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Responses to fire of Slender-billed Thornbills, *Acanthiza iredalei hedleyi*, in Ngarkat Conservation Park, South Australia. I. Densities, group sizes, distribution and management issues

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Abstract. The Slender-billed Thornbill, *Acanthiza iredalei hedleyi*, was studied in recently burnt, regenerating and mature heath (3, 10 and 22 years since fire respectively) in Ngarkat Conservation Park, South Australia. Data collected between 1991 and 2002 demonstrated that densities peaked seven years after fire at 0.26 birds ha^{-1}, while densities were lower and less variable in unburnt mature heath. Comprehensive searches in spring 2000 confirmed this trend, with densities varying from 0.02 birds ha^{-1} in mature heath, to 0.06 and 0.07 birds ha^{-1} in burnt and regenerating heath.

Between spring 2000 and autumn 2001 group sizes increased in the recently burnt heath from 4.3 to 6.3 birds per group. However, group sizes did not increase over the same period in the regenerating and mature heaths. Between 1991 and 2002 group sizes did not differ significantly between heaths that had been burnt since 1990 (2.7 birds per group) and mature heath burnt in 1978 (2.7 birds per group).

In the mature heath, Slender-billed Thornbills demonstrated strong fidelity for certain areas and were observed feeding juvenile birds on a number of occasions. This suggests that birds can persist in mature heath, albeit at low densities and in isolated areas of suitable habitat, and that frequent fires are not essential for population persistence. Furthermore, long-term records suggest that recolonisation of recently burnt heath is likely to occur from adjacent unburnt heath and is more successful after smaller fires. Therefore, in order to protect areas from which Slender-billed Thornbills can disperse into recently burnt habitats in Ngarkat, a spatial mosaic of habitats at different stages of post-fire succession is required.

Introduction

Inappropriate fire management is a major threatening process for Australia's avifauna. The most important variable in the management of fire for bird conservation is the frequency with which fire occurs (Woinarski and Recher 1997).

Fires create early post-fire successional habitats in which some insectivores and granivores can increase in abundance through efficient use of the more open landscape (Recher *et al*. 1985). However, frequent fires can have a detrimental impact on survival and breeding of birds (Brooker and Rowley 1991; Brooker and Brooker 1994; Brooker 1998). In the absence of fire, the structure, floristic composition and productivity of vegetation changes with growth and maturation (Specht *et al*. 1958; Woinarski and Recher 1997). Subsequently, infrequent fires also produce habitat features that are critical to the presence of certain bird groups, including hollow-dependent birds, frugivores, canopy dwellers and birds dependent on high densities of litter or vegetation (Woinarski and Recher 1997; Baker 2000).

Most threatened bird taxa within Australia that have been studied in relation to fire demonstrate a clear preference for infrequent fires (Woinarski and Recher 1997). For example, the Eastern Bristlebird, *Dasyornis brachypterus*, requires low, dense vegetation that develops only in the absence of fire (Baker 2000), and the long-term conservation of the Malleefowl, *Leipoa ocellata*, requires fire-free intervals of more than 60 years (Benshemesh 1990). However, the management of avifauna that prefer early post-fire successional habitats is rarely discussed. This is because such species are often habitat generalists whose populations are not threatened and therefore are of little concern to management (e.g. the Australian Magpie, *Gymnorhina tibicen*: Christensen *et al*. 1985).

The positive responses to fire of these early successional birds are usually documented in brief studies that only investigate changes in the composition and abundance of bird assemblages after fire (e.g. Christensen *et al*. 1985; Recher *et al*. 1985). Subtle responses to fire in demography, distribution and breeding activity, however, can be demonstrated only with more detailed studies (e.g. Brooker and Rowley 1991; Brooker 1998). Therefore, any positive responses to fire that may be demonstrated by birds of conservation

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significance warrants further investigation, and should not be assumed to indicate tolerance or preference for frequent fires.

The Slender-billed Thornbill, *Acanthiza iredalei hedleyi*, is particularly suited to such an investigation. Slender-billed Thornbills are small (9 cm, 7 g), sexually monomorphic, insectivorous birds with three subspecies broadly distributed across southern Australia (see Matthew 1994; Schodde and Mason 1999 for detailed distributions and taxonomy). The eastern subspecies (*A. i. hedleyi*, Slender-billed Thornbill hereafter) occurs in low, sclerophyllous heathland in north-western Victoria and south-eastern South Australia. In total, ~20 000 birds are thought to occur in subpopulations in Ngarkat Conservation Park (Ngarkat) in South Australia and in the Big and Little Deserts in Victoria, with as few as 4000 outside this area (Matthew 1994). Subsequently, it was recently classified as 'Lower Risk – Conservation Dependent' (Schodde and Mason 1999) and 'Near Threatened' (Garnett and Crowley 2000), because these populations were isolated in vegetation fragments, making them prone to extinction from large-scale perturbations such as fire (Croft *et al*. 1999; Garnett and Crowley 2000).

