and sedentary species (e.g. Lambrechts and Dhondt 1988; Korpimaki 1988; Przybylo et al. 2001), where individual fitness components should be strongly affected by variation in territory quality, because territory selection usually occurs only once in an individual’s lifetime. Habitat structure (e.g. Brooker and Rowley 1995; Pärt 2001a), food abundance (e.g. Gass et al. 1976; Poulsen et al. 1998), and nesting-site availability (e.g. Korpimaki 1988; Stokes and Boersma 1998; Luck 2002a) have been identified as major factors contributing to variation in the survival and reproductive success of birds. In view of the impact predators have on avian fitness components (in particular nesting success), the abundance of predators is also a crucial, yet commonly overlooked component of territory quality (Martin 1993; Weatherhead and Blouin-Demers 2004).

In this study, I measured multiple attributes of territory quality and related these to variation in survival and reproductive success of a highly sedentary species with limited dispersal capabilities, the Southern Emu-wren *Stipiturus malachurus*. This small insectivorous passerine occupies a diverse range of habitats along the southern and eastern coasts of mainland Australia, as well as Tasmania and several small offshore islands (Barrett et al. 2003). Three of eight recognised subspecies of the southern emu-wren are threatened (EPBC Act), mainly by the destruction and fragmentation of habitats (through draining and clearance of swampland for agriculture), heavy grazing, altered fire regimes, and invasion of heathland by introduced and native weeds (Littlely and Cutten 1996; Garnett and Crowley 2000). Identifying the habitat attributes correlated with higher breeding success and survival of southern emu-wrens is therefore a priority issue for conservation management. Emu-wrens appear to use certain habitat types more often than others (Chapter 3), and frequently-used habitats may have higher resource
value or lower predation risk. Here, I relate variation in territory quality (estimated from habitat quality, predator abundance and food availability) to reproductive success and survival during the breeding season in a population of the secure, nominate subspecies of southern emu-wren.

**Methods**

*Study sites*

Between July 2000 and March 2003, I collected information on territory quality and emu-wren breeding success and survival during the breeding season, within a stretch of coastal heathland in Portland, Victoria, Australia (38°23’ S, 141°36’ E). The area frequently experienced strong, moist on-shore winds, and had an annual rainfall of 821 mm, a mean minimum temperature of 5°C in July and a mean maximum of 24°C in January.

The main study area was a 16 ha wetland system owned and managed by Alcoa Portland Aluminium. This area was formerly a dumping site for smelter waste, but was later intensively modified and rehabilitated to create a wetland system (Brake *et al.* 1991). Originally a taxonomically rich stand of wet heath, the area now consists of a patchwork of vegetation communities including open and closed dry heath, tall shrubland, sedge/rushlands and swamps, and occasional stands of coast wattle (*Acacia longifolia* var. *sophorae*), brown stringybark (*Eucalyptus baxteri*) and myrtle wattle (*Acacia myrtifolia*). Heathlands are dominated by prickly teatree (*Leptospermum continentale*), scented paperbark (*Melaleuca squarrosa*) and scrub sheoak (*Allocasuarina paludosa*), and tall shrublands by coast beard heath (*Leucopogon parviflorus*).

In August 2002, I extended the study area to incorporate additional emu-wren habitat and increase the size of the study population. The study site boundary was extended southwards to include a 2 ha natural swamp. This section of heath has regenerated post-fire as thick coastal shrubland dominated by coast daisy (*Olearia axillaris*), seaberry saltbush (*Rhagodia condolleana*) and coast beard heath (*Leucopogon parviflorus*), with an understorey of coast sword-sedge (*Lepidosperma gladiatum*) and native tussock grass (*Poa labillardierei*). I also extended the study area further west to include 4 ha of coastal heathland. This section of heath is locally referred to as the ‘Dean’s Heath’ and is cooperatively managed by Portland Aluminium and the Department of Sustainability and Environment. The Dean’s Heath occurs within a broad
swale and has undergone intensive management for the control of coast wattle, including a prescribed burn in 1993 followed by hydro-axing. This 4 ha area of coastal dune is dominated by coast wattle, silver banksia (*Banksia marginata*), dusty miller (*Spyridium parvifolium*), winged spyridium (*Spyridium vexilliferum*), *Correa* spp. and occasional thickets of drooping she-oak (*Allocasuarina verticillata*).

**Identifying and measuring individuals**

Emu-wrens were captured in mist-nets and each bird was marked with a numbered metal ring (Australian Bird and Bat Banding Scheme) and a combination of three colour bands unique to that individual. I recorded the sex of the individual based on sexually dichromatic plumage: males can be distinguished from females by the presence of a lavender blue bib and supercilium. For each captured bird, I measured body mass to 0.1 g (using pesola scales), tail length (longest completely developed middle retrix, using a ruler), wing length (from carpal joint to flattened tip of longest primary; butt-ended ruler), male bib width and length (area covered with blue feathers; ruler), head-bill length and tarsus length to 0.1 mm (dial calipers).

Juveniles develop their adult plumage within 4-6 months of fledging and are thereafter indistinguishable from adults. Thus, if an individual was captured with adult plumage in August, I estimated age as 9 months, based on a minimum assumption that the individual had fledged in November the previous breeding season (the peak fledging period). I estimated the age of any individuals arriving at the study site in February and showing signs of juvenile plumage (more diffuse streaking, unstreaked ear coverts, duller colouration of bib, lores and supercilium, zero wear on primaries and retrices) as 3 months old.

Age was not correlated with any measure of physical morphology (Spearman correlations $p > 0.05$). There was no relationship between body mass and any measure of body size including tarsus, wing and head-bill length, so I was unable to formulate an index of body condition for emu-wrens. I therefore used Principal Components Analysis to reduce the number of morphological variables into three components for males and females, respectively (see table 1 for vector loadings).
**Population monitoring**

In South-western Victoria, the emu-wren breeding season extends from late July to early March (Maguire and Mulder 2004; Chapter 2). At each site, I conducted regular (4-6 days per week) census counts of colour-banded emu-wrens during each breeding season. During each non-breeding season, I made a one-week visit in June to survey the distribution of colour-banded birds during the winter. Intensive monitoring of the movements of emu-wrens over winter was not possible due to reduced calling frequencies and adverse weather conditions.

To facilitate navigation and enable precise geographic recording of the location of sighted individuals, I constructed a grid by erecting posts at 100 m intervals. I monitored sites using a spot-mapping area search approach (Pyke and Recher 1984; Bibby *et al.* 1992), following regular paths that were spaced about 15 m apart so that habitats across sites were surveyed with equal intensity. The starting location of area searches was alternated daily. Morning observations began one hour after sunrise and extended until noon. I resumed observations 3-4 hours before sunset and continued until nightfall. Emu-wrens were primarily observed when calling, hopping or flying, or when they were inadvertently flushed from vegetation. On calm days, the birds could be detected by the sound of movement from within vegetation. I used playback recordings of emu-wren song sparingly, to elicit a response from emu-wrens on days where bird activity was at a minimum. Playback was most effective when positioned as coming from a territory boundary or adjacent territory. For each emu-wren observed, I recorded: date, time (EST), group size, sex, colour-band identity, description of behaviour, and location using a Garmin GPS II+ unit with auto average capability and 5-10 m spatial accuracy.

Nests were found at various stages of development and where the hatching date was unknown, I estimated age of nestlings and fledglings using published descriptions (Pickett 2000; Maguire and Mulder 2004; Chapter 2). I visited nests every 1-2 days to monitor clutch size and dates of hatching and fledging, and to band and measure nestlings when they were between 11-14 days old. In some cases I found evidence of an active nest, but was unable to locate the nest. For example, I observed males or females carrying nesting material or prey to an unknown location. In cases where these observations were repeated over a week or more, I recorded this as a nesting attempt for the relevant pair.
Assessing territory quality

Territory size and habitat structure

I determined the territory size of each pair per season by plotting all GPS fixes (45 ± 4 fixes per territory per season) on to a projected aerial image in ArcView 3.2A (GIS by Environmental Systems Research Institute Inc. 1999). I initially determined territory boundaries using the Minimum Convex Polygon technique (Mohr 1947; Hooge and Eichenlaub 1997), but further refined these boundaries using the locations of territorial disputes, which occurred regularly between neighbouring groups. Within each breeding season, changes in territory ownership occurred, so that I generated separate maps for early (August-October), mid (November) and late breeding season (December-March). I calculated the area of each territory in hectares using the Spatial Analyst extension of ArcView.

Nesting substrate availability is often used as a measure of territory quality. However, emu-wrens used vegetation that is dense between ground level and 50 cm for nest placement, and this was abundant within territories (Chapter 3). Furthermore, nest placement was unrelated to the probability of emu-wren nesting success (Maguire and Mulder 2004; Chapter 2). I therefore excluded nesting substrate availability from estimates of quality. Instead, I calculated the proportion of each vegetation type, broadly referred to as habitat types, within territories. Habitat type ultimately influences resource levels, vulnerability to predation (related to protective cover) and travel costs associated with connectivity of cover. I mapped vegetation boundaries at each field-site through on-site surveys using the classification system of Specht et al. (1995) which differentiates vegetation communities based on the percentage of canopy cover of plant growth forms and average height of strata. I then transferred these GPS points onto an aerial image in ArcView and used the chlorophyll colour-tones of the image to delineate vegetation zones. I identified 5 vegetation types in total: closed heath (CH), heath (HTH), tall shrubland (SH), coast wattle stands (CWST) and closed sedge/rushland (SDG; detailed descriptions of each habitat type are provided in Table 2).

Abundance of predators

Snakes have been identified as major nest predators of emu-wrens (Maguire and Mulder 2004; Chapter 2). Furthermore, introduced predators are recognised as a major threat to emu-wren population persistence (Pickett 2000). I therefore recorded sightings of ground-dwelling
predators (including snakes, foxes and cats) during daily area searches of territories. As sightings of foxes and cats were infrequent and unlikely to be spatially constrained to the area where sighted, I excluded these from analyses assessing quality of individual territories. I used sightings of tiger snakes (Notechis scutatus) and common copperheads (Austrelaps superbus) in estimating total ‘snake’ density for each territory. The spatial positioning of each sighting was recorded using a Garmin GPS II+ unit. I also recorded habitat type, date and time of day, to explore variation in snake sightings.

Little is known about the home ranges and site fidelity of Australian elapid snakes. However, tiger snakes inhabit small ‘core’ areas within their home ranges for most of the season (with the exception of late spring and summer), and therefore their location within an area is quite predictable (Heath Butler, pers. comm.). I therefore used early spring sightings of tiger snakes to estimate density, and estimated length and width to distinguish between individuals. Common copperheads showed less variation in appearance (Ted Rohr, pers. comm.), but exhibit strong site fidelity, especially prior to their breeding season (late January to February) and when their prey source is stable (Ted Rohr, pers. comm.). At Portland, the majority of common copperhead sightings were in regular locations (within 2 m of a prior sighting) and therefore, most likely the same individuals. Furthermore, copperheads usually remained inactive when observed, so that thoroughly searching a territory within one morning or afternoon session would reveal most occupants. To reduce the likelihood of overestimating copperhead densities, I used the maximum number of sightings at unique positions within a territory on a single morning and afternoon session in spring, and divided this by territory size.

**Abundance of food resources**

Southern emu-wrens are insectivorous and obtain most of their food by gleaning insects and spiders from foliage, or by sallying and hawking for insects from the air (Fletcher 1913, 1915; Schodde 1982). Since very little is known about diet selectivity (Hutton 1991; Higgins *et al.* 2001), I obtained estimates of the productivity of territories by sampling aerial and foliage based insects in each of the different habitat types during spring (Sept-Nov 2002) and summer (Jan-Feb 2003) in the 2002 breeding season. These periods corresponded to when most birds at the site were nesting. Sampling during individual nesting attempts was considered too disruptive to the breeding pair. I conducted sampling on dry days and obtained a record of climatic conditions.
from the nearest weather station (Portland Airport, Victorian Regional Office of the Bureau of Meteorology). It was not possible to completely avoid the windy conditions characteristic of the area, so instead I ensured that the conditions for sampling were similar to those when video surveillance of nestling provisioning was carried out.

To target foliage insects, I used a pesticide ‘knockdown’ sampling method (Southwood 1978; Southwood et al. 1982). On the day preceding sampling, I selected four 1.5 m$^2$ areas of vegetation for sampling within each habitat type per territory, using a stratified random design. I started at the approximate centre of a habitat type within a territory and used random numbers to select a compass bearing and number of paces to a given area. This served as the starting point for the next randomly-selected area of vegetation. If the number of paces led beyond the territory border, I chose another random number. I flagged the shrubbery and recorded plant composition, heights and location using GPS. The next day, I visited flagged shrubs between 0700 and 1330 h. I spread a 1.5 m$^2$ white cotton sheet around the trunk to the edge of the canopy of each flagged shrub, or between the trunks and underneath the canopy of two or more shrubs. Using a backpack mister, I administered a pyrethrum insecticide (4g/L pyrethrins) with quick knockdown properties (16g/L piperonyl butoxide), recording the time of spraying. According to Kitching et al. (1993), 90% of insects fall from the canopy within three hours of spraying. I removed sheets after this time. Prior to removal, I shook the shrub vigorously, but this did not release many additional invertebrates. I carefully removed insects from drop sheets within 6 h of collection and placed these in 70% ethanol.

I used sweep netting to capture aerial insects flying close to foliage. Two areas were randomly selected as above. Within a 1.5 m$^2$ area, I took three sweep samples using a net of 50 cm diameter with 2 mm$^2$ meshing. Sampling occurred between 0720 and 1200, or between 1530 and 1930 h. I recorded average height of vegetation, time of day and a GPS-determined location for each sample. Using forceps, I collected insects from netting and placed these in 70% ethanol.

I identified arthropods to Order and where possible, to Family, using identification keys of Zborowski and Storey (1995) and New (1996). I measured body length of arthropods to the nearest 0.5 mm. Where specimens were incomplete, I used head length to approximate body length, based on sample averages for that taxon. In total, 23 insect orders and three additional
invertebrate orders, Araneae (spiders), Acari (ticks) and Pulmonata (slugs) were identified from 107 knockdown samples and 72 sweep samples (18 territories). I analysed data separately for each sampling method because these methods targeted independent arthropod communities (foliage versus aerial insects). I formulated a diversity index for each habitat type per territory per season, using the total number of insect orders (plus spiders) occurring within samples. I calculated average abundance and average insect and spider biomass (body lengths multiplied by abundance divided by sample number) for each sample. To explore potential sampling biases, I used linear regression to compare insect abundance measures with temperature, wind speed, humidity, time of day and height of vegetation sampled, and found no significant relationships ($p > 0.05$).

I analysed variation in the dependent variables (insect abundance, diversity and biomass), using Restricted Maximum Likelihood (REML) mixed modelling where season, habitat type and interactions were fixed factors, and territory was a random effect. Each dependent variable was checked for normality and equal variance, and transformed where necessary. Results were based on chi-square probabilities calculated from the Wald test, after the correction of each term for all other terms in the model. All analyses were carried out using GenStat version 7.1.

**Evaluating diet selectivity**

I set up miniature charge-coupled device (CCD) cameras near individual nests to collect data on provisioning rates and prey fed to nestlings. I recorded 8 h per day at each nest from the day of hatching until the day of fledging, starting at 0745 h each day. In total, I obtained 880 h of recording from 16 nests. I recorded the identities of visiting birds, arrival and departure times and the nature of the visit (provisioning, brooding or arrival without prey) from video recordings taken during the nestling feeding phase. For each pair, I calculated the average hourly provisioning rate across a subset of days (8-12) and standardised this according to brood size. I estimated prey size and grouped these into one of four classes: small ($\leq 1$ bill length; $< 9$mm), medium ($> 1$ to $\leq 2$ bill lengths; 9-17 mm), large (2-3 bill lengths; 18-27 mm), and very large ($> 3x$ bill length; $> 27$ mm). I was able to classify the size of 59% of prey items brought to the nest ($n = 10,937$). Furthermore, I was able to identify prey type on 53% of visits, with a slight bias towards larger insects with unique and highly visible features. In total, 12 insect orders and three invertebrate orders were identified as occurring in the nestling diet.
I assessed diet selectivity by comparing the proportions of prey observed in the nestling diet with their availability in the environment for the six prey categories common to all territories (adult coleoptera, diptera, hemiptera, lepidoptera, orthoptera and larvae). I made this comparison using Generalised Linear Modelling (GLM) with territory, sample type (nestling diet or availability), prey size or type, and their interactions as fixed factors. If the proportions of prey within size categories or types differed according to sample type (2-way interaction), then this would suggest that emu-wrens do not choose prey for nestlings based on availability.

*Modelling territory quality and fitness components of territory occupants*

For each pair, I estimated reproductive success using the total number of fledglings successfully produced per season. I also explored variation in the date of the first nesting attempt, average clutch size per brood per season, average nestling weight on day 11-14, hourly provisioning rate per nestling (days 8-12) and the number of days from hatching to fledging. These parameters are likely to vary with parental and/or territory quality and to influence the breeding success of pairs (e.g. Daan et al. 1988; Svensson and Nilsson 1995). In addition, I examined the duration (days) spent residing in the natal territory after fledging. Juvenile emu-wrens become nutritionally independent of parents 1.7 months after fledging. However, the period between independence and dispersal was highly variable across territories (5.7 ± 0.4 months after fledging, range 1.9-9.6 months, n = 36; Maguire and Mulder 2004; Chapter 2). Emu-wrens also occasionally bred cooperatively (Maguire and Mulder 2004; Chapter 2). On five territories juvenile males delayed dispersal and helped raise subsequent broods, remaining for at least 14 months after fledging. Presumably only high quality territories contain enough resources to support larger groups, and would confer benefits to individuals delaying breeding to become cooperative helpers (‘ecological constraints hypothesis’ Emlen 1982, 1984; Stacey and Ligon 1987).