The Slender-billed Thornbill is also one of the more secretive and least-known thornbills. Research to date has focused on its taxonomy and distribution (Matthew 1994; Schodde and Mason 1999), and documentation of its ecology has been anecdotal and based on few observations (Matthew 1994, 2002; Recher and Davis 2000). Little is also understood about the impacts of fire on Slender-billed Thornbills. Although birds are known to occur in heath recovering from fire (Matthew 1994), the mechanisms that are believed to drive the responses of heathland birds to fire, namely breeding success, survival, inherent patterns of habitat use and habitat productivity (Brooker and Rowley 1991; Brooker and Brooker 1994; Brooker 1998), are not known for the Slender-billed Thornbill.

This study presents 12 years of data collection in Ngarkat in which the densities of Slender-billed Thornbills were recorded in regenerating and mature heaths from 1991 to 2002 following a fire in the summer of 1990–91. It also makes a more detailed comparison of densities, group sizes and distribution of Slender-billed Thornbills between three contiguous heath habitats, each at a different stage of post-fire succession. In addition we also measured the relative availability of foliage invertebrates in the three types of post-fire heath as an indication of the quality of the different habitats to Slender-billed Thornbills. This information was used to (1) describe the numerical responses of Slender-billed Thornbills to fire, (2) determine the relative importance of heath at different stages of post-fire succession to Slender-billed Thornbills, and (3) provide information to assist with managing and conserving the species in Ngarkat Conservation Park.

Methods

Study area

The study was conducted at Ngarkat Conservation Park (Ngarkat), situated ~200 km south-east of Adelaide, South Australia (Fig. 1). With a total area of 262 700 ha, Ngarkat is the largest natural vegetation remnant in the agricultural region of South Australia (NPWS 1984) and makes up approximately one-third of the Ninety-Mile Desert and Big Desert in South Australia and Victoria (NPWS 1984). Mean annual rainfall is ~388 mm per year (recorded at Lameroo, 24 km north of Ngarkat: Bureau of Meteorology 2003); however, rainfall is probably spatially variable across the park. Average monthly rainfall for the period covered in this study is shown in Fig. 2.

The major vegetation association within the study area is low heath dominated by *Banksia ornata*, *Allocasuarina pusilla* and *Leptospermum myrsinoides*. In response to fire, *B. ornata* regenerates only from seed, *L. myrsinoides* regenerates from seed and by resprouting from lignotubers, and *A. pusilla* regenerates vigorously by resprouting (Specht *et al*. 1958). Frequent lightning strikes during dry summer thunderstorms ensure that wildfire is common in Ngarkat, and all parts of the park have been burnt at least once since 1945 as a result of at least 22 separate fires (Richards *et al*. 1999). Subsequently, a broad mosaic of vegetation communities at different stages of post-fire succession occurs.

This study primarily focused on three post-fire habitats situated in the north-west quarter of Ngarkat (35°39′S, 140°30′E) (Fig. 1): 'burnt' heath, 'regenerating' heath and 'mature' heath, which were last subject to wildfire in the summers of 1997–98, 1990–91 and 1978, respectively (Fig. 1). Before the fires in 1990–91 and 1997–98, the burnt and regenerating heaths were at the same stage of post-fire succession as the mature heath (i.e. they were all burnt in 1978).

Birds

In July 2000, initial attempts were made to trap and colour-band Slender-billed Thornbills. This was only marginally successful because of the very open habitat in recently burnt heaths and very low bird densities in mature heath. Only two birds, both caught in burnt heath, were banded. Therefore, in order to make detailed measurements of densities, spacing and site fidelity of Slender-billed Thornbills, systematic and comprehensive searches for unmarked groups were made in each habitat in September and October 2000 (spring). The area searched in each habitat type was determined by recording locations periodically throughout each searching period using a Global Positioning System (GPS), plotting these on a topographic map divided into 1-ha cells and then calculating the area searched. In each searching period, no area was searched more than once. Also, distances between groups were generally large enough to ensure that, during a searching period, groups were not counted and observed more than once.

Information regarding Slender-billed Thornbill groups was recorded upon location of a group during an 'observation bout'. Each observation bout continued until either the required amount of data was collected (detailed below and in Ward and Paton 2004) or the birds were disturbed by the observer's presence and moved too far away to observe. On completing an observation bout, searches for further groups of Slender-billed Thornbills were resumed. Searches were made from sunrise until sunset to ensure that observation bouts were spread as evenly as possible across daylight hours. In March 2001 (autumn) searches were limited to areas where birds had previously been located in both September and October 2000, in order to assess changes in group sizes over this time.

Long-term numerical responses of Slender-billed Thornbills to fire were assessed by counting birds along 1.5-km-long transects in winter each year from 1991 to 2002. In all, 58 permanent, fixed-width transects were originally established across Ngarkat in 1990 as part of assessing the effects of commercial honeybees on nectar resources of

Ngarkat heath plants (Paton 1996). A large fire in the summer of 1990–91 that burnt approximately half of these transects provided an ideal opportunity to measure the responses of birds to fire. In order to adequately document the responses of birds to additional fires, one additional transect was added in winter 1998 in response to a fire in the summer of 1997–98. Another six transects were added in winter 1999 in response to a large fire in the summer of 1998–99.

Each transect was divided into 15 100-m sections and all birds seen 50 m either side of the transect line were recorded by a single observer who walked slowly along the line (25 m min^{-1}). Each transect was walked twice ('out' and 'back') so that 15-ha cells were assessed twice over a 2-h period. This also increased the possibility that any birds present in the vicinity of the transect but not detected on the 'out' transect were detected on the 'back' transect. Each 'out' and 'back' transect was assessed in winter (June–August) of each year. In 1991–93, burnt transects were walked twice (once 'out' and once 'back'), while unburnt transects were walked 4–8 times. From 1994 onwards, all transects were walked only twice. A total of 75 partially burnt 1-ha cells (42, 7 and 26 cells in heath burnt in the summer of 1990–91, 1997–98 and 1998–99 respectively), were removed from bird density and group-size analysis because it was not possible to determine whether Slender-billed Thornbills were using burnt or unburnt heath. A completely burnt or unburnt cell was therefore the base sampling unit used for density calculations. Therefore, a minimum of 1694 1-ha cells, each a discrete sampling unit, were assessed in any of the census years.

In each year counts along all transects were conducted by up to six people experienced with the habitat and the identification of Slender-billed Thornbills by call and by sight. The open habitat in recently burnt and regenerating heath, and the consistent, low height of mature heath (~90 cm: Ward and Paton 2004), meant that the number of Slender-billed Thornbills within 50 m either side of the transect could be assessed with confidence. Birds were initially located either by sight or by call, and the numbers of birds within the transect was only ever assessed on the basis of the direct observation of birds. Since Slender-billed Thornbills call regularly, any bias in the ability to detect them between habitats was minimal.

Densities, group sizes, distribution and breeding

For each Slender-billed Thornbill group located in September and October 2000, the following data were recorded: the number of birds in the group, their initial location (by GPS), and any evidence of breeding. Densities of Slender-billed Thornbills (no. of birds per hectare) in each habitat type were determined by comparing the areas searched with the average number of birds located in September and October 2000.

Densities of Slender-billed Thornbills in burnt heaths (burnt in the summers of 1990–91, 1997–98 and 1998–99) and unburnt mature heath (burnt in 1978 or before) between 1991 and 2002 were calculated from transect data by totalling the number of birds seen in those 1-ha cells for burnt or unburnt heath, and dividing this by the total number of 1-ha cells assessed (given in Table 1).

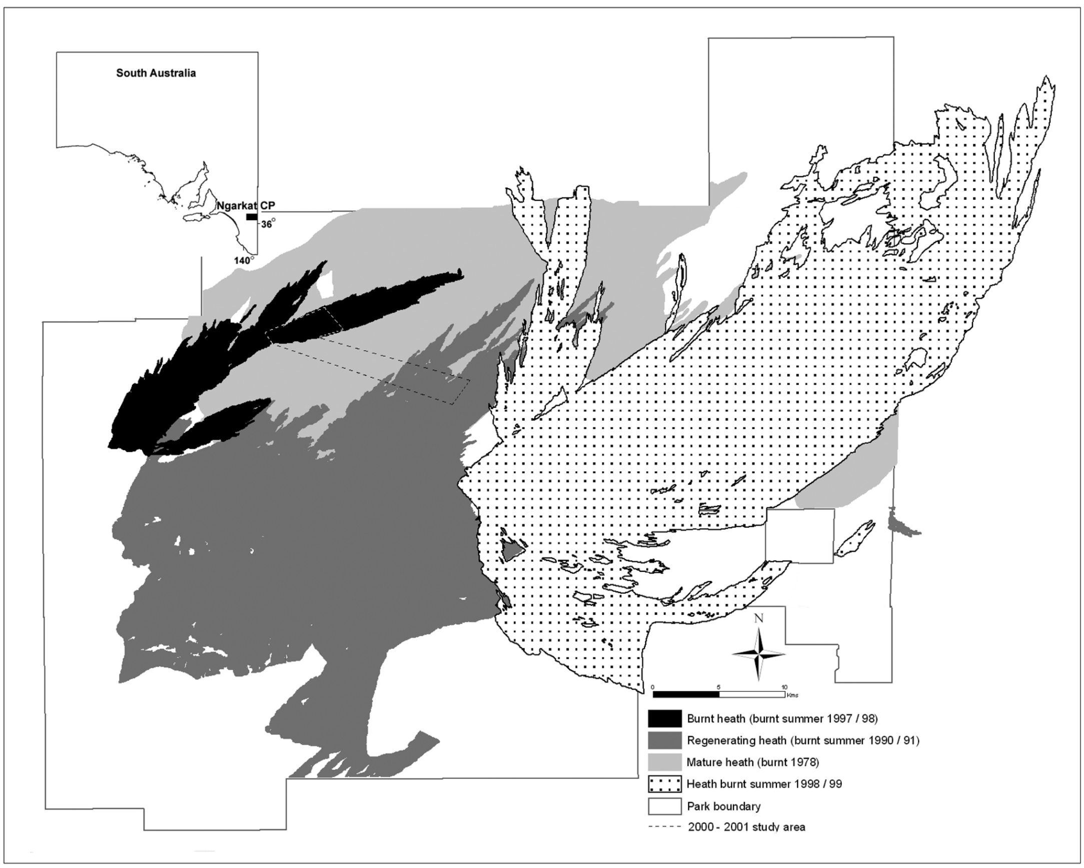

Fig. 1. Location of Ngarkat Conservation Park within South Australia, Ngarkat Conservation Park and the location of the 2000–01 study region, which spans areas burnt in 1978 (light grey), in the summers of 1990–91 (medium grey) and 1997–98 (black). The dotted area shows the extensive fire that occurred in the summer of 1998–99. Fire-history map of Ngarkat provided by Planning SA (Department for Transport and Urban Planning).