Parameters relating to reproductive success followed either a normal or Poisson distribution and hence I used GLM with normal (identity link) or Poisson error variances, to assess variation associated with territory size, area of available habitat types, male/female age in October, and male/female size (using principal components). The number of variables in a model was reduced using backward stepwise regression, which excludes variables in relation to the observed change in $r^2$. In analyses exploring variation in reproductive output, I excluded pairs whose nests failed.
completely prior to hatching. In a separate analysis, I explored the probability of a pair attempting to nest during a breeding season using logistic regression.

As a measure of survival during the breeding season, I used the time to disappearance of one member of a pair out of a possible eight months per breeding season (excluding cases of divorce; 8 of 62 partnerships). A 52 ha area surrounding the study sites was searched bi-monthly and no banded individuals were sighted, despite sightings of 89 unbanded individuals. It is therefore probable that if a banded individual disappeared from the site during the breeding season, it died rather than dispersed. Nevertheless, this estimate for survival of territory holders may be conservative. I used Spearman rank correlations to compare this measure of survival to the area of available habitat types, territory size and snake density. Finally, I explored the probability of nesting success using logistic regression.

Because individual quality can influence components of fitness and inter-correlate with territory quality (better quality or older individuals often occupying better territories; e.g. Dale and Slagsvold 1996; Buchanan and Catchpole 1997; Wolfenbarger 1999; Bart and Earnst 1999; but see Lambrechts and Dhondt 1988), I included these variables in analyses comparing the fitness components of pairs.

**Results**

**Territory size and configuration**

In 2000, there were 13 territories of an average $0.58 \pm 0.09$ ha on the main site at Portland, giving a density of 1.8 adults/ha (Fig. 1a). Two recently-dispersed juveniles occupied the smallest territory (0.27 ha), while the largest (1.23 ha) supported a cooperative group. In 2001, 77% of territories included at least one occupant from the previous season, but pair configurations had changed in all but three territories due to divorce and high mortality rates. A number of changes to territory boundaries occurred over the winter with some territories expanding and others retracting. Overall, there were 17 pairs at the beginning of August 2001 and an equivalent number of territories. Average territory size was $0.90 \pm 0.13$ ha (Fig. 1b). Mean population density was 2.3 birds per hectare and territory overlap was higher than previously observed. Nine individuals (including 1 pair) showed consistent occupancy of territories from 2001 to 2002 and reconfiguration of pairs was mostly due to mortality. Mean
territory size was $1.29 \pm 0.16$ ha in the main site, $1.12 \pm 0.10$ ha in Dean’s heath and $1.15 \pm 0.51$ ha in Burnt Hill (Fig. 1c). Population densities were 1.2, 3.5 and 2.5 birds/ha respectively. The largest territories were approximately 2ha. Midway through the season, the death of a number of individuals prompted changes in territory configuration across the main site. Adjacent pairs commonly expanded territories to include vacant areas.

Thirty nine percent of the variation in territory size was explained by female morphology, ages of the territorial pair, and the proportion of specific habitat types (GLM, $t = 5.73$, $n = 44$, $p < 0.001$; Table 3). Older males, and heavier and larger females tended to occupy larger territories. Territory size was also positively related to the proportion of heathland, coast wattle and tall shrubland.

*Variation in predator sightings*

The probability of sighting predators at Portland was unrelated to time of day. However, date and habitat type influenced the frequency of sightings of different predators. Sightings of cats were rare and more likely in closed habitats, namely closed heath, sedge/rushland or coast wattle stands bordering roadsides. Evidence of foxes (i.e. scats, scent markings, dens), was found across most habitat types. Snakes were sighted in all habitat types and the frequency of sightings was similar for dense and open habitats, suggesting habitat structure did not inhibit observer visibility (Mann-Whitney $U = 8$, $n = 164$, $p = 0.114$). However, there were significant relationships between habitat type and snake abundance. The area of sedge/rushland in a territory and snake abundance were positively correlated (Spearman correlation coefficient = 0.327, d.f. = 67, $p = 0.010$), while the area of closed heath (Spearman correlation coefficient = -0.252, d.f. = 67, $p = 0.003$) and coast wattle (Spearman correlation coefficient = -0.148, d.f. = 67, $p = 0.013$) were negatively correlated with snake abundance.

*Diet selectivity and abundance of food resources*

Emu-wrens more commonly fed nestlings medium (42%) and small prey (34%), while large (18%) and very large prey (6%) were less common ($n = 4484$). The size of prey emu-wrens fed to nestlings was not proportional to the availability of prey in those size classes in the environment (GLM, size class/sample type interaction: $\chi^2 = 91.76$, d.f. = 3, $p < 0.001$). Emu-wrens appear to be selective of medium and large prey, as these were selected in higher
proportions relative to their availability and particularly in view of the higher availability of small prey (Fig. 2). The availability of prey in size classes varied across territories (GLM, size class/territory interaction: $\chi^2 = 1.77$, d.f. = 33, $p = 0.004$), but emu-wren preferences were consistent (GLM, size class/territory/sample type interaction: $\chi^2 = 0.57$, d.f. = 33, $p = 0.978$).

There were also significant differences in the number of prey fed to nestlings according to prey type ($\chi^2 = -5.02$, d.f. = 7, $p < 0.001$). Lepidoptera, diptera and larvae (particularly caterpillars) dominated the nestling diet, while coleoptera and araneae were less abundant in the diet. The proportion of prey types fed to nestlings differed relative to their availability within the environment (GLM, prey type/sample type interaction: $\chi^2 = 24.84$, d.f. = 6, $p < 0.001$). Lepidopterans, orthopterans and larvae occurred in higher proportions in the nestling diet compared to their availability (Fig. 3). A smaller proportion of coleoptera occurred in the nestling diet than were available, while equivalent proportions of araneae, diptera and hemiptera occurred within the environment and nestling diet. Despite variable availability of prey types across territories (GLM, prey type/territory interaction: $\chi^2 = 1.80$, d.f. = 66, $p < 0.001$), emu-wren preferences remained consistent (GLM, prey type/territory/sample type interaction: $\chi^2 = 0.93$, d.f. = 66, $p = 0.644$).

The greatest diversity of arthropods (24 orders) occurred within foliage-based samples, while sweep netting was biased toward orders of flying arthropods as expected. Habitat type did not influence the total abundance or biomass of aerial insects, but significantly influenced diversity: tall shrubland, coast wattle and closed heathland had higher aerial insect diversity than sedge/rushland habitats (Table 4a). Season had significant effects on the mean biomass of aerial insects, and significant effects on abundance, biomass and diversity of foliage based insects (Table 4a, b). In a separate analysis, I explored variation in the total abundance and biomass (combining sweep and pesticide knockdown samples) of the prey types preferred/avoided by emu-wrens in relation to season and habitat type (Table 5). The same patterns were found when sweep and pesticide knockdown samples were analysed separately. Prey types that varied significantly with season were higher in abundance and/or biomass in spring compared to summer. Coleoptera occurred in highest abundance in closed heath and lowest abundance in sedge/rushland (Fig. 4). The opposite was true for diptera, where biomass and abundance were
highest in sedge/rushland and coast wattle stands, and lowest in closed heath and heath (Fig. 4). In closed heathland and sedge/rushland, the abundance of diptera was significantly lower in summer than spring, compared to minimal seasonal variation in heathland and tall shrubland. Hemiptera occurred in higher abundance and biomass in tall shrubland and closed heathland than other habitats (Fig. 4). A similar pattern was found for lepidoptera (Fig. 4). Araneae was the only prey type that was consistently available temporally and spatially.

Territory quality and fitness components
Females residing on territories with more tall shrubland available and paired to males with larger bibs (and shorter head-bill and tarsus lengths) produced larger clutches (GLM, $r^2 = 38.6$, $t = 3.30$, $n = 16$, $p = 0.026$; Table 6). However, the total number of fledglings successfully produced per season for those pairs that attempted nesting, was related solely to the vegetative properties of the territory: pairs occupying a greater area of tall shrubland and closed heathland produced more fledglings (GLM with Poisson error and logarithm link, dispersion fixed at 1: $t = 2.99$, $n = 27$, $p = 0.010$; Table 7). The time juveniles remained on the natal territory post-fledging was positively related to the area of tall shrubland available, and negatively related to maternal weight (GLM with Poisson error and logarithm link, dispersion fixed at 1: $t = 2.96$, $n = 16$, $p = 0.007$; Table 8). The date of the first nesting attempt was unrelated to the breeding output of pairs (GLM, $t = -1.00$, $n = 27$, $p = 0.317$), presumably due to the high rate of failure of first nesting attempts and the low occurrence of second broods. Furthermore, average nestling weight, provisioning rate and the number of days from hatching to fledging did not vary in relation to parental or territory parameters ($p > 0.05$). Logistic regression revealed that the probability of a pair attempting to nest within a given breeding season was unrelated to attributes of territory and individual quality ($\chi^2 = 0.21$, d.f. = 11, $n = 69$, $p = 0.99$).

Minimum estimated survival was not correlated with habitat structure or territory size ($p > 0.05$). The only factor to significantly reduce the persistence of a pair during the breeding season, that is, increase the likelihood of mortality of one or both members, was snake density (Spearman’s correlation coefficient = -0.328, d.f. = 67, $p = 0.002$). The probability of nest failure was unrelated to vegetative properties of territories ($p > 0.05$), but was positively correlated with the density of snakes within a territory (GLM, $t = 2.15$, d.f. = 44, $p = 0.032$).
Discussion
The reproductive success and survival of southern emu-wrens during the breeding season was closely linked with territory habitat structure and total abundance of snakes in a territory. Habitat type influenced the abundance and temporal stability of food resources, and correspondingly, emu-wren pairs inhabiting territories with a larger area of habitat associated with higher abundance of preferred prey types were more likely to produce larger broods. The exception to this was sedge/rushland, where high densities of snakes appeared to offset the benefits of abundant food resources. Nest success and adult survival during the breeding season was directly negatively related to the total density of snakes within a territory.

The relationship between territory size, habitat structure and food abundance
Southern emu-wrens exhibited strong territoriality, often engaging in aggressive physical contests and regularly maintaining territory boundaries through song displays. Investment in such territorial behaviour is likely to be energetically costly (Huntingford and Turner 1987), expose individuals to risk of injury (Neat et al. 1998) and heighten risk of predation through increased conspicuousness (Yasukawa 1989; Krams 2001; Hale 2004). In this study, emu-wren territory size was positively correlated with body size and age of the territorial pair. Larger and older individuals generally have competitive advantages associated with better territorial defense and local knowledge of an area, and should therefore gain access to better territories (Saether 1990; Fowler 1995; Pärt 2001b). Emu-wrens took advantage of opportunities to expand their territories following the death of neighbouring pairs, however, at times when population density was at its highest, pairs occupied smaller territories across the site. This suggests that the costs of defense act to limit territory size in the southern emu-wren.

Larger emu-wren territories appeared to have more foliage-based insects and spiders available, as the total biomass and abundance of insects and spiders sampled from foliage did not vary with habitat composition of territories. This initially suggested that territory size and resource abundance were closely linked. However, aerial insect catches were higher in certain habitats than others, specifically in coast wattle stands and closed heath where flowering trees and shrubs attracted a high abundance of pollinating insects (e.g. wasps, moths), and in sedge/rushlands bordering wetlands which had abundant insects with aquatic larvae (e.g. nematocerans). High aerial insect abundance within sedge/rush habitats may have compensated for the smaller than...
average size of territories containing sedge/rushland and hence the lower abundance of foliage-based insects.

Estimating food resource abundance is further complicated by preferences birds may have for particular prey types. Prey size and percentage of chitin are known to significantly affect diet selection in birds (Zach and Falls 1978; Karasov 1990; Kaspari and Joern 1993; Klasing 1998). When the nestling diet was examined, emu-wrens appeared to show preferences for adult lepidopterans and orthopterans, and larvae, in particular caterpillars. Lepidopteran larvae have low handling times due to low chitin content (Zach and Falls 1978; Kaspari 1991). Diptera and hemiptera were also common in the nestling diet but this was relative to their availability in the environment, and coleoptera, which contain high levels of chitin (Zach and Falls 1978; Kaspari and Joern 1993), were one of the least selected nestling prey types. Araneae are also considered highly valuable prey types due to high amino acid content and low chitin content (Zach and Falls 1978; Ramsay and Houston 2003; Magrath et al. 2004), but occurred in low proportions within the nestling diet despite consistent availability across seasons and habitats. Disparities between the proportions of prey types occurring in the nestling diet and those available in the territory might have occurred as a result of the insect sampling method employed (Norment 1987). However, the consistent preferences for given prey types across territories varying in prey availability suggests emu-wrens were selective of these prey types. Furthermore, sampling methods used in this study provided two relative indices of prey availability, and represented the microhabitats in which birds were most commonly observed foraging.

In this study, there is no evidence of a simple positive relationship between territory size and food resource abundance, particularly given the association between preferred prey types and habitat type. Tall shrubland appeared the most optimal habitat in terms of emu-wren nestling dietary preferences, with a high biomass and abundance of lepidoptera and hemiptera, and less temporal fluctuation in availability of diptera. Also closed heath and sedge/rushland contained a high abundance of frequently-selected nestling prey types, particularly aerial insects. In several studies of avian habitat quality, positive correlations between the abundance of insects and habitat structure have been reported (Conner et al. 1986; Huhta et al. 1998; van Horne and Bader 1990). This therefore suggests that habitat structure can be used as a proximate measure of emu-wren food abundance.
The effects of territory quality on fitness components of emu-wren pairs

Emu-wrens attempted to breed on all territories and nest failure was never attributed to starvation of nestlings (with the exception of nests tended by widowed females; Chapter 5). This suggests that despite variable territory size and habitat composition, all territories contained sufficient resources for breeding. Indeed, rates of parental care and offspring weight and age at fledging did not differ between territories. Clutch size, however, significantly differed between territories, suggesting that the abundance of preferred nestling food resources, related to the habitat composition of territories, might have been a constraint on total reproductive output. Emu-wrens at Portland had larger clutches and fledged more offspring when their territory contained more tall shrubland, the habitat which had the highest abundance of preferred nestling prey types. The area of closed heath occupied was also positively correlated with the number of fledglings produced, and this habitat contained abundant preferred nestling prey types and aerial insects. Lack (1947) suggested that clutch size in birds is adjusted to the maximum number of nestlings for which the parents can provide food, so that territory quality (available resources) must therefore be an important factor influencing optimum clutch size in territorial birds (see also Högstedt 1980; Hussell and Quinney 1985; Martin 1987; Sanz and Moreno 1995). Nest predation has also been recognised as a potential factor influencing clutch size in birds (Doligez and Clobert 2003; Ferretti et al. 2005), however, there was no evidence of such a relationship in this study.

The period between independence and juvenile dispersal was highly variable across territories and five juvenile males delayed dispersal for one year and assisted parents with the raising of subsequent offspring (‘cooperative helping’). Presumably only high quality territories contain enough resources to support larger groups, and would confer benefits to individuals that delay breeding (‘ecological constraints hypothesis’ Emlen 1982, 1984; Stacey and Ligon 1987), particularly in view of the short reproductive life-span of emu-wrens. In several cooperatively breeding fairy-wren species, group size is positively related to territory quality (Nias and Ford 1992; Brooker and Rowley 1995; Chan and Augusteyn 2003). In this study, offspring remained longer on the territory post-fledging and were more likely to become cooperative helpers, when the territory contained a greater area of tall shrubland. Cooperative groups had a higher likelihood of producing larger broods and two broods per season than pairs (Maguire and Mulder 2004; Chapter 2), either as a result of the provisioning efforts of helpers or territory quality.
Thus, territories containing tall shrubland appear to be of higher quality. Similar positive associations between vegetation (‘habitat’) types and reproductive success have also been reported for several bird species (Conner et al. 1986; Braden et al. 1997; Luck 2002a), including the splendid and superb fairy-wrens (Nias and Ford 1992; Rowley and Russell 1990; Brooker and Rowley 1995; Chan and Augusteyn 2003), which are close relatives of the southern emu-wren.

While the reproductive success of pairs was closely linked with territory quality, clutch size was also positively correlated with male bib-size (and negatively with male tarsus and head-bill lengths). Bib size has been found to function as an honest signal of phenotypic quality and male status in birds (e.g. Møller 1987; Veiga 1993; Pärt and Qvarnstrom 1997). Production of a bib is considered energetically non-costly (Rohwer and Ewald 1981; Jarvi and Bakken 1984), however, behavioural maintenance of status signals (Møller 1987), higher susceptibility to infection through maintenance of high testosterone levels (Zuk et al. 1990) and increased risk of predation through increased conspicuousness (Møller 1989; Slagsvold et al. 1995), are the hypothesised costs. Bib size may therefore function as an honest indicator of male quality in this species, especially given the display of the bib during territorial contests. The effects of individual quality, however, appear to have less impact on the reproductive success of pairs, because ultimately the probability of a brood successfully fledging is influenced by territory attributes.

Predators are responsible for most nest failure of passerines in the Southern and Northern Hemispheres (Martin 1993, 1995; Russell 2000; Weatherhead and Blouin-Demers 2004), but very few studies directly assess the impact of predator densities on the survival and reproductive success of birds (Roseberry and Klimstra 1970; Komdeur and Kats 1999; Sergio and Newton 2003). Instead, most studies make inferences concerning the protective value of vegetation (Martin 1988, 1992; Nias and Ford 1992; Candolin and Voigt 2001). I found that the probability of emu-wren nesting failure and adult survival during the breeding season, was directly related to the density of snakes present within a territory. An experiment comparing the breeding success of pairs with predator-protected versus unprotected nests was attempted in 2002 (Maguire unpublished), but this had to be abandoned because birds did not return to the nest within 3 hours of introducing a wire mesh cage around the nest. Nevertheless, snakes have been identified as major nest predators of emu-wrens, through direct observation and video surveillance of nests
Snakes are also the major nest predators of the closely related fairy-wrens *Malurus splendens* (Rowley *et al.* 1991) and *Malurus cyaneus* (Warham 1958). While I have no direct evidence that snakes are successful at preying upon adult emu-wrens, females are clearly vulnerable during incubation and brooding of nestlings, and this was when most female disappearances occurred (Maguire and Mulder 2004; Chapter 2).