Initial locations of groups found during the 2000–01 searching period were plotted on a topographic map divided into 1-ha cells and used to calculate the minimum distance between groups (metres) in each searching period. Means were compared between habitats using one-way analysis of variance (ANOVA) and Tukey Honestly Significant Difference (HSD) tests. The percentage of all Slender-billed Thornbill groups that demonstrated breeding activity (primarily adult birds feeding fledglings and presence of juvenile birds) in spring 2000 was documented to determine whether breeding occurred in each habitat. Group-size data documented from both the 2000–01 searching period and the 1991–2002 transects were compared between habitat types within sampling periods and between sampling periods within habitat types using one-way ANOVA, *t*-tests and Tukey HSD tests.

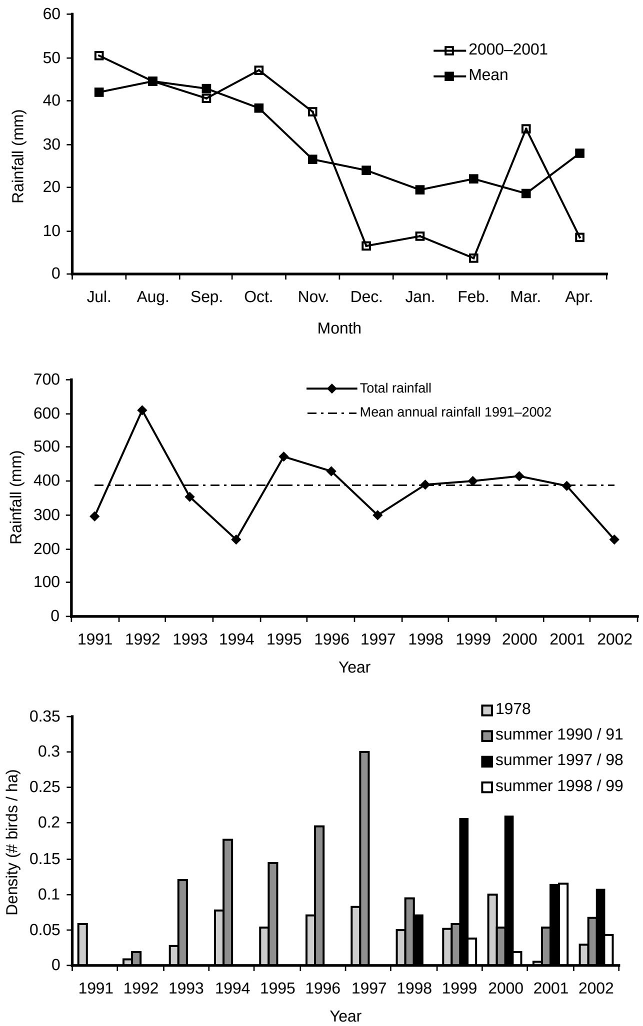

Fig. 2. *Top*: Monthly rainfall over the 2000–01 study period, compared with mean rainfalls for each month (Bureau of Meteorology 2003). *Middle*: yearly rainfall for Lameroo, 24 km north of Ngarkat, 1991–02, and mean annual rainfall for the same period (Bureau of Meteorology 2003). *Bottom*: Winter densities of Slender-billed Thornbills in the unburnt heath (burnt in 1978 or before) and in heaths burnt in the summer of 1990–91, 1997–98 and 1998–99 between 1991 and 2002. Figures show the number of birds per hectare. In each year birds were counted along transects (1.5 km long × 100 m wide), each divided into 15-ha cells, at 58–65 sites across Ngarkat (see Table 1). A total of 75 partially burnt 1-ha cells were not included in density analysis over the 1992–2002 period, and from a total of 669 records of Slender-billed Thornbills 41 records were not included in density analysis because they occurred in partially burnt 1-ha cells. Therefore, density calculations were made from 225, 295, 79 and 29 records of Slender-billed Thornbills collected over 12 years in cells burnt in or before 1978, in the summer of 1990–91, 1997–98 and 1998–99, respectively.

Site fidelity

Initial attempts to individually mark Slender-billed Thornbills were unsuccessful and only two birds were colour-banded in the burnt heath in August 2000. Because birds were not individually marked, site fidelity measures described here represent the repeated use of certain areas by Slender-billed Thornbills, but not necessarily by the same birds.