Snake abundance was highly correlated with certain habitat types. A number of biotic and abiotic factors can lead to potential bias in estimating snake population density (weather, season and habitat type; Sun *et al.* 2001). I was careful to avoid these biases by conducting surveys under conditions and in seasons when snakes show limited movement, and by employing very thorough search methods in all habitats. My finding of no difference between sighting frequency of snakes in closed versus open habitats at Portland suggests that my estimates of density were not affected by the visibility of snakes. Snakes are known to occur in higher densities where prey is abundant or highly clumped (Sun *et al.* 2001), and at Portland, frogs (a major prey source for tiger snakes and copperheads; Mirtschin and Davis 1983), were most abundant in wetland habitats. Correspondingly, snakes were most abundant in stands of sedges and rushes, and least abundant in coast wattle stands and closed heath. Despite high prey availability in closed heath and sedge/rushland, only emu-wrens occupying a greater area of the former habitat experienced high reproductive success. This suggests that the benefits of food availability in sedge/rushland were offset by the high density of snakes present in this habitat type.

Snakes appear to have a significant impact on emu-wren survival during the breeding season. The intensive land modifications that have occurred within the Portland area and the subsequent local extinctions of a number of small native mammal, amphibian and reptilian species (Coulson *et al.* 1999; Ellen Mitchell, pers. comm.) may have disrupted the natural equilibrium between snakes and their sources of prey. Habitat fragmentation may further enhance the conspicuousness of ground-dwelling birds, making them more vulnerable to predators. This might suggest that in more pristine habitats, natural predators might have less impact on population viability.

The findings of this study suggest that preservation of tall shrubland and closed heathland habitats are a key conservation priority for maintaining emu-wren population viability. These habitats have a high degree of shrub cover, which appears to offer abundant food resources and
better protection from predators. Nevertheless, as Lambrechts et al. (2004) point out, winter habitat requirements for birds may differ from those important for breeding, particularly as food may become more limited during this time. In order to make predictions about population viability and habitat quality as accurate as possible, it will be desirable to estimate winter survival and habitat use of emu-wrens.


**Table 1.** Principal Components loadings for southern emu-wren male and female body size attributes treated independently.

<table>
<thead>
<tr>
<th></th>
<th>PCA1</th>
<th>PCA2</th>
<th>PCA3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Male</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>-0.388</td>
<td><strong>0.701</strong></td>
<td>0.073</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>0.101</td>
<td><strong>0.861</strong></td>
<td>0.002</td>
</tr>
<tr>
<td>Head-bill length (mm)</td>
<td><strong>0.645</strong></td>
<td>0.138</td>
<td>-0.214</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td><strong>0.837</strong></td>
<td>0.137</td>
<td>-0.017</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>-0.266</td>
<td>0.268</td>
<td><strong>0.720</strong></td>
</tr>
<tr>
<td>Bib size (mm²)</td>
<td><strong>-0.750</strong></td>
<td>-0.207</td>
<td>-0.247</td>
</tr>
<tr>
<td><strong>Female</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>-0.179</td>
<td><strong>0.780</strong></td>
<td>0.336</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>-0.455</td>
<td><strong>0.685</strong></td>
<td>0.067</td>
</tr>
<tr>
<td>Head-bill length (mm)</td>
<td>0.357</td>
<td><strong>0.558</strong></td>
<td>-0.251</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>0.125</td>
<td>0.242</td>
<td><strong>-0.869</strong></td>
</tr>
<tr>
<td>Body mass (g)</td>
<td><strong>-0.862</strong></td>
<td>-0.161</td>
<td>-0.085</td>
</tr>
</tbody>
</table>
Table 2. Summary of the characteristics of the habitat types available within Portland territories. Values presented are means and standard errors calculated from vegetation sampling along 20 m line transects at Portland (Chapter 3).

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Description</th>
<th>Strata height (cm)</th>
<th>Bare ground cover (%)</th>
<th>Shrub cover (%)</th>
<th>Sedge cover (%)</th>
<th>Grass cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed heath (CH)</td>
<td>Dense cover of low to medium shrubs interspersed with tall sedges and grasses</td>
<td>55 ± 4</td>
<td>5 ± 1</td>
<td>95 ± 10</td>
<td>35 ± 4</td>
<td>24 ± 5</td>
</tr>
<tr>
<td>n = 32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heathland (HTH)</td>
<td>Moderately dense cover of low to medium shrubs, with inter-shrub spaces dominated by short purple flag (<em>Patersonia fragilis</em>) or tassel rope rush (<em>Hypolaena fastigiata</em>)</td>
<td>51 ± 8</td>
<td>12 ± 2</td>
<td>65 ± 7</td>
<td>28 ± 5</td>
<td>31 ± 6</td>
</tr>
<tr>
<td>n = 20</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tall Shrubland (SH)</td>
<td>Dominated by medium to tall shrubs such as coast beard heath (<em>Leucopogon parviflorus</em>) and coast daisy (<em>Olearia axillaris</em>)</td>
<td>73 ± 11</td>
<td>4 ± 2</td>
<td>55 ± 14</td>
<td>31 ± 11</td>
<td>29 ± 13</td>
</tr>
<tr>
<td>n = 12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coast Wattle stand (CWST)</td>
<td>Mature stand of coast wattle (<em>Acacia longifolia</em>) with sparse understorey</td>
<td>178 ± 18</td>
<td>21 ± 5</td>
<td>39 ± 9</td>
<td>50 ± 12</td>
<td>22 ± 4</td>
</tr>
<tr>
<td>n = 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Closed Sedge/rushland (SDG)</td>
<td>Dense cover of sedge and rush species such as pithy sword sedge (<em>Lepidosperma longitutudinae</em>), flat cord rush (<em>Restio complanatus</em>) and sea-rush (<em>Juncus krausii</em>)</td>
<td>71 ± 7</td>
<td>16 ± 7</td>
<td>37 ± 8</td>
<td>66 ± 7</td>
<td>12 ± 12</td>
</tr>
<tr>
<td>n = 16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Generalised linear model (GLM) output for log territory size versus southern emu-wren male and female age and morphological characteristics, and the proportional availability of habitat types (%). Analysis is based on a normal distribution. Asterisks indicate significant results (*, $p < 0.05$; **, $p < 0.01$; ***), $p < 0.001$).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Estimate</th>
<th>s.e.</th>
<th>$\chi^2$ (44)</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.341</td>
<td>0.263</td>
<td>-5.09</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Female PCA1 (-ve weight)</td>
<td>-0.199</td>
<td>0.066</td>
<td>-3.04</td>
<td>0.004**</td>
</tr>
<tr>
<td>Male age in October</td>
<td>0.029</td>
<td>0.010</td>
<td>2.93</td>
<td>0.005**</td>
</tr>
<tr>
<td>% Heathland</td>
<td>0.654</td>
<td>0.236</td>
<td>2.77</td>
<td>0.008**</td>
</tr>
<tr>
<td>Female PCA2 (+ve tail, wing, head-bill)</td>
<td>0.144</td>
<td>0.064</td>
<td>2.24</td>
<td>0.030*</td>
</tr>
<tr>
<td>% Coast Wattle stand</td>
<td>1.496</td>
<td>0.676</td>
<td>2.21</td>
<td>0.032*</td>
</tr>
<tr>
<td>% Tall shrubland</td>
<td>0.670</td>
<td>0.319</td>
<td>2.10</td>
<td>0.042*</td>
</tr>
<tr>
<td>Female age in October</td>
<td>0.019</td>
<td>0.013</td>
<td>1.46</td>
<td>0.152</td>
</tr>
</tbody>
</table>
Table 4. Output from REML model for square-root transformed average insect and spider biomass, body length and abundance, and diversity collected from a) sweep-netting, and b) pesticide knockdown sampling of southern emu-wren territories at Portland. Analysis is based on a normal distribution. Asterisks indicate significant results (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th></th>
<th>Territory</th>
<th>Season * Habitat type (d.f. 4, 73)</th>
<th>Season (d.f. 1, 73)</th>
<th>Habitat type (d.f. 5, 73)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimated variance</td>
<td>s.e.</td>
<td>( \chi^2 )</td>
<td>( p )</td>
</tr>
</tbody>
</table>

**a) sweep netting samples**

- Insect and spider abundance: -0.015, 0.089, 1.68, 0.151, 0.88, 0.347, 1.00, 0.418
- Insect and spider biomass: 0.437, 0.683, 1.86, 0.762, 12.24, < 0.001***, 4.72, 0.452
- Diversity index (# insect orders + spiders): 0.214, 0.262, 8.82, 0.066, 3.91, 0.048*, 14.64, 0.012*

**b) pesticide knockdown samples**

- Insect and spider abundance: 0.119, 0.239, 2.36, 0.501, 5.98, 0.014*, 6.20, 0.184
- Insect and spider biomass: 0.335, 0.859, 2.98, 0.395, 4.25, 0.039*, 2.81, 0.591
- Diversity index (# insect orders + spiders): 0.169, 0.209, 2.94, 0.402, 9.56, 0.002**, 7.65, 0.105
**Table 5.** Variation in the abundance and biomass of five arthropod orders collected through sweep and pesticide knockdown sampling, according to season, habitat type and interaction factors, with territory as a random effect. REML model output is presented, where asterisks indicate significant results (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Arthropod Order</th>
<th>Component</th>
<th>Territory Component, s.e.</th>
<th>Season (d.f. = 1) ( \chi^2, p )</th>
<th>Habitat Type (d.f. = 4) ( \chi^2, p )</th>
<th>Season*Habitat (d.f. = 4) ( \chi^2, p )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lepidoptera</strong></td>
<td>Abundance</td>
<td>0.027, 0.033</td>
<td>6.15, 0.013*</td>
<td>3.39, 0.009**</td>
<td>0.81, 0.519</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>0.049, 0.043</td>
<td>3.30, 0.069</td>
<td>1.72, 0.142</td>
<td>1.15, 0.332</td>
</tr>
<tr>
<td><strong>Diptera</strong></td>
<td>Abundance</td>
<td>0.027, 0.022</td>
<td>5.71, 0.017*</td>
<td>4.05, 0.003**</td>
<td>3.33, 0.019*</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>-0.335, 0.399</td>
<td>4.38, 0.036*</td>
<td>6.11, &lt; 0.001***</td>
<td>2.45, 0.061</td>
</tr>
<tr>
<td><strong>Hemiptera</strong></td>
<td>Abundance</td>
<td>-0.048, 0.143</td>
<td>0.18, 0.670</td>
<td>3.07, 0.016*</td>
<td>1.48, 0.219</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>-0.135, 0.208</td>
<td>0.22, 0.640</td>
<td>3.13, 0.014*</td>
<td>1.44, 0.230</td>
</tr>
<tr>
<td><strong>Araneae</strong></td>
<td>Abundance</td>
<td>0.108, 0.061</td>
<td>1.72, 0.190</td>
<td>1.57, 0.178</td>
<td>0.32, 0.866</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>0.081, 0.061</td>
<td>0.30, 0.582</td>
<td>0.18, 0.951</td>
<td>0.50, 0.732</td>
</tr>
<tr>
<td><strong>Coleoptera</strong></td>
<td>Abundance</td>
<td>0.046, 0.038</td>
<td>11.35, &lt; 0.001***</td>
<td>7.62, &lt; 0.001***</td>
<td>2.12, 0.076</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>-0.053, 0.025</td>
<td>6.32, 0.012*</td>
<td>5.01, &lt; 0.001***</td>
<td>1.06, 0.374</td>
</tr>
</tbody>
</table>
Chapter 4  Territory quality and emu-wren fitness components

**Table 6.** Generalised linear model output for southern emu-wren clutch size per brood per season (square-root transformed). Asterisks indicate significant results (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>estimate</th>
<th>s.e.</th>
<th>t (16)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>1.412</td>
<td>0.238</td>
<td>5.92</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Area of tall shrubland (ha)</td>
<td>0.630</td>
<td>0.234</td>
<td>2.69</td>
<td>0.016*</td>
</tr>
<tr>
<td>Male PCA1 (+ve head-bill and tarsus, -ve bib)</td>
<td>-0.216</td>
<td>0.082</td>
<td>-2.64</td>
<td>0.018*</td>
</tr>
<tr>
<td>Area of closed heath (ha)</td>
<td>0.518</td>
<td>0.297</td>
<td>1.75</td>
<td>0.100</td>
</tr>
<tr>
<td>Territory size (ha)</td>
<td>-0.229</td>
<td>0.142</td>
<td>-1.61</td>
<td>0.127</td>
</tr>
<tr>
<td>Female PCA3 (+ve tarsus)</td>
<td>-0.151</td>
<td>0.094</td>
<td>-1.60</td>
<td>0.128</td>
</tr>
<tr>
<td>Male age in October</td>
<td>0.014</td>
<td>0.013</td>
<td>1.09</td>
<td>0.294</td>
</tr>
</tbody>
</table>

**Table 7.** Generalised log-linear model output for the total number of fledglings produced by southern emu-wren pairs that attempted nesting. Analysis is based on a Poisson distribution. Asterisks indicate significant results (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>estimate</th>
<th>s.e.</th>
<th>t (26)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-0.654</td>
<td>0.261</td>
<td>-2.50</td>
<td>0.012</td>
</tr>
<tr>
<td>Area tall shrubland (ha)</td>
<td>0.908</td>
<td>0.367</td>
<td>2.48</td>
<td>0.013*</td>
</tr>
<tr>
<td>Area closed heath(ha)</td>
<td>1.000</td>
<td>0.469</td>
<td>2.13</td>
<td>0.033*</td>
</tr>
<tr>
<td>Male PCA3 (+ve weight)</td>
<td>0.314</td>
<td>0.184</td>
<td>1.71</td>
<td>0.088</td>
</tr>
<tr>
<td>Male PCA1 (+ve head-bill and tarsus, -ve bib)</td>
<td>-0.248</td>
<td>0.152</td>
<td>-1.63</td>
<td>0.104</td>
</tr>
<tr>
<td>Area of sedge/rushland (ha)</td>
<td>0.745</td>
<td>0.904</td>
<td>0.82</td>
<td>0.410</td>
</tr>
</tbody>
</table>
### Table 8. Generalised log-linear model output for the months southern emu-wren juveniles remained on the natal territory post-fledging. Analysis is based on a Poisson distribution. Asterisks indicate significant results (*, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>estimate</th>
<th>s.e.</th>
<th>( t ) (16)</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>1.714</td>
<td>0.346</td>
<td>4.95</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Area tall shrubland (ha)</td>
<td>1.048</td>
<td>0.448</td>
<td>2.34</td>
<td>0.019*</td>
</tr>
<tr>
<td>Female PCA1 (-ve weight)</td>
<td>0.333</td>
<td>0.156</td>
<td>2.13</td>
<td>0.033*</td>
</tr>
<tr>
<td>Territory size</td>
<td>-0.804</td>
<td>0.428</td>
<td>-1.88</td>
<td>0.061</td>
</tr>
<tr>
<td>Area of closed heath (ha)</td>
<td>1.083</td>
<td>0.662</td>
<td>1.64</td>
<td>0.102</td>
</tr>
<tr>
<td>Area of heath (ha)</td>
<td>0.452</td>
<td>0.374</td>
<td>1.21</td>
<td>0.227</td>
</tr>
<tr>
<td>Male age in October</td>
<td>-0.027</td>
<td>0.023</td>
<td>-1.17</td>
<td>0.241</td>
</tr>
</tbody>
</table>
Fig. 1. Southern emu-wren territory configurations at Portland for the middle of each breeding season in a) 2000, b) 2001 and c) 2002. Permanent bodies of water appear as grey shaded areas and roads are outlined in bolded black.
**Fig. 2.** The mean proportion of insects per size category collected from the environment through sweep netting and pesticide knockdown sampling, and fed to nestlings as observed from video surveillance of southern emu-wren nests at Portland.
Fig. 3. The mean number per sample of insects per prey category collected from the environment through sweep netting and pesticide knockdown, and fed to nestlings as observed from video surveillance of southern emu-wren nests at Portland. Only the most common prey types were included in this analysis, and larvae were placed in a separate category to adult prey types.
Fig. 4. The mean abundance of hemiptera, lepidoptera, coleoptera and diptera within each habitat type, sampled using sweep netting and pesticide knockdown at Portland. Habitat types are abbreviated as closed heath (CH), coast wattle stand (CWST), heathland (HTH), sedge/rushland (SDG), and tall shrubland (SH).
Parental contributions and allocation of care in the Southern Emu-wren

Abstract
Parental care of individual offspring within a brood may be influenced by the relative contributions of parents, the energetic requirements of the offspring, and potential returns to the parents on their investment. I studied parental care in the southern emu-wren, a sexually dichromatic, cooperatively breeding passerine. Only male offspring assist parents as helpers. Males are also larger and more colourful than females. Because sons may have higher energetic needs, and are more likely than daughters to repay the costs of their investment by means of local resource enhancement, parents might be expected to bias investment toward sons. I estimated provisioning rates to nestlings over two years through video surveillance of 16 nests from hatching to fledging. Nestlings developed sexually dichromatic plumage seven days after hatching, providing a visible cue of nestling sex to parents. The provisioning rate and prey load of male parents was consistently greater than that of their female partners. Female provisioning rate was inversely related to the time spent brooding nestlings. Neither parent was able to successfully raise offspring independently. In broods of one offspring, parents contributed equally, however, in larger broods, only the male increased his provisioning rate. There were no differences in feeding rates across broods differing in sex ratio, or to sons versus daughters. However, parents fed sons larger prey items closer to fledging age. Furthermore, sons and daughters were fed different proportions of prey types. The sexes fledged in similar body condition and no biases in mortality were evident. The effects of sex-biased provisioning may therefore be a potential mechanism for biasing the population sex ratio in times of low food supply.