Short-term site fidelity was assessed by recording the position of all groups located throughout the 2000–01 study period and in each habitat type on a topographic map divided into individual 1-ha cells. Long-term site fidelity was assessed from the 1991–2002 transect data. For both datasets comparisons were made of the proportion of multiple records of Slender-billed Thornbills over the respective study periods that occurred within the same individual 1-ha cells, within a contiguous group of three 1-ha cells, within a contiguous group of five 1-ha cells, and those that were isolated records (i.e. were recorded only once in an isolated individual 1-ha cell over the respective study periods). Site fidelity was subsequently described as the percentage of records that occurred in individual 1-ha cells, within groups of three contiguous 1-ha cells, and within groups of five contiguous 1-ha cells. The observed frequency distribution of Slender-billed Thornbill records in cells was also calculated for the long-term records. The 'goodness of fit' of this distribution was tested with frequencies expected from a Poisson (random) and negative binomial (clumped) distribution. If Slender-billed Thornbills repeatedly used certain areas of heath, they would be expected to demonstrate a clumped distribution.

Insect abundance and activity

Insect assemblages in the three habitat types were assessed in November 2000 (spring) and March 2001 (autumn) using two methods (for simplicity we refer to all arthropods as 'insects'). First, the abundance of foliage insects was estimated from foliage clippings taken from six randomly chosen *Leptospermum myrsinoides* plants in each habitat at five locations where Slender-billed Thornbills had initially been located, chosen randomly from all initial locations recorded. Therefore, 30 clippings were obtained for each habitat type in each of spring and autumn. In spring, a ratio of four non-flowering plants to two flowering plants was sampled in each habitat type. *L. myrsinoides* did not flower in March. *L. myrsinoides* was used because Slender-billed Thornbills were known to forage on it and it was the only plant species from which equivalent-sized samples could be obtained in each habitat given the structural differences between habitat types, and the sizes of other plant species at different successional stages (Ward and Paton 2004). Samples were taken by placing a 30 cm × 60 cm clear plastic bag over the foliage, which was cut at the base of the bag (so that each foliage sample was ~60 cm long), and then inverted. After vigorous shaking, each clipping was thoroughly inspected for insects on both the foliage and within the plastic bag. Each clipping was dried and weighed, and the abundance of insects on the foliage for each habitat type was calculated as the number of insects per 100 g dry weight of foliage (including the branches of each sample). The abundances of foliage insects were compared between habitat types and seasons using two-way ANOVA and Tukey HSD tests.

Second, insect activity was assessed by visually inspecting the insects on the vegetation, the ground and in the air. At each of the five locations where foliage clippings were made in each habitat type, the total number of individual insects (excluding flies attracted to the observer) seen during two minutes of observation of a 1-m^3 area were

Table 1. Summary of the number of 1-ha cells assessed in transect data between 1991 and 2002

Each transect was walked at least twice in each year (once 'out' and once 'back'), so that every 1-ha cell was assessed at least twice in each year, and between 1991 and 1993 transects located primarily in unburnt mature heath were assessed more than twice. An additional transect was added after the fire in the summer of 1997–98, and six transects were added following the 1998–99 fire. Some transects were partially burnt. Unburnt cells located primarily in burnt transects were included in analysis of unburnt heath, and partially burnt cells were removed from analysis

Census year	Years cells burnt	No. of 1-ha cells	No. of times searched	Total no. of unburnt cells	No. of 1-ha cell assessments	No. of partially burnt cells	Total no. of 1-ha cells assessed
1991	≤1978	450	4	n/a	1868	0	2594
	1990–91	420	2	68	772	46	
1992	≤1978	450	6–8	n/a	3128	0	3854
	1990–91	420	2	68	772	46	
1993	≤1978	450	6–8	n/a	2768	0	3494
	1990–91	420	2	68	772	46	
1994–97	≤1978	450	2	n/a	968	0	1694
	1990–91	420	2	68	772	46	
1998	≤1978	330	2	n/a	728	0	1717
	1990–91	420	2	68	772	46	
	1997–98	135	2	0	270	7	
1999–2002	≤1978	330	2	n/a	728	0	1875
	1990–91	420	2	68	772	42	
	1997–98	135	2	0	270	7	
	1998–99	90	2	0	180	26	

recorded in both November 2000 and March 2001. A total of 100 2-min counts for each habitat type were made over the entire study period. The abundances of active insects were compared between habitat types and seasons by applying a square-root transformation to the count data and using a two-way ANOVA and Tukey HSD tests.

Results

Densities

In order to locate Slender-billed Thornbills, a larger area was searched in the mature heath, with ~1100 ha searched in each of September and October 2000, compared with 790 ha and 940 ha in the burnt and regenerating heaths, respectively. Despite this, more birds were found in the burnt and regenerating heath than in the mature heath (Table 2). In the burnt heath, 43 birds (19 groups) and 56 birds (16 groups) were found in September and October, respectively, while 68 birds (16 groups) and 62 birds (17 groups) were found in the same periods in the regenerating heath. However, in the mature heath, only 25 birds (10 groups) and 23 birds (8 groups) were found in September and October, respectively.

Densities of Slender-billed Thornbills were therefore higher in the burnt and regenerating heath than in the mature heath. The mean number of birds found in spring in the burnt, regenerating and mature heath was 50, 65 and 24, respectively, giving densities of 0.06, 0.07 and 0.02 birds per hectare (Table 2).