Introduction
Parents have limited resources to allocate towards reproduction, and investment in caring for offspring can come at a cost to adult survivorship (Nur 1988; Lessells 1991; Siikimäki et al.)
1997), future reproductive success (Gustafsson and Sutherland 1988; Nilsson and Svensson 1996; Wernham and Bryant 1998), or opportunities to seek additional mates. Therefore the degree to which each parent invests in the current brood should be governed by the costs and benefits of care, relative to the impact on that parent’s ability to invest in additional offspring (Trivers 1972).

The relative contributions of parents to offspring care can be viewed as the evolutionary outcome of conflict between the sexes. Males are expected to invest similar amounts of care as females when biparental care is necessary for offspring survival, for example young are altricial or require high levels of brooding and provisioning (reviewed by Wittenberger and Tilson 1980; Martin 1987; Wolf et al. 1988). Reduced male care might be expected, however, in environments where food is abundant, permitting females to successfully raise offspring unaided and males to increase their reproductive success through mating opportunities with other females (Silver et al. 1985; Davies 1992). Nevertheless, male contributions might increase the size or quality of the brood that can be raised (reviewed by Martin 1987; Wolf et al. 1988). In general, males rarely contribute more care to offspring than females (Silver et al. 1985; Clutton-Brock 1991).

Parental investment is further complicated by interactions with the differential costs and benefits of raising offspring that vary in size or sex (Lessells 1998, 2002). Allocation of care is expected to be biased when offspring differ according to (1) sex-related energetic requirements arising from size dimorphism (red-winged blackbirds *Agelaius phoeniceus*: Teather 1992; zebra finches *Taeniopygia guttata*: Martins 2004; brown songlarks *Cinclorhamphus cruralis*: Magrath et al. 2004), (2) differential dispersal behaviour (giving higher fitness payoffs to greater body reserves at the time of independence of the dispersing sex; Greenwood 1980; budgerigars *Melopsittacus undulatus*: Stamps et al. 1987; Stamps 1990), or (3) the potential reproductive value of the sexes (Trivers and Willard 1973). Moreover, the costs and benefits of producing one sex of offspring can differ between parents. For example, if philopatric sons compete with their fathers for matings or local resources, this may make investment in daughters more profitable for fathers (eastern bluebirds *Sialis sialis*: Gowaty and Droge 1991).

Sex-biased provisioning has been reported in several sexually dimorphic species (Anderson et al. 1993; Nishuimi et al. 1996; Magrath et al. 2004), but also in monomorphic species related to
variation between the sexes in local resource competition (Stamps et al. 1987; Gowaty and Droge 1991). Parents can use multiple cues to allocate feeds to offspring, including offspring size (Stamps et al. 1985; Price and Ydenberg 1995; Mock and Parker 1997) or behavioural cues such as begging intensity or location in the nest (Kacelnik et al. 1995; Kolliker et al. 1998; Kilner 2002; Whittingham et al. 2003).

I studied the relative contributions of male and female parents to nestling provisioning in a socially monogamous passerine with biparental care, the southern emu-wren (*Stipiturus malachurus*). Emu-wrens are small (~7g), sexually dichromatic passerines endemic to coastal Australia. They form long-term pair bonds and occasionally breed cooperatively, with philopatric male offspring helping raise subsequent broods (Maguire and Mulder 2004; Chapter 2). Adult males are slightly larger than females and have a blue, as opposed to rufous-brown, bib and supercilium (Schodde 1982). These plumage differences develop at an early stage, approximately mid-way through the nestling period when young are only seven days old (Maguire and Mulder 2004; Chapter 2). This provides a unique opportunity to explore parental investment relative to offspring sex, as parents must be able to easily distinguish between male and female offspring.

Biased provisioning in relation to offspring sex may be expected in southern emu-wrens for several reasons. First, male emu-wren nestlings are larger than their female siblings (Maguire and Mulder 2004; Chapter 2) and may therefore have greater energetic requirements. Second, their plumage is more colourful than that of female nestlings. The structural colours of the male bib may require further energetic or nutritional investment to develop (Andersson 1999; Fitzpatrick 1998; Keyser and Hill 1999). Finally, biased provisioning of male offspring may be related to the tendency for males to become cooperative helpers (‘repayment hypothesis’ see Emlen et al. 1986), and the enhanced reproductive success experienced by cooperative groups (Maguire and Mulder 2004; Chapter 2).

In this study I examined: 1) allocation of care in relation to offspring sex (signalled by dichromatic plumage and size) and behavioural cues (begging intensity and position in the nest), and 2) contributions by male and female parents to offspring care (including provisioning and brooding, and size and type of prey).
Methods

This study was conducted over two breeding seasons in the years 2001-2003; each breeding season extended from late July to early March. The study population inhabited 16 ha of wet heath, and an adjoining 7 ha of coastal heathland, in Portland, southwestern Victoria, Australia (38°23’ S, 141°36’ E). Vegetation across the site was dense and consisted of a variety of flowering shrubs, sedges/rushes and native grasses, and emu-wrens occupied territories of between one and two hectares (Chapters 3 and 4).

I captured individuals using mist-nests and banded each with a unique combination of colour-bands for identification. I visited the field site daily to locate nests and follow the progress of each nesting attempt. General breeding parameters are provided in Chapter 2. I monitored parental care at 14 nests attended by two parents, and two nests attended by the breeding pair and a male helper (2001/2 n = 6, 2002/3 n = 10). Average clutch size was 2.6 (range 2-3 eggs). Females start to incubate eggs when the clutch is complete, and therefore chicks hatch synchronously. Nests were found at various stages of development (building n = 4, incubation n = 6, nestling stage n = 6), and in cases where laying date was unknown, I calculated backwards from the age of the nestlings or fledglings, using the mean incubation period (19 ± 2 days). I estimated age of nestlings and fledglings using published descriptions (Pickett 2000; Maguire and Mulder 2004; Chapter 2). I banded and measured nestlings when they were 11-14 days old.

At each nest I placed a charge-coupled device (CCD) colour camera with audio 30 cm from the nest entrance. The camera was linked to a VCR via a 15 m extension lead and both units were powered by a 12-volt car battery, using an inverter. I recorded ~8 h per day at each nest (mean 8.4 ± 0.4 h). Recording began at 0745 h EST. For nests found during the building phase, cameras were set up the day after the last egg was laid (one day after incubation began) to minimise disturbance to the nesting pair. Cameras and video equipment did not appear to disturb the birds as they returned to the nest on average 7.2 ± 1.1 min after recording commenced. I recorded a total of 880 h during the nestling period at 16 nests (mean 8.7 ± 0.4 h on 6.9 ± 0.9 days per nest; n = 14 females) and noted the identities of visiting birds, arrival and departure times and the nature of the visit (direct feeding of nestlings, delivery of prey item to female parent for ingestion or redistribution to nestlings, arrival without prey, brooding). I identified prey items to the level of Order (visible on 59% of visits, n = 10,937) and estimated their size, grouping them
into one of four classes: small ($\leq$ 1 bill length; < 9 mm), medium (1 to $\leq$ 2 bill lengths; 9-17 mm), large (2-3 bill lengths; 18-27 mm), and very large (> 3x bill length; > 27 mm).

When nestlings reached seven days of age, I was able to record the sex and position of the offspring fed, the direction of approach of the attending adult, and the number of offspring that begged ($n = 12$ nests, 3.6 ± 0.9 days per nest). Nests entrances were ~10 cm high and nestlings frequently stretched their necks above the nest rim when begging. I used a transparent sheet with 1 cm gridlines placed over the video screen during transcription to estimate the height reached by the nestling that was fed, compared to the next highest begging offspring that was not fed. Begging order was not treated as a separate variable because it was correlated with begging height. Begging vocalisations could not be measured because these are largely inaudible to the human ear. I recorded the number of feeds delivered to individual offspring and calculated the proportion of feeds and average prey size received by offspring in relation to offspring sex and position in the nest. I calculated the relative heights of offspring per visit for begging data analyses.

**Statistical analyses**

I transformed data using logarithmic or square root transformations where assumptions of a normal distribution or equal variance were not met. Due to repeated sampling of nests over time, I used mixed models fitted by REML with ‘nest’ as a random factor. Daily means of visitation rates and duration of visits were calculated for each nest. All models included clutch size, age of brood (where day 1 is the day of hatching) and interaction terms as covariates. Additional fixed factors included sex ratio (the proportion of males in a brood) or brood composition (single-sex versus mixed-sex). Non-significant terms were sequentially removed until only significant terms remained ($p < 0.05$). Variation associated with weather parameters, time of day, year and period within the breeding season revealed no significant relationship with visitation rate or duration, and I therefore exclude these factors from further analyses.

In analyses comparing the proportion of feeds and size and type of prey fed to sons and daughters by parents, I included data from cooperative groups to increase my sample size. I examined any effect of this by including ‘cooperative’ and ‘non-cooperative’ as a factor, and found no significant interactions with this factor. The lack of a significant interaction could arise
due to a very small sample size and thus I cannot comment on whether parents in unassisted and assisted pairs vary in parental behaviour.

I collapsed prey types to nine categories (Araneae, Coleoptera, Diptera, Hemiptera, larvae, Lepidoptera, Orthoptera, winged, other) and determined the proportion of prey observed within each category provided to offspring, in relation to sex of the attending adult, age of the brood and sex of the nestling. This was analysed using REML models for log-transformed proportions of each order separately.

Begging data were analysed with a mixed logistic REML model, which estimated the influence of various factors on the binomial response whether the highest-gaping offspring was fed or not. Factors included the height difference between gaping offspring, maximum height reached, sex of the attending adult, sex of the offspring fed, age of the brood, the number of offspring that begged and position within the nest. Nest was included as a random factor.

I calculated an index of nestling body condition using the residuals of a regression of body mass by tarsus length (Dowling 2003). These were used in a REML analysis with nest as a random factor, and brood size and parental feeding rates as fixed factors.

**Results**

**Allocation of care**

**Offspring sex**

There were no differences in the proportion of feeds ($\chi^2 = 2.81, n = 12, p = 0.094$) or the size of prey ($\chi^2 = 0.56, n = 12, p = 0.455$) fed to sons and daughters. However, the size of prey fed to offspring of different sex varied significantly with offspring age ($\chi^2 = 5.10, n = 12, p = 0.024$; Fig. 1). The sexes received similar sized prey early in the nestling phase (days 6-9), however, parents fed sons larger prey as they approached fledging, and daughters smaller prey. Parents also varied the proportion of prey taxa fed to sons and daughters. Sons received more lepidopterans, dipterans, coleopterans and hemipterans than daughters ($\chi^2 = 32.38, \text{d.f.} = 8, n = 10, p < 0.001$; Fig. 2).
There was no evidence that parents responded differently to sons and daughters with regard to prey size delivered ($\chi^2 = 0.14, n = 12, p = 0.713$) or proportion of feeds ($\chi^2 = 0.15, n = 12, p = 0.702$). Furthermore, within broods, there were no biases in the size of prey or number of feeds to individual offspring of the same sex (paired $t$-tests $p > 0.05, n = 10$). Nestling body condition did not vary with brood size or parental feeding rates ($p > 0.05, 10$ nests, $21$ nestlings).

**Behavioural cues**

On most visits, only one prey item was brought to the nest and only one offspring was fed ($91\%$ single feeds, $n = 4054$). On $50\%$ of visits, the offspring that gaped the highest when begging was fed ($n = 4054$) and in $14\%$ of visits there was no difference in the begging heights of offspring that were fed and not fed. However, the highest begging offspring was unsuccessful on $20\%$ of visits, and on $16\%$ of occasions, offspring did not beg at all. Overall, the number of offspring gaping ($\chi^2 = 22.17, n = 10, p < 0.001$), the relative height of the offspring fed in relation to its siblings ($\chi^2 = 99.78, n = 10, p < 0.001$), and the maximum height reached ($\chi^2 = 12.51, n = 10, p < 0.001$), were important predictors of whether the highest gaping chick was fed. Offspring sex did not interact significantly with any variable of begging behaviour to increase the likelihood of parents responding to begging ($p > 0.05$), however, female offspring reached greater heights on average than male offspring ($f = 5.2 \pm 0.04$ cm, $m = 4.7 \pm 0.04$ cm; $t = 7.09$, d.f. = 2747, $p < 0.001$).

Parents responded differently to begging cues. Males responded more strongly to relative height differences between begging nestlings ($\chi^2 = 4.55, n = 10, p = 0.033$, estimated effect: $f = 0.39$, $m = 0.69$) and females more strongly to the maximum height reached when begging ($\chi^2 = 3.90, n = 10, p = 0.048$, estimated effect: $f = 0.19$, $m = -0.01$). There was, however, no relationship between the likelihood of a parent feeding a begging offspring and the sex of that offspring ($p > 0.05$).

Emu-wrens build dome shaped nests with a side entrance, and adults at a given nest tended to approach the nest either directly or from one side. There were no differences in the direction male and female parents approached the nest ($\chi^2 = 1.17, n = 7, p = 0.279$). Parents fed the nestling in closest proximity to their approach on $45\%$ of occasions ($n = 4053$), but this was not
significant and did not vary with sex of the parent ($\chi^2 = 2.44, n = 7, p = 0.876$). Offspring were very active in the nest from day five post-hatching and would re-arrange themselves within the nest frequently throughout the day. There was, however, no advantage of being in a given position within the nest in terms of the average prey size ($\chi^2 = 0.59, \text{ d.f.} = 2, n = 7, p = 0.744$) or proportion of feeds received ($\chi^2 = 2.78, \text{ d.f.} = 2, n = 7, p = 0.250$).

**Parental contributions to offspring care**

On average, there were 6.0 visits per hour to each nest (5.5 visits where nestlings were fed per hour, $n = 14$). Males provisioned offspring at a significantly higher rate than females ($\chi^2 = 90.17, n = 16, p < 0.001$; Table 1). Feeding frequencies varied according to the age and size of the brood. Female provisioning rates increased steeply as the brood approached fledging, while male feeding rates increased gradually ($\chi^2 = 11.61, n = 16, p < 0.001$; Fig. 3). For broods of one offspring, female and male provisioning rates were similar. For larger brood sizes (two or three offspring), male effort exceeded female effort ($\chi^2 = 7.52, n = 16, p = 0.006$; Fig. 4). Parental provisioning rates did not vary with sex ratio of the brood ($\chi^2 = 1.46, n = 16, p = 0.227$).

Total brood provisioning rates varied significantly according to the number of attending adults. At nests where one parent died and the other was left to raise the young alone, nestlings either died in the nest of starvation or hypothermia ($n = 3$, early nestling phase) or were preyed upon ($n = 2$, late nestling phase). The sexes responded differently in the absence of their partner; males increased their provisioning rate by almost double ($\chi^2 = 21.25, n = 2, p < 0.001$), while females did not change their provisioning rate ($\chi^2 = 0.04, n = 2, p = 0.847$). At nests tended by cooperative groups, there was a trend towards a higher total provisioning rate than at nests tended by unassisted pairs, primarily due to the extra feeds provided by helpers (total feeds/hr: cooperative $6.7 \pm 3.9, n = 2$; pairs $5.5 \pm 4.1, n = 14$; $\chi^2 = 4.16, n = 11, p = 0.04$).

Parents varied in the proportion of time they spent at the nest. Females spent a significantly longer proportion of the day at the nest than males ($\chi^2 = 122.12, n = 14, p < 0.001$; Table 2) as a consequence of brooding, which is exclusively a female role. Males further reduced time spent at the nest per visit by passing prey on to the brooding female to distribute to offspring on 18% of visits ($n = 5,928$ male visits). The female brooded nestlings on 22% of visits and on half of these
visits, the female did not bring prey to the nest \((n = 3,829\) female visits). The number of brooding visits per hour (and duration of brooding visits) decreased with age of the brood, declining significantly seven days after hatching \((\chi^2 = 76.33, n = 16, p < 0.001)\). There was no relationship between female brooding effort and brood size \((\chi^2 = 0.01, n = 16, p = 0.924)\).

Parents differed in the duration spent feeding nestlings per visit according to brood size \((\chi^2 = 7.87, n = 16, p = 0.005)\). Females spent significantly longer at the nest than males when feeding broods larger than one (Fig. 5). Feeding duration was unrelated to age of the brood \((\chi^2 = 1.01, n = 16, p = 0.315)\). Parents did not differ in the amount of time spent at the nest during non-feeding visits, which were primarily for nest sanitation and what appeared to be nest guarding. Nor did the duration of non-feeding visits vary according to brood size or age \((p > 0.08)\).

Both parents increased the size of prey delivered to offspring over the nestling period \((\chi^2 = 6.07, n = 13, p = 0.014)\). However, parents did not vary the size of prey delivered to broods of different sizes \((\chi^2 = 0.00, n = 13, p = 0.954)\). Overall, males brought larger prey items to the nest than females \((\chi^2 = 4.34, n = 13, p = 0.037); \) predicted means (log-prey size): \(f = 1.01, m = 1.15)\).

Parents most commonly brought larvae, winged insects and lepidopterans to the nest, while beetles and spiders were brought less frequently (Fig. 6). The breadth of the nestling diet increased with nestling age, significantly increasing mid way through the nestling phase (after day 7 post-hatching). Parents brought a greater proportion of coleoptera to nestlings as they approached fledging \((\chi^2 = 7.35, n = 10, p = 0.007)\). This was the only prey type that varied in frequency of delivery with age of the brood. Parents varied in the proportions of prey they collected. In particular, males brought a smaller proportion of larvae \((\chi^2 = 5.12, n = 10, p = 0.024)\), winged insects \((\chi^2 = 9.40, n = 10, p = 0.002)\), coleoptera \((\chi^2 = 10.85, n = 10, p < 0.001)\), and ‘other’ prey types \((\chi^2 = 10.29, n = 10, p = 0.001)\) than females.

**Discussion**

In line with my predictions, I found evidence of biased provisioning in favour of male offspring. Sons were allocated more profitable prey types than daughters and received larger prey items.
than daughters in the late nestling phase. Below I examine the potential cues that parents may respond to when allocating prey and the fitness payoffs that may drive this bias. In the southern emu-wren, biparental care appears essential to offspring survival. Brooding was exclusively a female role, while male parents contributed higher provisioning efforts than female parents. This was even more evident in larger broods, where male contributions were higher than for a single offspring, while female effort remained constant.

**Allocation of care**

Sons received higher proportions of lepidoptera, diptera, coleoptera and hemiptera than daughters. In several studies of prey choice, birds have shown consistent preferences for prey with lower chitin and toxins, namely larvae, lepidopterans and spiders (Zach and Falls 1978; Kaspari 1991; Brodmann and Reyer 1999). In a study relating emu-wren prey selectivity to availability, lepidoptera were identified as a highly preferred prey type. Diptera and hemiptera also contributed to the bulk of the nestling diet (Chapter 4). Thus, sons receive prey types that are preferentially selected by parents (with the exception of coleoptera which form only a minor part of the nestling diet), and that are presumably high in quality. Given the profound influence nutritional content of prey could have on offspring growth and quality (Perrins 1976; Tinbergen 1981), it is surprising that this is only the second study (after Magrath et al. 2004), to consider prey quality as a means of biasing care to offspring.

Prey size is another component of parental investment that is commonly overlooked. In the few studies that have compared the size of prey allocated to male and female offspring, no bias was detected (Lessells et al. 1998; Magrath et al. 2004). Male and female emu-wren offspring received similar sized prey in the early nestling phase. However, towards the late nestling phase parents allocated larger prey items to sons than daughters, suggesting higher energetic investment in male offspring. This age-related effect might arise as a result of offspring sex becoming more apparent with age, in particular due to the development of sexually dichromatic plumage. The size differences between male and female offspring within mixed broods may also become more obvious closer to fledging (e.g. red-winged blackbirds Agelaius phoeniceus: Fiala and Congdon 1983; Teather 1992). I did not measure emu-wren nestlings in the early nestling phase. However, within mixed broods male offspring were 5% heavier than females in the late nestling phase, 4% larger in skeletal measurements and feathers were 6% more developed.
(Maguire and Mulder 2004; Chapter 2). It is questionable as to whether these size differences are large enough to generate biased responses from parents. Instead dichromatic plumage cues may be important.

Competitive ability may also differ between the sexes or become more evident with increasing age-related energetic requirements. The responsiveness of emu-wren parents to begging does not appear as strong as in other species (Teather 1992; Leonard and Horn 1996; Dearborn 1998; Kilner 2002). Parents only fed the highest begging nestling on 50% of occasions (although in another 14% of visits the offspring fed was equal in height to its begging sibling). Parents - in particular fathers - appeared to be more responsive to competitive differences between siblings, since the correlation between preferential feeding of begging offspring was stronger when more offspring were gaping and when the relative height difference between nestlings was large. Furthermore, parents - in particular mothers - were more likely to feed nestlings according to how high they reached above the nest rim. It is widely assumed that the parent spending more time at the nest would be better able to assess the needs of the brood (Stamps et al. 1985; Gottlander 1987; MacGregor and Cockburn 2002). Given the length of time female emu-wrens spend at the nest when brooding and feeding large broods, begging height may therefore be a reliable cue of hunger. On average, female offspring reached higher when begging than male offspring. It is common for the smaller sex to beg more actively or at higher rates than the larger sex (e.g. Ryden and Bengtsson 1980; Bengtsson and Ryden 1983; Greig-Smith 1985; Stamps et al. 1989). However, this did not translate into a direct preference for allocating feeds to begging male or female offspring.

It appears as though parents respond to a combination of plumage or size cues, as well as behavioural cues signalling hunger and competitive vigour, when allocating prey. Ultimately, male offspring appear to benefit by receiving prey of higher energetic and nutritional value, a pattern which may become even more apparent post-fledging (e.g. Harper 1985; Slagsvold 1997).

*Why might parents favour sons?*  
Male emu-wren offspring may have higher energetic needs than females related to size or plumage dimorphism. Sons and daughters fledge in equivalent body condition despite the
disproportionate energetic content of prey received. This might infer that males have higher energetic demands. It has been widely demonstrated that larger nestlings have higher metabolic rates than smaller nestlings (Fiala and Congdon 1983; Teather and Weatherhead 1988; Anderson et al. 1993; Krijgsveld et al. 1998; Boulet et al. 2001). Sex-biased provisioning has been reported in sexually dimorphic species where there are large-size differences between nestlings (Ryden and Bengtsson 1980; Fujioka 1985; Greig-Smith 1985; Drummond et al. 1986; Litovich and Power 1992; Kilner 1995; Price and Ydenberg 1995; but see Stamps et al. 1985). However, when size differences between nestlings are small (in the range of 5%), sex-biased provisioning is more commonly absent (Smiseth et al. 1998; Whittingham et al. 2003). Nevertheless, small differences may potentially generate disproportionate energetic requirements especially in the late nestling phase (e.g. Leonard and Horn 1996).

The energetic costs of structural plumage colouration have not been widely studied. However, it has been suggested that plumage reflectance can be affected by minute changes in feather growth, and therefore the amount and regularity of the colour-producing nanostructure might carry production costs or be nutritionally dependent (Fitzpatrick 1998; Andersson 1999; Keyser and Hill 1999). The size of the bib appears to be correlated with male reproductive success in emu-wrens (Chapter 4), and as with other species, UV-reflectance of the bib may also signal male quality (Andersson and Amundsen 1997; Keyser and Hill 2000; Siefferman and Hill 2003). Hence, preferential care of sons may result in higher benefits to parents if reproductive success of males is more condition-dependent than in females.

Alternatively, parents may allocate more investment to sons due to the tendency for sons to become cooperative helpers and to repay the costs of this investment (‘repayment hypothesis’ see Emlen et al. 1986). Cooperative helpers increase the reproductive success of the breeding pair, with cooperative groups being more likely to produce larger broods, and two broods in a breeding season (Maguire and Mulder 2004; Chapter 2). Furthermore, as evident from this study, the total provisioning rate at cooperative nests appears to be higher than at nests tended by pairs. Thus, the quality or condition of offspring may also be enhanced by the presence of helpers, or offspring may reach independence more quickly, which would account for the higher likelihood of double broods. Nevertheless, only 19% of males surviving to independence became
cooperative helpers, so that the likelihood of parents receiving this benefit was quite low \((n = 26,\) Maguire and Mulder 2004; Chapter 2).

There was no evidence of a population-wide sex-ratio bias at the study site (Chapter 2), although male biases have been reported in other populations of southern emu-wrens (Pickett 2000), as well as in nesting records and museum specimens (Schodde 1982). Under conditions of low food supply, preferential allocation of care to sons may result in higher mortality of daughters in the nest or after fledging (Clotfelter 1996). Males, however, might be more susceptible to starvation than females if their energetic demands are indeed higher (Teather 1992). Food supplementation experiments and manipulation of brood size and sex ratio are needed to help unravel the evolutionary significance of sex-biased provisioning in the southern emu-wren.

**Parental contributions to offspring care**

Male emu-wrens were primarily responsible for provisioning of offspring, visiting at almost double the female’s rate and bringing larger prey per visit. Females, on the other hand, were exclusively responsible for brooding offspring, spending lengthy periods of time at the nest. In birds where one parent is engaged in non-feeding activities, such as nest guarding or brooding, the other parent commonly provisions at a higher rate (Woodard and Murphy 1999). Females increased their provisioning efforts as brooding declined (offspring became more endothermic from day seven post-hatching). Males did not respond to increased female assistance by decreasing their provisioning effort, instead older broods were provisioned at higher rates overall. A positive relationship between provisioning rate and brood age is a common pattern in birds (e.g. Moreno 1987; Karlsson 1994; Green 2002; Whittingham et al. 2003), presumably because offspring energetic requirements are higher closer to fledging.

Male emu-wrens were capable of adjusting their contribution of care to offspring, increasing their provisioning rates in the absence of the female (when widowed), or when brood sizes were large. Females were less flexible in their provisioning rates than males, especially during the early nestling phase. The lower flexibility of female provisioning efforts is evident from several studies involving experimental manipulation of brood size (great tit *Parus major*: Smith et al. 1988; red-winged blackbird: Whittingham 1989; pied flycatcher *Ficedula hypoleuca*: Källander and Smith 1990; Moreno *et al.* 1995; American kestrels *Falco sparverius*: Dawson and Bortolotti...
Female contributions may not vary greatly because they have already invested heavily during laying, incubation and brooding, and are working at some physiological maximum (Drent and Daan 1980; Nishiumi et al. 1996), or because time available for foraging is reduced as a consequence of time spent brooding (Wright and Cuthill 1990; Dickinson and Weathers 1999). Female emu-wrens do not vary brooding effort according to brood size, so that the time restrictions on foraging would appear to remain fixed regardless of the energetic demands of the brood.

Male emu-wrens appear to be less constrained than females in responding to increases in brood size. Nevertheless, high provisioning rates are likely to be energetically costly (Bryant 1988; Pärt et al. 1992; Moreno et al. 1995; Siegel et al. 1999) and expose individuals to higher predation risks (Lack 1954, 1966; Welty 1975; Breitwisch 1989). For this reason, only high quality males or those defending high quality territories may be able to afford elevated provisioning rates, and hence be capable of rearing larger broods. Elsewhere I report (Chapter 4) that clutch sizes of southern emu-wren pairs were positively correlated with male bib-size and territory quality, but unrelated to female attributes.

Biparental care appears to be necessary for successful fledging of offspring, since all nests tended by widowed birds failed. Older nestlings of widowed birds were predated; perhaps because they were left unattended for longer periods (e.g. Woodard and Murphy 1999), and/or louder begging vocalisations of hungry nestlings attracted predators (e.g. tree swallows Tachycineta bicolor, Leech and Leonard 1997). Among younger nestlings, starvation was a common cause of death when nestlings were fed by the female alone. It is more likely that mortality of recently-hatched nestlings raised by solitary males was related to hypothermia in the absence of brooding (see also western bluebirds Sialia mexicana, Dickinson and Weathers 1999). Starvation in this context was unlikely, since these males maintained the same level of overall provisioning as at biparental nests. Although the sample of widowed birds in this study was low, it appears that parents of either sex cannot fully compensate for loss of care by their partner, thus constraining emu-wrens to social monogamy (Wittenberger and Tilson 1980).
Table 1. The mean (± standard error) hourly provisioning rates of southern emu-wren parents at 16 nests. All nests were tended by pairs, with the exception of two nests tended by cooperative groups, each with one male helper (denoted by an asterisk). Numbers appearing in parentheses are the number of days nests were monitored by video surveillance.

<table>
<thead>
<tr>
<th>Nest (days)</th>
<th>Female</th>
<th>Male</th>
<th>Total mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>BURNT HILL (5)</td>
<td>5.06 ± 0.34</td>
<td>5.96 ± 1.05</td>
<td>5.51 ± 0.54</td>
</tr>
<tr>
<td>BYND23 (8)</td>
<td>7.69 ± 2.64</td>
<td>4.92 ± 0.37</td>
<td>6.31 ± 1.34</td>
</tr>
<tr>
<td>BLUEPEA (6)</td>
<td>1.05 ± 0.26</td>
<td>4.04 ± 0.68</td>
<td>2.55 ± 0.57</td>
</tr>
<tr>
<td>GMRY3 (11)</td>
<td>2.84 ± 0.66</td>
<td>7.91 ± 1.03</td>
<td>5.37 ± 0.81</td>
</tr>
<tr>
<td>GORSE (6)</td>
<td>3.29 ± 0.93</td>
<td>5.04 ± 1.29</td>
<td>4.16 ± 0.80</td>
</tr>
<tr>
<td>POLE 2_2 (5)</td>
<td>2.86 ± 0.57</td>
<td>10.08 ± 1.81</td>
<td>6.47 ± 1.50</td>
</tr>
<tr>
<td>POLE 2_3 (4)</td>
<td>7.29 ± 1.31</td>
<td>8.15 ± 0.74</td>
<td>7.72 ± 0.72</td>
</tr>
<tr>
<td>POLE 20 (4)</td>
<td>1.68 ± 0.44</td>
<td>13.65 ± 1.17</td>
<td>7.66 ± 2.33</td>
</tr>
<tr>
<td>POLE 22 (6)</td>
<td>5.91 ± 1.40</td>
<td>10.79 ± 0.86</td>
<td>8.35 ± 1.08</td>
</tr>
<tr>
<td>POLE 23 (4)</td>
<td>0.38 ± 0.38</td>
<td>5.06 ± 0.81</td>
<td>3.18 ± 0.91</td>
</tr>
<tr>
<td>POLE 6 (4)</td>
<td>0.53 ± 0.10</td>
<td>7.41 ± 0.68</td>
<td>3.97 ± 1.34</td>
</tr>
<tr>
<td>POLE 9 (4)</td>
<td>2.53 ± 1.01</td>
<td>4.37 ± 0.81</td>
<td>3.45 ± 0.69</td>
</tr>
<tr>
<td>SHEOAK (1)</td>
<td>1.81</td>
<td>6.97</td>
<td>4.39 ± 2.58</td>
</tr>
<tr>
<td>YMYY (4)</td>
<td>8.50 ± 0.77</td>
<td>7.35 ± 0.57</td>
<td>7.93 ± 0.49</td>
</tr>
<tr>
<td>*DH SE (9)</td>
<td>6.82 ± 0.80</td>
<td>6.95 ± 1.02</td>
<td>6.72 ± 0.48</td>
</tr>
<tr>
<td>*HILLSIDE (15)</td>
<td>4.75 ± 1.27</td>
<td>8.50 ± 0.93</td>
<td>6.59 ± 0.70</td>
</tr>
<tr>
<td>Total mean (96)</td>
<td>3.94 ± 0.41</td>
<td>7.32 ± 0.34</td>
<td>5.65 ± 0.27</td>
</tr>
</tbody>
</table>
Table 2. The mean (± standard error) proportion of the day spent at the nest by southern emu-wren parents at 16 nests. All nests were tended by pairs, with the exception of two nests tended by cooperative groups, each with one male helper (denoted by an asterisk). Numbers appearing in parentheses are the number of days nests were monitored by video surveillance.

<table>
<thead>
<tr>
<th>Nest (days)</th>
<th>Female</th>
<th>Male</th>
<th>Total mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>BURNT HILL (5)</td>
<td>0.06 ± 0.18</td>
<td>0.02 ± 0.02</td>
<td>0.04 ± 0.17</td>
</tr>
<tr>
<td>BYND 23 (4)</td>
<td>0.10 ± 0.15</td>
<td>0.02 ± 0.01</td>
<td>0.06 ± 0.21</td>
</tr>
<tr>
<td>GMGG (2)</td>
<td>0.25 ± 0.44</td>
<td>0.35 ± 0.36</td>
<td>0.30 ± 0.32</td>
</tr>
<tr>
<td>BLUEPEA (6)</td>
<td>0.41 ± 0.18</td>
<td>0.26 ± 0.15</td>
<td>0.34 ± 0.22</td>
</tr>
<tr>
<td>GMRY3 (9)</td>
<td>0.37 ± 0.27</td>
<td>0.33 ± 0.22</td>
<td>0.35 ± 0.25</td>
</tr>
<tr>
<td>GORSE (6)</td>
<td>0.40 ± 0.30</td>
<td>0.06 ± 0.06</td>
<td>0.23 ± 0.46</td>
</tr>
<tr>
<td>POLE 20 (4)</td>
<td>0.12 ± 0.39</td>
<td>0.06 ± 0.05</td>
<td>0.09 ± 0.31</td>
</tr>
<tr>
<td>POLE 22 (5)</td>
<td>0.40 ± 0.34</td>
<td>0.07 ± 0.08</td>
<td>0.23 ± 0.47</td>
</tr>
<tr>
<td>POLE 23_2 (6)</td>
<td>0.57 ± 0.14</td>
<td>0.19 ± 0.09</td>
<td>0.38 ± 0.35</td>
</tr>
<tr>
<td>POLE 9 (4)</td>
<td>0.42 ± 0.44</td>
<td>0.11 ± 0.20</td>
<td>0.26 ± 0.51</td>
</tr>
<tr>
<td>POLE2_2 (5)</td>
<td>0.31 ± 0.36</td>
<td>0.03 ± 0.02</td>
<td>0.17 ± 0.48</td>
</tr>
<tr>
<td>POLE2_3 (4)</td>
<td>0.13 ± 0.17</td>
<td>0.05 ± 0.07</td>
<td>0.09 ± 0.20</td>
</tr>
<tr>
<td>YMYY (5)</td>
<td>0.06 ± 0.25</td>
<td>0.02 ± 0.05</td>
<td>0.04 ± 0.23</td>
</tr>
<tr>
<td>*DH SE (9)</td>
<td>0.04 ± 0.19</td>
<td>0.04 ± 0.19</td>
<td>0.03 ± 0.01</td>
</tr>
<tr>
<td>*HILLSIDE (15)</td>
<td>0.23 ± 0.44</td>
<td>0.02 ± 0.03</td>
<td>0.10 ± 0.03</td>
</tr>
<tr>
<td>Total mean (89)</td>
<td>0.26 ± 0.42</td>
<td>0.10 ± 0.25</td>
<td>0.18 ± 0.45</td>
</tr>
</tbody>
</table>
Fig. 1. Prey size (square-root transformed) fitted values (from REML analysis with nest as a random factor, and brood size, day and offspring sex as factors) delivered to emu-wren nestlings of different sex, according to the age of those nestlings. [REML estimated effects (square-root mean prey size): f = -0.049, m = 0.039].
**Fig. 2.** The mean proportion of feeds containing different prey types allocated to male and female offspring.
Fig. 3. Hourly provisioning rate (square-root transformed) of southern emu-wren parents at 16 nests, versus age of brood (days after hatching). [REML estimated effects: $f = 0.16$, $m = 0.08$].
Fig. 4. Mean hourly provisioning rate of southern emu-wren parents according to brood size ($n = 16$ nests). [REML estimated effects: $f = -0.02$, $m = 0.38$].
Fig. 5. Variation in the mean duration of a feeding visit (s) for southern emu-wren parents according to brood size.
Fig. 6. The mean proportion of prey types brought to the nest by adult male and female emu-wrens. Significant results ($p < 0.05$) are denoted by an asterisk.
Chapter 6

Low levels of extra-pair mating and cooperative breeding in the Southern Emu-wren

Abstract
The frequency of extra-pair paternity (EPP) varies considerably across avian species, with some of the highest rates recorded within the fairy-wrens (Maluridae). A number of hypotheses attempt to explain this interspecific variation, including the ‘constrained female’, ‘restricted schedule’ and ‘adult survival’ hypotheses. I investigated the genetic mating system of the Southern Emu-wren (*Stipiturus malachurus*), a socially monogamous passerine occurring within the Australian family Maluridae. Southern emu-wrens are cooperative breeders with high levels of paternal care and low annual survival. Each of these characteristics predicts varying levels of EPP according to the major hypotheses. I developed microsatellite markers to assess paternity within 27 emu-wren broods. Overall, 12% of 50 genotyped offspring were sired by a male other than the social father, and 15% of all nests contained at least one extra-pair young. Mate choice by female emu-wrens appears to be limited by the importance of high levels of paternal care for offspring survival, as suggested by the ‘constrained female’ hypothesis. Moreover, a tradeoff between paternal care and EPC may be unlikely for males (‘restricted schedule’ hypothesis) given the costs of reduced care and the relatively low benefit of EPP. Within the fairy-wrens, the prevalence of cooperative breeding appears to facilitate high levels of extra-pair paternity, as helpers compensate for reduced paternal care. The low occurrence of cooperative breeding in the southern emu-wren may thus help explain the extreme differences in the frequency of extra-pair paternity between these genera. Low annual survival of emu-wrens does not lead to higher EPP but may instead make divorce a less costly means of improving mate (or territory) choice.