Transect data from 1991–2002 demonstrated that very few Slender-billed Thornbills occurred in heath in the two years after it was burnt in the summer of 1990–91, with no birds recorded in 1991 and only 0.008 birds ha^{-1} in 1992 (Fig. 2). This slow response recovery may have been influenced by the below-average rainfall in 1991. Following this, densities increased steadily, peaking at 0.3 birds ha^{-1} seven

Table 2. Summary of searching, density, distribution and breeding data for Slender-billed Thornbills in Ngarkat Conservation Park for September and October 2000 in the burnt, regenerating and mature heath

The mean number of birds found in each habitat type is based on two independent assessments, one made in September 2000 and the other in October 2000. Means and totals given in 'combined' were calculated from data across habitat types

	Habitat types: Burnt	Regenerating	Mature	Combined
Total area searched (ha)	790	940	1100	2830
No. of birds (no. of groups) located in September	43 (19)	68 (16)	25 (10)	136 (45)
No. of birds (no. of groups) located in October	56 (16)	62 (17)	23 (8)	141 (41)
Mean no. of birds (no. of groups) located in spring (September and October)	50 (18)	65 (17)	24 (9)	139 (43)
Bird density (no. of birds ha^{-1})	0.06	0.07	0.02	0.05
Group density (no. of groups ha^{-1})	0.020	0.018	0.008	0.015
Minimum distance (m) between groups (mean ± s.e.)	344 ± 29	513 ± 49	1061 ± 106	549 ± 42
Percentage of groups breeding	27.3	56.7	17.4	33.0

years after the fire in 1990–91. Densities of Slender-billed Thornbills declined between 1994 and 1995 and between 1997 and 1998, coinciding with below-average rainfall in 1994 and 1997, respectively. Following the sharp decline in 1997–98, densities did not increase beyond 0.06 birds ha^{-1} for the remainder of the sampling period (Fig. 2).

In contrast, Slender-billed Thornbill densities increased more rapidly after the fire in the summer of 1998–99. In the first year after the fire, 0.07 birds occurred per hectare of recently burnt heath, and in the second year after fire densities were 0.21 birds ha^{-1} (Fig. 2). Densities remained at this level before declining in 2001 and 2002 (0.11 birds ha^{-1} in each year: Fig. 2).

Slender-billed Thornbills also used recently burnt heath in the first two years after the extensive fire that affected Ngarkat in the summer of 1998–99, although densities remained low (0.04 and 0.02 birds ha^{-1} in 1999 and 2000, respectively: Fig. 2). Densities increased slightly in winter 2001 (0.1 birds ha^{-1}) and then declined to 0.04 birds ha^{-1} in 2002.

Densities of Slender-billed Thornbills within the unburnt mature heath generally remained lower, yet more stable, than in heaths that had been burnt, although there were sharp declines in density in 1992 and 2001 (0.01 birds ha^{-1} in both years: Fig. 2). The mean density of Slender-billed Thornbills in areas that that had been burnt within the last 12 years (0.11 birds ha^{-1}) was significantly higher than for unburnt mature heath not burnt in at least 12 years (0.05 birds ha^{-1}) (t = 2.31, d.f. = 31, P = 0.03).

Distribution and group sizes

The location of all Slender-billed Thornbill groups found in the study region over the 2000–01 study period are represented in Fig. 3. The minimum distance between groups of Slender-billed Thornbills differed significantly between each habitat type (F = 40.9, d.f. = 2,88, P < 0.0001) with, on average, 1061 m, 513 m and 344 m separating groups in the mature, regenerating and burnt heath, respectively (Table 2).

In total, 56.7%, 27.3% and 17.4% of all Slender-billed Thornbill groups exhibited breeding behaviour in the regenerating, burnt and mature heath respectively (Table 2). Breeding behaviours observed included courtship behaviour (presentation of a feather to another bird), nest attendance and primarily the presence of juvenile birds and adult birds feeding fledglings in September and October 2000.

Slender-billed Thornbill groups differed significantly in size between habitats in spring and autumn during the 2000–01 study period (Fig. 4). In spring the average group size in the regenerating heath was 4.3 birds per group, significantly larger than those occupying the burnt heath (2.9 birds per group) and the mature heath (2.6 birds per group) (F = 9.8, d.f. = 2,84, P < 0.0001). In autumn the average group size in the burnt heath was 6.3 birds per group, significantly higher than the average group size in the regenerating