Introduction
The profusion of studies exploring extra-pair paternity (EPP) over the past 15 years has revealed considerable variation in rates of EPP, even between closely related species (Birkhead and Möller 1995; Westneat and Sherman 1997; Westneat *et al.* 1990). Original attempts to explain
interspecific variation in rates of EPP concentrated on opportunities for extra-pair copulations (EPC) associated with ecological conditions (e.g. breeding synchrony: Stutchbury and Morton 1995; Stutchbury 1998; breeding density: Birkhead et al. 1987; Møller and Birkhead 1992). However, these hypotheses received little support from comparative analyses (Westneat and Sherman 1997; Weatherhead and Yezerinac 1998; Bennett and Owens 2002; Møller 2003). Instead, three hypotheses focusing on tradeoffs associated with EPP in relation to parental care and adult survival have gained better comparative support (Birkhead and Møller 1996; Arnold and Owens 2002; Bennett and Owens 2002; Møller 2003).

The ‘constrained female’ hypothesis was originally proposed to explain the high rates of extra-pair paternity recorded in the superb fairy-wren (*Malurus cyaneus* 76% EPP within broods: Mulder et al. 1994). Female fairy-wrens control fertilizations and are highly selective of certain extra-pair males (Mulder and Magrath 1994; Mulder et al. 1994; Dunn and Cockburn 1999). However, female mate choice appears to be constrained by the social environment and the resultant contributions of males to parental care. Fairy-wrens form socially monogamous pair bonds but more commonly occur in cooperatively breeding groups (57% of group/seasons: Green et al. 1995). Within pairs, male fairy-wrens contribute more parental care and experience higher within-pair paternity than dominant males in cooperative groups. In cooperative groups, helpers compensate completely for reduced paternal assistance (Mulder et al. 1994; Dunn and Cockburn 1996). Thus, it appears that a change in the female’s social environment tips the balance of costs and benefits to favour one reproductive strategy over another. The contributions of helpers liberate females from the constraints of dependence on a single male for paternal care, facilitating unrestricted mate choice without a compromise to offspring viability. The benefits of EPP to females potentially include acquiring ‘good genes’ for offspring (Dunn and Cockburn 1999) or in the highly philopatric splendid fairy-wren (*M. splendens*), reducing the likelihood of inbreeding (65% EPP occurs within broods: Brooker et al. 1990).

The ‘restricted schedule’ hypothesis (Møller and Birkhead 1993; Ketterson and Nolan 1994; Schwagmeyer et al. 1999) may not be mutually exclusive of the predictions of the constrained female hypothesis, but instead focuses on the costs and benefits of EPP to males. High levels of paternal investment may restrict time available for males to seek and engage in EPC. This can include male contributions to nestling provisioning and nest guarding, but restrictions appear to
be greater for males that contribute to incubation (Møller and Birkhead 1993; Ketterson and Nolan 1994; Schwagmeyer et al. 1999). If the benefits of paternal care are high relative to the benefits of EPP, it is expected that males will be unlikely to tradeoff time allocated to paternal care, leading to a lower likelihood of EPP. In cooperative breeders, the contributions of helpers may minimise the costs of reduced paternal care and enable males to seek EPC opportunities. For example, in the superb fairy-wren, males with reduced workloads engage more frequently in extra-pair courtship displays, and this increases extra-pair mating success (Green et al. 1995).

Finally, the ‘adult survival’ hypothesis (Mauck et al. 1999; Wink and Dyrcz 1999) predicts that in short-lived species, selection should favour males that invest in the current brood, due to the uncertainty of future breeding opportunities. Thus, reducing the likelihood of retaliation by males (through desertion or reduced paternal care) in response to lowered paternity. This would therefore liberate females from constraints on mate choice, leading to a greater tolerance for EPP in species with high adult mortality compared to those with long reproductive life spans.

The Southern Emu-wren (*Stipiturus malachurus*), a close relative of the fairy-wrens, exhibits high levels of paternal care, is a facultative cooperative breeder and has low annual survival (Maguire and Mulder 2004; Chapter 2). Here, I investigate the genetic mating system of the species using microsatellite markers and examine the predictions of the three described hypotheses in relation to the life-history characteristics of the southern emu-wren. Two of these hypotheses predict opposite levels of EPP frequency in this species. In line with the restricted schedule and constrained female hypotheses, high levels of paternal care may limit male opportunities for EPC and constrain female mate choice. The low prevalence of cooperative helping in the southern emu-wren would suggest lower rates of EPP than in the fairy-wrens. Alternatively, low adult survival (Pickett 2000; Maguire and Mulder 2004; Chapter 2) may reduce apparent constraints on female mate choice and result in higher rates of EPP.

**Methods**

*Population monitoring*

I monitored a population of emu-wrens inhabiting 16 ha of wet swamp and heathland and an adjoining 6 ha of coastal heathland in Portland, southwestern Victoria, Australia (38°23’S, 141°36’E) over three breeding seasons, August to March, in the years 2000-2003. General
demographic and breeding information is provided in Chapter 2. I captured individuals using mist-nets and banded each with a unique combination of colour-bands for identification. From each captured bird, I took a 10-µl blood sample from the brachial vein using a capillary tube and stored this in 100% ethanol. In the three breeding seasons, 69, 74 and 81% of males in the population were captured and bled (2000/01: 5 unbanded, 11 banded; 2001/02: 5 unbanded, 14 banded; 2002/03: 5 unbanded, 22 banded). I observed a total of 59 pairs and three cooperative groups containing 1-2 male helpers. Helpers were distinguished from breeding males on the basis of several behaviours, including proximity to the breeding female, courtship feeding and territorial behaviour.

I visited the field site daily to locate nests and followed the progress of each nesting attempt. Average clutch size was 2.7 (range 2-3 eggs). At three nests where eggs were abandoned prior to hatching, I collected and dissected the embryo and stored tissue in 100% ethanol (n = 5 eggs). From another brood, DNA was extracted from an unhatched, fertilised egg. At 14 nests, I banded nestlings when they were between 11-14 days old and took blood samples as above. I collected dead nestlings from 3 abandoned nests, dissected their hearts and livers, and stored tissues in 100% ethanol. Where offspring fledged earlier than expected or fledglings appeared on territories where nests had not been located (n = 8 families), I captured these juveniles in mist-nets, banded them and took blood samples. In each of these families, I had observed the captured male feeding or herding offspring prior to capture.

In total, DNA samples for 28 broods were obtained (53 offspring; 1.9 ± 0.2 nestlings per brood). In six broods, I was unable to capture one of the offspring in the brood, and in another nest, only one member of the brood was sampled, as the two other nestlings died and were removed from the nest by the breeding female. I excluded a brood of three raised by a cooperative group from my analysis, as the social father could not be captured. Three of the 27 remaining broods were raised by cooperative groups (two groups), and 24 by unassisted pairs (22 unique pairs; 17 males, 20 females).

Development of microsatellite markers

I extracted DNA from blood samples and tissue taken from eggs and dead nestlings, using a salting-out procedure (Bruford et al. 1992). Extracted DNA was stored in low EDTA-TE buffer
(10mM Tris pH7.5, 0.1mM EDTA). I enriched genomic DNA for GA, GT and GAAA repeat-containing fragments using the method of Gardner et al. (1999) with modifications as detailed in Adcock and Mulder (2002). I amplified positive clones in 50µl reactions and purified PCR products using the Qiaquick PCR purification kit (QIAGEN) following the manufacturer’s instructions. PCR products were sequenced commercially (SUPAMAC, Sydney, Australia and MACROGEN, Seoul, Korea).

The 184 colonies screened in the GAAA, 372 in the GA and the 200 in the GT-enriched genomic library, yielded respectively, 3, 58 and 18 colonies that were sequenced. Primers were manufactured (Invitrogen) for the 26 of these that contained eight repeats or more and flanking sequence suitable for primer design. One primer in each pair was manufactured with a 5’-M13 (5’CACGACGTTGTAAAACGAC) tail for use in the universal dye-labelling method described by Boutin-Ganache et al. (2001). I tested primer pairs that gave consistent, specific products for polymorphism by typing at least 20 putatively unrelated individuals at each microsatellite locus. Reactions (10µl) were performed in 0.2ml microtitre plate (Greiner) wells layered with a drop of mineral oil (Sigma) on a Corbett Research PC-960C thermocycler. All PCRs contained Taq polymerase (0.25 units), MgCl$_2$ (see Table 1 for concentrations), reaction buffer (10mM Tris-HCl, 50mM KCl, 0.1% Triton X-100) and dNTPs (200µM) supplied by Promega. Reactions contained an M13 primer (200 nM) 5’-labelled with a Beckman Coulter dye (D3 or D4), the locus-specific tailed (15nM) and untailed (200nM) primer, and 40ng of genomic DNA. A total of 40 cycles of amplification were performed: one cycle of 60s at 95C followed by 40 cycles of 94C for 20s, the optimal annealing temperature for 30s and 73C for 90s. PCR products (0.25µl) were electrophoresed on a Beckman Coulter 8000XL automated sequencer using the CEQ 8000XL fragment analysis kit (Beckman Coulter) according to the manufacturer’s instructions. I estimated fragment sizes using the Beckman Coulter 8000XL fragment analysis software. Primer sequences, optimum annealing temperatures and MgCl$_2$ concentrations are listed in Table 1.

Seven loci were polymorphic ($N_A = 2-9$, $H_E = 0.32-0.75$, Table 1). Using tests implemented in GENEPOP 3.3 (Raymond and Rousset 1995), no loci showed linkage disequilibrium ($p > 0.05$) and only $Smm4$ significantly deviated from Hardy-Weinberg expectations with a highly significant heterozygote deficiency. Analyses of individuals of known sex indicated that $Smm4$
was Z-chromosome linked. All genotyped females were homozygous at this locus compared with 30% homozygosity in males.

**Paternity assignment**

I genotyped all nestlings and adults at 7 loci (Smm1, 2, 3, 4, 5, 6 and 7). These loci gave a probability of 0.956 for unambiguously identifying the genetic father of each nestling when maternal alleles had been assigned. No two males in the population had identical genotypes.

I used a two-step procedure to assign parentage. I first compared offspring genotypes to those of their putative mothers. When these matched, I subtracted the maternal alleles from the nestling’s genotype, and then compared the allelic profile of the offspring to that of the social father. For one-allele mismatches, I searched for any other males in the population providing a better match than the social father. In cases where genotypes differed at two or more loci, I assumed that the nestling was sired by an extra-pair male. Using a database containing all genotyped males in the population, I attempted to identify the most likely father of the nestling based on male genotype. In cases where multiple males were potentially the father of a nestling, I conservatively assigned the male in closest proximity as the most likely father (Double and Cockburn 2000). I compared my assignments to those obtained using the maximum likelihood procedure in the computer programme CERVUS (Marshall et al. 1998), setting the minimum confidence level of correctly assigning paternity to 80%. In all cases, the most likely fathers as determined from the exclusion method were identical to those nominated by CERVUS.

**Results**

I was able to assign paternity to 44 of the 50 (88%) genotyped nestlings (Table 2). Non-maternal alleles in the offspring matched the social father exactly in 42 cases. One-allele mismatches between the social father and offspring occurred in a further three cases. Of these one-allele mismatches, two offspring occurred in broods where all other offspring in the nest matched the social father, and where there was no better allelic match with another male in the study population. I assumed these mismatches arose as a result of mutations, especially as offspring alleles were only separated by two base pairs from the paternal allele at the mismatching locus. Across species, mutation rates of microsatellite loci regularly exceed 1% (Jeffreys et al. 1988; Beck et al. 2003), and the majority of mutations result in changes of only one repeat unit (Neff
and Gross 2001; Beck et al. 2003). An additional offspring mismatching the social father at one allele occurred in a brood where another extra-pair offspring was present and differed by four base pairs from the paternal allele. I assumed this was an extra-pair offspring, but could not find the paternal match within the banded population.

Offspring alleles mismatched the social fathers at three or four alleles in the remaining five cases and I assumed extra-pair males fathered these offspring. One was the sole offspring of a pair captured post-fledging, two occurred within the same brood (and the third member of the brood escaped capture), and two belonged to broods each containing two other within-pair offspring, one of which was raised by a cooperative group. I could not match the paternal alleles of four extra-pair offspring with any other captured male, but one offspring matched two males on the neighbouring territories.

Overall, 12% of all offspring genotyped ($n = 50$) were sired by an extra-pair male and 15% of all nests ($n = 27$) contained at least one extra-pair offspring. All but one brood that was cuckolded contained three offspring. No bias in the sex ratio of cuckolded broods was evident ($\chi^2 = 1.52, p = 0.218$).

There was little evidence to suggest that male helpers engaged in EPCs. In one cooperative family, both helpers were identified as sons and no EPP occurred within the two broods raised by this group. However, my microsatellite markers were not polymorphic enough to distinguish between the social father and helper male as potential sires of one offspring. In the other cooperative group for which I was able to obtain DNA from the breeding pair and all offspring, I was unable to capture the helper and thus could not determine whether he was a son of the breeding pair, or whether he sired the extra-pair nestling in the brood. At another cooperative family, I was unable to capture the dominant male. I was nevertheless able to exclude the helper as a potential sire, as he did not match any of the three offspring at different combinations of two loci.

**Discussion**

In the southern emu-wren, extra-pair paternity occurred in 15% of nests and accounted for 12% of offspring. This rate of EPP is similar to that reported for many other small passerines, but is
notably low compared to frequencies of EPP reported for the closely related fairy-wrens 
(*Malurus splendens* 65% of nests: Brooker *et al.* 1990; *M. cyaneus* 76% of nests: Mulder *et al.* 1994; *M. melanocephalus* 74.5% of nests: Karubian 2002). Despite their taxonomic affinities, fairy-wrens and emu-wrens differ in a number of life-history attributes, and these may help to explain the difference in frequency of EPP.

**Constraints on extra-pair mate choice for female emu-wrens**

One significant and general cost of EPC to female reproductive success is the risk of retaliation (reduced paternal assistance or desertion) by males in response to reduced paternity (Arnqvist and Kirkpatrick 2005). While in some monogamous passerines females are capable of raising offspring unassisted (reviews by Wolf *et al.* 1988; Ketterson and Nolan 1994; Gowaty 1996), biparental care of offspring appears to be necessary for successful reproduction in southern emu-wrens. Female emu-wrens were unable to successfully raise broods alone (Chapter 5), and provisioning rates at nests attended by solitary females were lower than at nests attended by two parents (Chapter 5). Given this extreme dependence on male cooperation for successful reproduction, any benefits of EPC to females may be low compared to the possible costs of withheld paternal care or desertion.

In cooperatively breeding species, the contributions of helpers to offspring provisioning may reduce this constraint on extra-pair mate choice by females (the ‘constrained female hypothesis’; Mulder *et al.* 1994). For instance, in the superb fairy-wren, helpers compensate for reductions in paternal care, mitigating potential costs to females engaging in EPC. This emancipation from paternal care in cooperative groups is closely correlated with the prevalence of EPP in fairy-wrens; in groups with helpers, the proportion of offspring fathered by the dominant male is significantly lower than in pairs, even though the helpers themselves rarely gain paternity (Mulder *et al.* 1994; Dunn and Cockburn 1996).

If helpers liberate females from constraints on extra-pair mate choice, the likelihood of EPP should also be higher in cooperative groups of emu-wrens than it is in pairs. In this study, EPP occurred in one of two cooperative groups sampled, compared to 14% within pairs (*n* = 22). Paternity assignment among a much larger sample of pairs and cooperative groups will be necessary to provide convincing evidence of any systematic difference in the frequency of EPP.
in these two contexts. Nevertheless, the infrequent occurrence of cooperative breeding in southern emu-wrens (5%, \(n = 62\), Maguire and Mulder 2004; Chapter 2) offers a potentially parsimonious explanation for the low frequency of EPP in the species.

An important assumption of the ‘constrained female’ hypothesis is that males are able to modify their parental care in response to changes in extra-pair paternity. Males might be able to assess paternity in their broods by several means, including monitoring of female departures (Kempenaers et al. 1992; Sheldon 1994) or territorial intrusions by extra-pair males (Phillip and Gross 1995). It has nevertheless been argued that males cannot reliably distinguish their own offspring within a brood of mixed paternity (Davies et al. 1992; Leonard et al. 1995). If so, in species where males have short reproductive tenure, they should be less likely to reduce care because of the possible costs of mistakenly disadvantaging genuine offspring (reviewed by Whittingham et al. 1992; Westneat and Sherman 1993; Sheldon 2002; Westneat and Stewart 2003). Although this scenario is plausible, it predicts (Mauck et al. 1999) high rates of extra-pair paternity in southern emu-wrens, which contradicts the observed pattern.

**Trade-offs for males between within- and extra-pair paternity**

Male emu-wrens contribute to nest-building, guard the nest during incubation, provision the female when she leaves the nest after each incubation bout, and contribute the greatest share of provisioning of nestlings and fledglings (Maguire and Mulder 2004; Chapter 2). Thus, as well as constraining female mate choice, the substantial investment made by males in paternal care may restrict opportunities for seeking and engaging in EPCs (‘restricted schedule’ hypothesis; Möller and Birkhead 1993; Ketterson and Nolan 1994; Schwagmeyer et al. 1999).

In cooperatively breeding fairy-wrens, helper contributions afford dominant males greater flexibility in departing the territory to display to extra-pair females, which in turn enhances their likelihood of obtaining EPCs (Mulder et al. 1994; Green et al. 1995; Dunn and Cockburn 1996; Mulder 1997). In contrast, male emu-wrens do not appear to reduce their care to offspring in the presence of helpers (Chapter 5). Instead, the total brood provisioning rate is higher for broods provisioned by groups than those provisioned by pairs (Chapters 2 and 5).
The benefits of EPP to males may furthermore be small relative to the costs of reduced care (Maynard Smith 1977). Although I was unable to assign extra-pair paternity to individual males, it is unlikely that any male in this population sired more than one extra-pair offspring. One-third of male emu-wrens at the site survived for only a single breeding season and only 7% survived beyond two seasons \((n = 30)\), so that the lifetime reproductive success of most males was generally determined by their reproductive output in a single breeding season. Given the necessity of paternal care to offspring survival and the limited options for future breeding, the optimal response for males should be to invest in the current brood (Mauck et al. 1999).

*Causes and consequences of female dependence on male care*

Why do emu-wrens appear to be more dependent on male contributions to parental care than fairy-wrens? One possible explanation is that limited food availability selects for dependency on paternal care. In the fairy-wrens, habitat preferences are broader (Higgins et al. 2001) and resources may not be as limited. This may also potentially account for the differences in the frequency of cooperative breeding in the two genera. Presumably only high quality territories with abundant resources could support additional group members and would confer benefits to juveniles that delay breeding to become cooperative helpers (‘ecological constraints hypothesis’ Emlen 1982, 1984; Stacey and Ligon 1987). In several fairy-wren species, the number of helpers within a group is positively related to territory quality (Nias and Ford 1992; Brooker and Rowley 1995; Chan and Augusteyn 2003).

The important role of paternal care in maximising reproductive success further suggests that females may gain greater fitness benefits by discriminating among males on the basis of direct (parental), rather than indirect (genetic) benefits. If so, females may exercise mate choice primarily through divorce, rather than extra-pair fertilisation. Low adult survival results in abundant breeding territory vacancies becoming available each year (Maguire and Mulder 2004; Chapter 2). Divorce occurs in 40% of pairs that survive across seasons \((n = 10)\), and when divorce takes place, the female usually disperses from the territory after a failed breeding attempt (Maguire and Mulder 2004; Chapter 2). By divorcing a male and emigrating to another territory, females stand to gain access to both improved resources and a male of potentially higher quality.
Conclusion

In conclusion, biparental care appears pivotal to the reproductive success of male and female emu-wrens. The most likely explanation for the need for biparental care is that emu-wrens occupy environments in which resources are limited. Dependence on male care may both constrain females from engaging in unrestricted mate choice (‘constrained female’ hypothesis) and males from engaging in EPC (‘restricted-schedule’ hypothesis). The low frequency of cooperative breeding means that females are rarely emancipated from the need for male care. The importance of paternal care for offspring fitness may select for female mate choice of males based on direct benefits (the provision of high levels of paternal care; Hoelzer 1989), rather than indirect genetic benefits (genes inherited by the offspring; Fisher 1930; Zahavi 1975; Hamilton and Zuk 1982). Under such conditions, females may exercise mate choice by means of divorce, rather than extra-pair mating.
Table 1 Characterisation of microsatellite loci in the southern emu-wren (*Stipiturus malachurus*). The final annealing temperature (T<sub>M</sub>) is in °C and the MgCl<sub>2</sub> concentration in mM. The number of individuals genotyped (N), number of alleles (N<sub>A</sub>), allele size range in base pairs (bp), and observed (H<sub>O</sub>) and expected (H<sub>E</sub>) heterozygosity are listed for each locus. An asterix denotes a sex-linked locus, and observed and expected heterozygosity and exclusion probabilities are calculated from males only. The M13 prefix in the primer sequence denotes a 5’ M13 tail (CAGGACGTTGGTAAAAACGAC), attached to the primer sequence. Cloned sequences have been deposited with GenBank under Accession numbers DQ160179-DQ160186.

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<th>N&lt;sub&gt;A&lt;/sub&gt;</th>
<th>Bp</th>
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Table 2. The number of within and extra-pair young among 28 southern emu-wren broods. Families are divided on the basis of the social mating system (cooperative groups and pairs). Families are alphabetically coded and numbers refer to first and second broods by the same pair. In all pairs/groups, the social mother and father were captured, with the exception of family Y where the dominant male was not captured. [I included this brood in analyses exploring potential sires within the population, including the helper from this group.] The number of offspring typed and those I failed to capture are given. Those denoted with an asterisk were captured post-fledging, while a plus sign denotes nests where eggs or dead nestlings were collected. In all other nests, offspring were banded and bled when 11-14 days old.

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Chapter 7

General discussion

The findings of this thesis contribute to our understanding of the breeding biology and habitat requirements of the southern emu-wren, and more generally, the evolution of sex-biased parental care, and the role of detailed population studies in avian conservation. Below I highlight the most important findings of my research and offer suggestions for future research.

A low frequency of extra-pair paternity, compared to other Malurids

In the literature on EPP in birds, fairy-wrens of the genus *Malurus* within the family Maluridae stand out because of their high frequencies of extra-pair fertilisations (Brooker et al. 1990; Mulder et al. 1994; Karubian 2002). *Stipiturus* is the first Malurid genus outside *Malurus* for which parentage analyses have now been completed, and my findings show that the frequency of EPP in this group is dramatically lower. Why have emu-wrens evolved a less genetically promiscuous mating system than the fairy-wrens, despite sharing many ecological traits with this genus? The most likely explanation appears to be that emu-wrens occupy environments in which resources are limited and survival is low. As a result, female emu-wrens depend on paternal care to an extreme degree. Because cooperative breeding occurs at a low frequency, alternative sources of parental care that might emancipate females from the need for male care and facilitate unrestricted mate choice, are rarely available. It appears that females may gain greater fitness benefits by discriminating among males on the basis of direct (parental), rather than indirect (genetic) benefits, and thus, females may exercise mate choice primarily through divorce, rather than extra-pair fertilisation.

Biased provisioning of sons and daughters in the late nestling stage

Southern emu-wren parents allocated larger prey items to sons than daughters in the late nestling phase and also biased the proportion of different prey types fed to each sex, so that sons appeared to receive more profitable prey items. The number of feeds allocated to offspring tends to be the focus of most studies reporting biased provisioning in birds. This is only the second study (after Magrath et al. 2004) to investigate differences in prey type and size allocated to sons and
daughters, and both have revealed this as a potential mechanism for biasing care to offspring. For species such as the southern emu-wren, where size differences are in the order of 5%, energetic demands are not expected to be large enough to generate disproportionate investment in sons and daughters. However, size-related energetic requirements are only one possible explanation for sex-biased care, and male and female southern emu-wrens differ in a number of respects, including plumage dichromatism and the degree of natal philopatry.

*Impact of predators on breeding success and adult survival*

Predation appears to be a profoundly important selective agent both on adults and nestlings. Midway through one breeding season, the number of adults within the study population crashed to below 50% of the original level, and this coincided with a rise in predator numbers. This event highlighted the potential vulnerability of this small population to sudden extinction in the absence of effective predator control, and the importance of immigration of individuals from surrounding populations for population recovery. Deployment of video cameras at emu-wren nests provided direct evidence that nest predation by snakes and feral cats is the principal cause of nest failure in southern emu-wrens. Emu-wren nests were built close to the ground, making them easily accessible to these two ground-dwelling predators. When cat numbers rose dramatically in one year of my study, this had widespread effects on the local bird fauna, including the southern emu-wren population. This rise was partially attributed to a decline in fox numbers, highlighting the need for simultaneous control of introduced predator populations so that predator-prey dynamics are not disturbed.

The strong positive correlation I found between the density of snakes and emu-wren nest failure and adult mortality during the breeding season, indicates that high quality food resources and protective cover were of modest value to emu-wrens if territories with these attributes also harboured high densities of snakes. The impact of snakes on emu-wren numbers may have been exacerbated by a decline in alternative prey sources in the local area. Human land-use practices and altered water quality have contributed to the decline (and local extinction) of many small mammal and frog species. Habitat fragmentation, degradation and edge effects may also contribute to increased exposure to predators (Heske *et al.* 2001; Huhta *et al.* 2004), particularly because snakes have been found to prefer edge habitats due to thermoregulatory benefits and higher abundance of prey (see review of Weatherhead and Blouin-Demers 2004). Potentially
effective conservation measures for reducing the impact of snakes on emu-wrens, include the re-establishment of local biodiversity and enhancement of habitat connectivity.

Population viability and habitat management

The dispersal of individuals between habitat patches clearly can sustain populations following local catastrophic events (such as the population crash observed in this study). Proximity to a source population appears to be essential, as populations subject to catastrophic reductions in numbers elsewhere have not recovered (Mt Lofty Ranges; Recovery Team Reports 1994-1998). Emu-wrens disperse relatively short distances (in the maximum range of 1.2-2.5 km; see also Pickett 2000) and this behaviour is influenced by the degree of ‘connectivity’ (vegetated corridors) between patches of suitable habitat. Emu-wrens have been known to move through tracts of highly unsuitable habitat (including stands of weeds) so that the habitat specifications of corridors appear to be more generalised than those of breeding habitat. Nevertheless, even in areas less subject to fragmentation, very few juveniles are sighted after dispersal from the natal territory. This implies that high costs are associated with dispersal. In fragmented landscapes, greater dispersal distances presumably increase physiological costs and exposure to predators (Dale 2001). Exchange of individuals between populations also helps sustain levels of genetic diversity and reduces the deleterious effects of inbreeding. It is unknown whether hatching failure increases with high relatedness of individuals, but in other avian species this has been a significant contributor to population decline (Westemeier et al. 1998).

Given the effect of habitat fragmentation on population viability, it appears that habitat management may be best directed at a landscape level. In Victoria, the remaining inland populations (Bunyip State Park, Yellingbo Reserve and Grampians National Park) and those in highly urbanised areas (Cranbourne Botanical gardens and Langwarrin Flora and Fauna Reserve) are of greatest conservation concern, primarily due to their isolation. Preservation of fine-scale habitat structure is also a priority. Vegetation structure is an important component of the species habitat, influencing use and the subsequent survival and breeding success of emu-wrens. The degree of cover, vertical foliage density, height and diversity of plant species all contribute to habitat suitability for emu-wrens. Vegetation must offer structural support and concealment for nests and provide food resources (influencing abundance, diversity and temporal availability of insects), cover from predators and shelter from extreme climates and strong winds, as well as
facilitate emu-wren movement. Particular attention must be paid to management of invasive weeds, which have the potential to alter vegetation structure. An appendix to this thesis includes a set of habitat management guidelines specifically developed for conservation of the Portland population of emu-wrens.

Future directions

What factors limit juvenile dispersal and natal philopatry in emu-wrens? Cooperative breeding occurred at low frequency in the southern emu-wren. Helping appears to have benefits associated with raising non-descendant kin and residing on high quality territories, but what causes juveniles to delay dispersal and postpone independent breeding? A comparative study of populations varying in demographics, particularly in territory and breeding vacancies, should advance our understanding of the ecological conditions likely to affect natal philopatry in the southern emu-wren. I detected few cases of successful juvenile dispersal, but southern emu-wrens are extremely difficult to detect. Radio-transmitters are a costly, but potentially more effective method of investigating juvenile dispersal. To understand the ecological factors promoting cooperative breeding in emu-wrens, but also to obtain information fundamental to population conservation management, it will be necessary to obtain information on the distances juveniles disperse (whether they are capable of crossing large tracts of agricultural land) and whether any sex bias exists in philopatry or survival during dispersal (such information would incidentally enable more accurate determination the effectiveness of habitat corridors, and possible barriers to dispersal).

Genetic markers may also be useful tools for determining whether dispersal occurs between populations. Preliminary testing of microsatellite markers (developed in Chapter 7 for paternity analysis) in different southern emu-wren populations has revealed considerable variation in the levels of heterozygosity and allele frequencies between populations (Maguire unpublished). These markers are therefore potentially valuable for assessing genetic exchange between populations, population viability, inbreeding depression and bottlenecking events (Nunney and Campbell 1993). Genetic markers would also be a valuable tool for identifying source populations for translocations.
Does cooperative breeding facilitate EPP in the southern emu-wren?
The correlation between high frequency of EPP and cooperative breeding in fairy-wrens, and low
frequencies of EPP and cooperative breeding in emu-wrens supports predictions of the
‘constrained female’ hypothesis. Nevertheless, it remains to be demonstrated that the frequency
of EPP is indeed higher within cooperative emu-wren groups than unassisted pairs, as the sample
size within this study was too small to make any such conclusion. Two assumptions of the
‘constrained female’ hypothesis are that a) females are more likely to engage in extra-pair
fertilisations when they are less dependent on male contributions (e.g. when food supply is
abundant or helpers are present) and b) that males reduce paternal care in response to lowered
paternity. The former assumption predicts that across populations, the frequency of EPP should
be correlated with food abundance or the incidence of cooperative breeding. Within populations,
year-to-year variation in resource availability or the frequency of cooperative breeding should
also be correlated with the rate of EPP. Experiments in which food is supplemented, or helpers
are removed from cooperative groups, should also result in an increase or decrease in the
frequency of EPP. Food supplementation should both reduce the dependence of females on male
care and restrictions on male opportunities to seek EPP (‘restricted schedule’ hypothesis).
Detailed observations of the time experimental and control males allocate to parental care
(including nest guarding and foraging), extra-territory excursions and mate guarding should
reveal the nature of tradeoffs between these mutually exclusive activities. Cross-fostering of
offspring between nests may reveal whether males are capable of recognising their own
offspring.

What are the fitness consequences of sex-biased provisioning?
Emu-wrens survive well in captivity and have the potential to breed successfully (Hutton 1991).
The growth rates of male and female nestlings could be measured under experimentally varied
dietary regimes to determine whether biases in the size and type of prey allocated to sons lead to
higher energetic and nutritional gain. Furthermore, to determine whether parents respond to
plumage cues when allocating prey to nestlings, these cues could be manipulated using non-toxic
paints that have similar spectrophotometric properties to emu-wren plumage. Alternatively, size
cues might be important. Parental responses to mixed broods varying in the magnitude of size
differences between offspring could also be investigated by means of cross-fostering.
Chapter 7  General discussion

What is the role of sexual dichromatism in emu-wrens?
Emu-wrens develop sexually dichromatic plumage as nestlings, an unusual phenomenon among birds. In view of the short lifespan of emu-wrens, early plumage maturation may facilitate territory acquisition or mate attraction for newly independent young, enabling breeding in their first year. Sexual dichromatism among adults is usually associated with polygynous or highly promiscuous mating systems. In the southern emu-wren, the mating system appears to be monogamous, and this raises the question of why males should be dichromatic. Males are important contributors to nestling feeding and females could use male bib size or colouration to assess their potential as providers (‘good parent’ process of sexual selection; Hoelzer 1989). In the field, male reproductive success (using within- and extra-pair matings) could be correlated with measurements of the size and colouration of the bib (using reflectance spectrophotometry). The bib size and colour could then be experimentally manipulated to observe any resultant changes in territory size/ownership, mate switching or reproductive success. Aviary-based experiments manipulating diet (arthropod sources as identified by this study) could be used to evaluate whether structural colouration of adults is condition-dependent. This may help explain the observed biased provisioning of sons and daughters.

How important are resources versus predators in determining territory quality?
This study has revealed that habitat quality, in particular food abundance, and predation pressure are major factors influencing the survival and breeding of southern emu-wrens. Nevertheless, the relative importance of each of these factors still requires further investigation. Field-based experiments manipulating food availability (through food supplementation) and predation pressure (protected vs. unprotected nests) and comparing the subsequent breeding success (e.g. clutch size, fledging success) of pairs would be highly informative. For these experiments, choice of a field site homogenous in habitat structure and pairs similar in age/breeding experience would help minimise potential confounding variables.

Does emu-wren habitat suitability change temporally?
The composition and structure of heathland habitats along the Southern coast of Australia are likely to change considerably in the long-term, due to weed invasions and reduced fire frequency. This study confirmed the importance of habitat structure for emu-wren occupancy and use, but little is known of how habitat structure changes temporally and how emu-wrens
respond to these changes. By measuring vegetation structure and species diversity within different aged heathlands or areas of variable fire history, optimal ‘age’ or ‘burn’ classes of habitat can be determined. Within the Portland region, mosaic burning of the heathlands will be implemented over the next ten years to target invasive weeds (Hill 2005). This creates an opportunity to collect pre- and post-fire botanical data and to measure responses of the local emu-wren population.