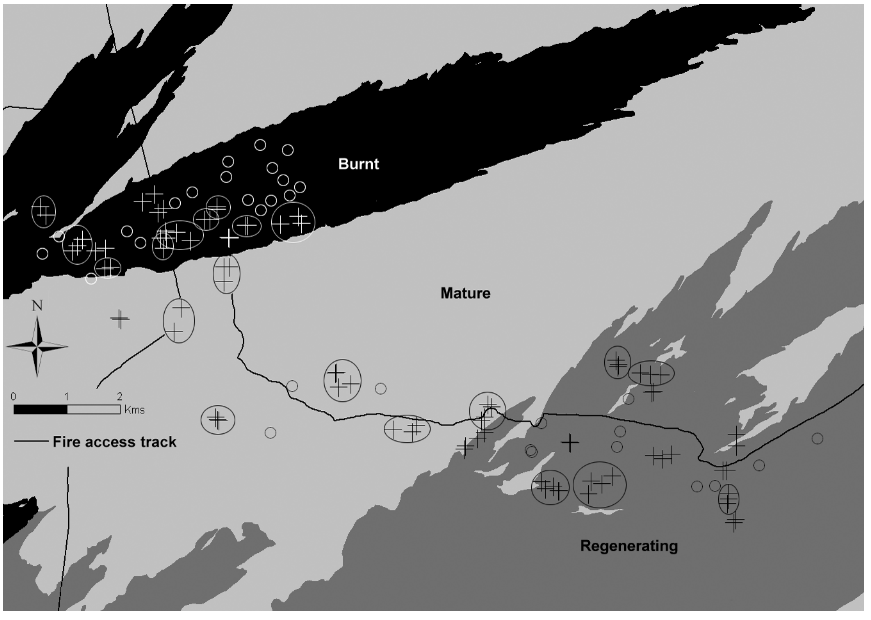

Fig. 3. Location of all birds found in burnt, regenerating and mature heath in Ngarkat over the entire study period (September 2000–March 2001). Crosses (+) represent groups that were seen repeatedly in the same area over September and October. Open circles (○) represent groups that were located only once in that area over the entire study period. Crosses with circles around them represent groups that persisted in an area over the entire study period, having been located in that particular area in September and /or October, and March.

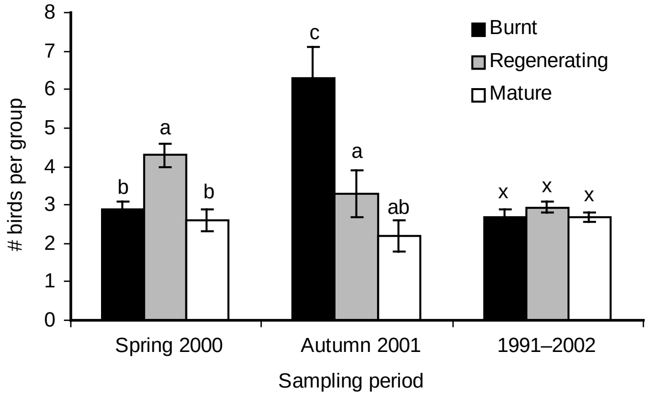

Fig. 4. Comparison of group sizes (mean ± s.e.) of Slender-billed Thornbills in the burnt, regenerating and mature heath in Spring 2000 and Autumn 2001 in Ngarkat Conservation Park, as well as from long-term average group sizes recorded in winter from 1991 to 2002. For 1991–2002 records, 'mature' heath was heath burnt in or before 1978, 'regenerating' heath was burnt in 1990, and 'burnt' heath was burnt in the summer of 1997–98. Different labels within each sampling period and between sampling periods (a, b, c, d, x and y) indicate a significant difference at $\alpha = 0.01$ (Tukey Honestly Significant Difference Test). Note, however, that sampling periods were compared only between similar habitats. For the burnt, regenerating and mature heaths, $n = 37$, 31, 23, respectively, for Spring 2000, and 12, 7 and 6 for Autumn 2001. For the burnt, regenerating and mature heaths, $n = 79$, 295 and 225, respectively, for the 1991–2002 transect data. Of a total of 669 records of Slender-billed Thornbills, 41 records occurred in partially burnt 1-ha cells and were not included in group size analysis, as were 29 records of Slender-billed Thornbills in heath burnt in 1999.

heath (3.3 birds per group) and the mature heath (2.2 birds per group) ($F = 6.9$, d.f. = 2,21, $P = 0.0049$). No differences occurred in the group sizes of Slender-billed Thornbills between spring and autumn in the mature ($t = -0.765$, d.f = 27, $P = 0.4508$) and regenerating heath ($t = -1.256$, d.f. = 35, $P = 0.2173$). However, in the burnt heath, group sizes were significantly larger in autumn than in spring ($t = 5.754$, d.f. = 47, $P < 0.0001$). Between 1991 and 2002 group size in winter in the heaths burnt in or before 1978 and in the summers of 1990–91 and 1997–98 averaged 2.7 ($n = 225$), 2.9 ($n = 295$) and 2.7 ($n = 79$) birds per group, respectively ($F = 1.11$, d.f. = 2,596, $P = 0.33$) (Fig. 4).

Site fidelity

Slender-billed Thornbills showed strong short-term fidelity for certain areas. The two birds colour-banded in August 2000 were observed in the same hectare in October 2000, and within 3 ha in March 2001. Across the 2000–01 study period and study area, 72% (84 of 116 records) of all records of Slender-billed Thornbill groups occurred more than once within groups of three contiguous 1-ha cells, while 89% (103 of 116 records) of observations occurred more than once within groups of five contiguous 1-ha cells (Table 3). Site fidelity was greatest in the mature heath, with 31% (9 of 29 records) of Slender-billed Thornbill groups located occurring more than once within individual 1-ha cells, compared with 8% (4 of 49 records) and 11% (4 of 38 records) in the burnt and regenerating heath, respectively (Table 3).