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Appendices

APPENDIX 1. MANAGEMENT GUIDELINES FOR THE CONSERVATION OF THE SOUTHERN E MU-WREN: A REPORT TO PORTLAND ALUMINIUM

Introduction

In 1991, Portland Aluminium adopted a management plan for ‘The Smelter in the Park’ (Brake et al. 1991). The main priority of this plan was to ensure that the Aluminium smelter operates in a natural setting that maintains the biological diversity of the area and is aesthetically pleasing to the local community. The plan designated five zones with different land use goals, the largest of which was committed to conservation of flora and fauna (Zone D: Habitat for Wildlife). Following implementation of this plan, major rehabilitation works were undertaken to recreate the wetlands, heathlands and shrublands that once existed in the 200 ha smelter buffer zone. As part of the management program, a comprehensive survey of wildlife present within the smelter management zones was carried out and several species of conservation significance were identified, including the southern emu-wren (Coulson et al. 1999). The southern emu-wren has been described as a habitat specialist and hence a major concern of Portland Aluminium is the conservation and enhancement of habitat for this threatened species.

The southern emu-wren (Stipiturus malachurus) is a small Australian passerine that is threatened in several parts of its range. The Mount Lofty Ranges subspecies is classified as endangered, and the Dirk Hartog Island and Eyre Peninsula subspecies are classified as vulnerable nationally (EPBC Act). Elsewhere in Australia, the southern emu-wren is considered secure. However, threats to local populations are ongoing. These include loss and fragmentation of habitat, changes to habitat structure arising from altered fire regimes, heavy grazing and weed invasions, and depredation from cats and foxes (Littlely and Cutten 1994, 1996; MLR Southern Emu-wren Recovery Team 1998). Southern emu-wrens are poor fliers and are highly adapted to densely vegetated habitats including heathland, shrubland and swampland. Fragmentation of habitat patches contributes to the inability of emu-wren populations to recover after catastrophic events such as wildfire, because distances between patches exceed the species’ dispersal capacity. Susceptibility to predation is also enhanced by degradation of habitat. Current management
strategies for the endangered subspecies of southern emu-wren include habitat mapping, population monitoring, restoring degraded habitats and translocating individuals to areas within the subspecies’ former range (Littlely et al. 1997; MLR Southern Emu-wren Recovery Team 1998; Pickett 2000).

At Portland, the most significant issues for the management of the southern emu-wren are the preservation of coastal heathland and shrubland habitats, and control of introduced predators. Coastal heaths and shrubland are becoming severely degraded within the area due to an interaction between reduced fire frequency and invasion of these habitats by coast wattle (Acacia sophorae; see McMahon et al. 1994), gorse (Ulex europaeus) and blue pea (Psoralea pinnata). Foxes and feral cats are highly abundant in the area and are major predators of local native wildlife.

Conserving the population of southern emu-wrens occupying the buffer zone around the smelter has been identified by Portland Aluminium land managers as a main priority, particularly because resolving the issues threatening the local persistence of this species would encompass the conservation needs of several other bird and mammal species within the area. During 2000-2003, a study aimed at identifying the habitat requirements of the southern emu-wren and threats to local population persistence was undertaken. The results of this study have been formulated into management guidelines detailed below.

**Methods**
Research into the population demographics, breeding success and habitat preferences of the southern emu-wren was carried out within the Portland Heathland. Three field sites were arbitrarily defined with some interchange of emu-wrens occurring between these. Each site varied in plant species composition and management history.

The main study site was a 16 ha wetland system occurring within the Portland Aluminium buffer zone. This area was formerly a dumping site for smelter waste, but was later intensively modified and rehabilitated to create a wetland system (Brake et al. 1991). Originally a taxonomically rich stand of wet heath, the area now consists of a patchwork of vegetation
communities including open and closed dry heath, tall shrubland, sedge/rushlands and swamps, and occasional stands of coast wattle (*Acacia longifolia* var. *sophorae*), brown stringybark (*Eucalyptus baxteri*) and myrtle wattle (*Acacia myrtifolia*). Heathlands are dominated by prickly teatree (*Leptospermum continentale*), scented paperbark (*Melaleuca squarrosa*) and scrub sheoak (*Allocasuarina paludosa*), and tall shrublands by coast beard heath (*Leucopogon parviflorus*).

The second site was a 2 ha natural swamp at the southern end of the wetland area. This area has regenerated post-fire as thick coastal shrubland dominated by coast daisy (*Olearia axillaris*), seaberry saltbush (*Rhagodia condolleana*) and coast beard heath (*Leucopogon parviflorus*), with an understorey of coast sword-sedge (*Lepidosperma gladiatum*) and native tussock grass (*Poa labillardierei*). The third site extended west of the smelter property, occurring within the ‘Dean’s Heath’ which is cooperatively managed by Portland Aluminium and the Department of Sustainability and Environment. The Dean’s Heath occurs within a broad swale and has undergone intensive management for the control of coast wattle, including a prescribed burn in 1993 followed by hydro-axing (McMahon *et al.* 1994). This 4 ha area of coastal dune is dominated by coast wattle, silver banksia (*Banksia marginata*), dusty miller (*Spyridium parvifolium*), winged spyridium (*Spyridium vexilliferum*), Correa spp. and occasional thickets of drooping she-oak (*Allocasuarina verticillata*).

Over three breeding seasons (August to February) in the years 2000-2003, the breeding success and survival of emu-wren pairs inhabiting the wetlands and coastal heaths within the smelter buffer zone were monitored (Maguire and Mulder 2004; Chapter 2). This involved capturing and banding individual birds with unique combinations of colour bands, and monitoring their daily movements within each breeding season.

Emu-wren habitat use was monitored during each breeding season. Daily visits were made to the site and GPS locations of colour banded birds recorded. Locations of birds were mapped and territory size for each pair determined using GIS. Availability of habitat types was mapped across the site, and the proportion of their use by emu-wrens then compared to availability within
territories. Variation in habitat use was investigated in relation to vegetation structural and floristic characteristics using statistical modeling (Chapter 3).

Prey abundance, vegetation structure and density of predators have been highlighted as important variables that might influence the breeding success and survival of birds. Hence the quality of emu-wren habitats was investigated through intensive insect sampling of emu-wren territories, and estimates of snake (copperhead *Austrelaps superbus* and tiger snake *Notechis scutatus*) densities. Variation in the breeding success and survival of emu-wren pairs was then explored in relation to these territory attributes (Chapter 4).

**RESULTS**

*Population demographics*

Resighting rates of banded birds from one breeding season to the next were low (30-59%), suggesting high mortality of emu-wrens within the Portland Heathland. Midway through the 2001 breeding season, 50% of banded adults suddenly disappeared from the wetland site. Despite regular searches of surrounding heathland, these banded adults were never resighted so that death was a more probable cause than dispersal. The climate during the 2001 breeding season was no different than previous years (Victorian Regional Office of the Bureau of Meteorology), hence food availability should also have been similar given the strong association between insect abundance and climate (e.g. Pyke 1984; Cucco and Malacarne 1996). A more likely possibility was that depredation of adult birds was high that year. The sudden population decline coincided with the laying of fox baits across the study site and increased sightings of feral cats in the area (Kevin Saunders and Ron Jeffries, Portland Aluminium, personal communication). This was the first year in which the frequency of fox baiting was increased from biannually to three times per year; this apparently resulted in more effective reductions in fox numbers (Kevin Saunders, Portland Aluminium, personal communication). This may in turn have led to enhanced survival of feral cats, by reducing competition and predation pressure, as has been found for other populations (Risbey *et al.* 1999, 2000; Read and Bowen 2001). Feral cats are known to be more significant predators of small passerines than foxes (Risbey *et al.* 1999; Read and Bowen 2001) and video monitoring at Portland has shown that cats prey on southern emu-wrens. Degradation of habitat probably further contributes to the predation of
southern emu-wrens within the area (as for the Eurasian treecreeper (*Certhia familiaris*): Huhta *et al.* 2004).

Emu-wrens have a slow breeding rate (i.e. a long breeding season, small clutch size and high rate of nest failure) typical of small passerines in the Southern Hemisphere (Russell 2000). Nest failure was commonly attributed to death of one of the pair or predation of eggs or nestlings by snakes or feral cats. Adult mortality was also high, with individuals living to 1.6 years on average. It therefore appears as though the wetland area at Portland is a population sink for emu-wrens, where mortality exceeds fecundity. Numbers are sustained within the area through dispersal of emu-wrens from other populations occupying the surrounding coastal heath and shrubland. This dispersal is perhaps aided by the connectivity of vegetation along the Portland to Nelson coastline. In the Mount Lofty Ranges, mortality and fecundity rates of sub-populations are similar to those at Portland, however, dispersal is prevented due to the isolation of habitat patches within bare, agricultural landscapes (Pickett 2000).

*Habitat use and quality*

Emu-wrens used habitat variably in response to structural rather than floristic characteristics. Habitats with dense vertical foliage density of shrubs, grasses and sedges/rushes between ground level and 100 cm, and dense horizontal cover of shrubs, with the exception of low growing shrubs (maximum height = 70 cm) were used most frequently by emu-wrens. However, when availability of habitat was taken into account, habitat use was negatively correlated with species richness and the vertical foliage density of low shrubs. Within habitats, emu-wrens more frequently used plant species that had a dense canopy cover (26 ± 2% of total cover, crown diameter 93 ± 5 cm), high foliage density between 50-100 cm, and average heights of around 1 m. Plant species in which emu-wrens nested comprised ~14% of total canopy cover and were densest between ground level and 50 cm. Canopy cover, vegetation height and vertical foliage density were consistently important variables related to emu-wren habitat use at multiple fine-scales.

Animals should choose to occupy and use habitats that maximise their breeding success and survival. In heterogeneous environments, high quality areas should be preferentially used over
poorer-quality areas (Fretwell and Lucas 1970). However, limited dispersal opportunities or habitat saturation may force individuals to occupy ‘suboptimal’ habitats and this can come at a cost to their reproductive success or longevity. Understanding the implications of habitat selection in terms of individual breeding success or survival is particularly important for land managers attempting to preserve or restore habitat for threatened species.

Habitat type and the density of snakes within territories significantly influenced the breeding success and survival of southern emu-wrens at Portland. Prey abundance, based on total insects and preferred nestling prey types, varied significantly across territories according to habitat type. Tall shrubland, closed heath and sedge/rushland were identified as having high numbers of preferred nestling prey types. Accordingly, reproductive success was high in territories containing a greater proportion of tall shrubland and closed heath. However, the benefits of food abundance appeared to be offset by the density of snakes within a territory. Sedge/rushland habitats had the highest recorded abundance of tiger snakes and copperheads. These snake species had significant negative impacts on emu-wren pair survival and nesting success. At Portland, it is possible that the natural balance between snakes and their prey has been disrupted by intensive land modifications and the subsequent local extinctions of a number of small native mammal, amphibian and reptilian species (Coulson et al. 1999, Ellen Mitchell, pers. comm.).

**MANAGEMENT GUIDELINES**

The main threats to the persistence of southern emu-wrens within the Portland Aluminium management zone are modification of habitats, particularly from weed invasions, and the impacts of introduced and native predators. Therefore, the central issues for conservation of southern emu-wren populations in Portland are habitat preservation and restoration, including maintaining connective corridors between habitat patches, and control of predator numbers.

*Habitat preservation and restoration*

Control of invasive weeds is of primary concern. Coast wattle is a natural component of the coastal heathland system at Portland and juvenile forms of the species act as valuable habitat to southern emu-wrens. However, a number of factors have contributed to invasive proportions of
A. sophorae at Portland, namely a marked decrease in the frequency of fire and an increase in numbers of introduced bird species, e.g. starlings (Sturnus vulgaris), which disperse the seed (McMahon et al. 1994). Coast wattle has a severe impact on the structure and composition of emu-wren habitat. Coast wattle invasions can structurally alter habitat from low heath (30-50 cm high) to a closed shrubland (200-300 cm high) within three to five years (McMahon et al. 1994). Older stands of coast wattle are structurally unsuitable habitat for southern emu-wrens, despite this habitat being incorporated within several emu-wren territories at Portland. Fire is a proven effective control of coast wattle within the Portland Heathland (McMahon et al. 1994). It is recommended that control burns occur during Autumn rather than December to lessen the impact on populations of many passerines whose breeding seasons occur in the spring and summer. The southern emu-wren is known to rapidly recolonise burnt areas and to achieve optimal population densities in mid-successional habitats (Jordan 1987; McFarland 1988; Littlely and Cutten 1996). McFarland (1988) recommended a fire regime of seven to eight years in areas where emu-wrens occurred in small, isolated fragments. However, in contiguous stretches of habitat, the optimal fire regime is recommended as closer to three years (Jordan 1987). Managers should ensure that strips of vegetation around the allocated burn areas are left intact as corridors for dispersal of emu-wrens and other fauna into unburnt areas of suitable habitat.

Blue pea (Psoralea pinnata) is another weed species regularly used by southern emu-wrens at Portland and a common component of tall shrubland habitat. Tall shrubland was identified as one of the most beneficial habitats for emu-wren breeding and survival. However, it must be noted that P. pinnata proliferates rapidly and eliminates the growth of natives so that its long-term subsistence would reduce the suitability of habitat. The species is unsuitable as nesting substrate and impacts greatly on the floral diversity of habitats. Fire is a non-effective means of control for blue pea and it is recommended that the species be removed manually prior to autumn when the species germinates (Michael Rosier, DSE, pers comm.). Larger shrubs should be cut at the base and painted with herbicide to prevent resprouting (Michael Rosier, pers. comm.).

Following clearance of weeds, it is recommended that areas be replanted during spring to minimise the impacts of fine-scale habitat loss. Areas should be replanted with native species propagated from local seed banks and the most desirable outcome would be to recreate habitat.
resembling the natural heathlands or tall shrublands present within the area. Managers should choose species of shrubs, tussock-like grasses and sedges/rushes that have sprawling crowns between 50-100 cm, that grow to between 1-2 m and that are densely branched from 0-100 cm. A dense mix of tall and medium shrubs, interspersed with native tussock grasses and sedges/rushes is ideal. Tree species with stunted growth forms are also suitable for emu-wrens. Sedge and rushlands should be fringed by shrubbery and trees to encourage use by emu-wrens, however, it must be kept in mind that these habitats are associated with high densities of snakes at Portland and hence are not ideal breeding habitats.

Layering of vegetation within the understorey is also an important component of emu-wren habitat. Managers should aim to create layered habitats, which provide greater vertical foliage density. These not only offer appropriate habitat structure for emu-wrens but also contain abundant food resources. Plants with asynchronous flowering are of particular benefit to emu-wrens, especially to the successful rearing of broods in summer because resource abundance commonly declines in summer compared with spring. The following examples of late flowering species are therefore valuable components of habitat: silver banksia *Banksia marginata*, scented paperbark *Melaleuca squarrosa*, prickly moses *Acacia verticillata*, heath teatree *Leptospermum myrsinoides*, pale turpentine bush *Beyeria lechenaultii* and twiggy daisy bush *Olearia ramulosa*.

Although certain habitat types have been identified as less suitable for emu-wrens, it must be noted that these habitats may still be important for maintaining connectivity of habitat throughout the landscape. Emu-wrens, in particular dispersing juveniles, were commonly sighted in areas with unsuitable habitat, such as senescent stands of coast wattle, disturbed roadside regrowth and narrow stretches of sparse shrubbery and bare ground. Hence, the spatial configuration of habitats throughout the landscape and connectivity of habitat patches must also be considered when formulating management plans.

*Predator control*
Snakes are a natural component of the wetland and heath system at Portland, however, they are having a great impact on the fecundity and survival of southern emu-wrens and other small passerines within the area. Returning the balance to the food chain in this heavily degraded
wetland ecosystem is therefore vital, and this will require immediate management action to prevent further decline of amphibian, reptile and small mammal populations within the area.

Regular 1080 fox baiting should be continued within the Portland buffer zone, however, feral cats also need to be simultaneously managed within the area. The source of feral cats needs to be identified and the local community should be made aware of the impacts of cat predation on local wildlife. The number of feral cats within the area is likely to decrease with active involvement from the community, as well as eradication of existing feral cats through a comprehensive trapping program.

*Population monitoring*

The southern emu-wren population at Portland must be monitored each breeding season in order to determine the effectiveness of any management action undertaken and also to ensure the continued persistence of the population through time. The timing of emu-wren population counts would appear to be most important to accurately estimating effective population size ($N_e$), particularly because in the late breeding season dispersing juveniles form cohorts or establish pair bonds, but are not yet of breeding age. If the aim of the survey is to estimate the size of the local population of adult emu-wrens only, then it is best to do this in late August when pair bonds appear stable and before young are produced (Fig. 1). However, birds may be nesting at this time and more secretive, hence harder to observe. If a survey is being carried out to determine whether the population is successfully breeding, then it would be better to do this in November or January, when the conditions are best for surveying and emu-wrens are highly conspicuous (vocal and visible) because they are moving about as family groups. If group size was recorded for each observation, the number of adults could still be estimated, being careful to distinguish between family groups (cohesive) and birds in close proximity during territorial disputes (aggressive).

Detecting emu-wrens is heavily dependent on the weather and therefore you should aim to survey an area on a day with mild to no wind, no rain and with mild temperatures up to 26° C. When searching an area, weave your way through, stopping every so often (10-20 m depending on visibility) to look around and scan the tops of vegetation or gaps in foliage for any movement.
Sometimes it is necessary to make a pishing sound to elicit a response from the wrens. Allow for 7 m either side of you when searching a territory, that is, you may have to walk up and down a number of times to thoroughly search an area. Typically if you walk in close proximity to an emu-wren, it will emit an alarm call (a sharp ‘steet’ similar to a cricket). If alarmed the emu-wren will usually stay within cover and this can be for long periods of time, depending on the level of disturbance. It is best to stand very quietly or to sit level with the vegetation, until the emu-wren resumes its behaviour. If singing is heard from a distance, you should head toward that location, keeping an eye on emergent vegetation (including dead trees or taller shrubs standing out above the heath), as this is where emu-wrens commonly sing from.

Fig. 1. Average frequency of sightings of emu-wrens per month, based on the 2001 and 2002 breeding seasons. The majority of sightings occurred in August, September and January.
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