Strong site fidelity for certain areas was also demonstrated over a longer temporal scale (Table 4). In total, 669 records of Slender-billed Thornbills were made in Ngarkat between 1991 and 2002, and these records occurred in 906 (46.5%) of the total 1950 1-ha cells that were assessed in this period. Of these 669 records, 55.8% occurred more than once within individual 1-ha cells, 94.6% occurred within a group of three consecutive 1-ha cells, 98.2% occurred within a group of five consecutive 1-ha cells and 1.8% were isolated records (i.e. were recorded only once in an isolated individual 1-ha cell over the entire period: Table 4). Also, over this period, Slender-billed Thornbills did not demonstrate differences in site fidelity between the mature and the burnt and regenerating heaths, with 55.9% and 55.8% of Slender-billed Thornbill records occurring within individual 1-ha cells in the burnt/regenerating and mature heaths, respectively. The frequency distribution of Slender-billed Thornbills matched that of a negative binomial ($\chi^2 = 3.87$, d.f. = 7, $P = 0.79$) and not that of a Poisson distribution ($\chi^2 = 277.95$, d.f. = 7,

Table 3. Measures of short-term site fidelity for Slender-billed Thornbills in Ngarkat Conservation Park

The percentage of all records of Slender-billed Thornbill groups located within each habitat type (in September and October 2000, and March 2001), that were found more than once within 1-ha cells, within groups of three and five contiguous 1-ha cells, and those that were isolated records (i.e. were recorded only once in an isolated 1-ha cell over the entire study period)

	All habitats	Mature habitat	Regenerating habitat	Burnt habitat
Total no. of 1-ha cells assessed	2830	1100	940	790
No. of 1-ha cells with no records	2732	1081	907	746
Total no. of records of Slender-billed Thornbill groups	116	29	38	49
Repeated records in 1-ha cells (% of total records)	15	31	11	8
Repeated records in 3 contiguous 1-ha cells (% of total records)	72	79	82	61
Repeated records in 5 contiguous 1-ha cells (% of total records)	89	83	90	92
Groups recorded only once in an isolated 1-ha cell (% of total records)	11	17	10	8

Table 4. Measures of long-term site fidelity for Slender-billed Thornbills in Ngarkat Conservation Park

The percentage of all records of Slender-billed Thornbill groups annually located along marked fixed-width transects in Ngarkat during winter from 1991 to 2002 that were found more than once in single hectare cells, within groups of three and five continuous hectare cells and those that were isolated records (i.e. were recorded only once in an isolated individual hectare cell over the entire study period). 'Burnt / regen.' habitat refers to heaths burnt since 1990, 'mature' refers to heath burnt in 1978 or before. The # ha cells assessed and the # ha cells with no records of Slender-billed Thornbills are not given for the separate habitat types because this figure changed with time as more fires affected the study site

	All habitats	Mature habitat	Burnt or regenerating habitat
No. of individual 1-ha cells assessed	975	–	–
No. of 1-ha cells with no records	522	–	–
Total no. of records of Slender-billed Thornbill groups	669	228	441
Repeated records in single 1-ha cells (% of total records)	55.8	55.8	55.9
Repeated records in 3 contiguous 1-ha cells (% of total records)	94.3	94.3	94.7
Repeated records in 5 contiguous 1-ha cells (% of total records)	97.4	94.6	98.6
Groups recorded only once in an isolated 1-ha cell (% of total records)	1.8	2.7	1.4

$P < 0.001$), indicating that Slender-billed Thornbills had a clumped distribution within transects.

Insect abundance and activity

Over the entire sampling period, 3.9 kg of *L. myrsinoides* foliage was sampled, and 345 insects were sampled from this foliage. Although no analyses of size classes were made, nearly all insects sampled were of the size (2–10 mm long) that Slender-billed Thornbills would consume (authors' observations), including small larvae and adult Lepidoptera (moths), Arachnida (spiders and mites), Diptera (flies) and Hemiptera (bugs).

Two-way ANOVA showed that insect abundances on foliage differed between habitats and seasons (F = 16.4, d.f. = 5,174, $P < 0.0001$). In spring, foliage insects were generally less abundant, but not significantly so, in mature heath than in regenerating and burnt heath (Fig. 5). For the entire study period the mature heath supported fewer insects (8.4 per 100 g *L. myrsinoides* foliage) than did the regenerating heath (16.3 per 100 g *L. myrsinoides* foliage). However, abundances in the burnt heath (12.4 per 100 g *L. myrsinoides* foliage) were not different from those in either the regenerating or mature heaths (Fig. 5). Seasonal shifts in the abundance of foliage insects saw fewer foliage insects in autumn (mean across habitat types: 3.9 insects per 100 g *L. myrsinoides* foliage) than in spring (mean across habitat types: 21.0 insects per 100 g *L. myrsinoides* foliage), and this seasonal effect was similar in each habitat type (Fig. 5), with no significant interaction between habitat type and season (F = 0.24, d.f. = 2,174, P = 0.7846).

Insect activity also differed significantly between habitat types and between seasons (F = 6.57, d.f. = 5,294, $P <$ 0.0001). For example, insect activity over the entire study period in the burnt heath (5.1 insects seen every 2 min) and regenerating heath (3.9 insects seen every 2 min) was greater than in the mature heath (2.1 insects seen every 2 min) (Fig. 6). The effect of season, however, did not influence

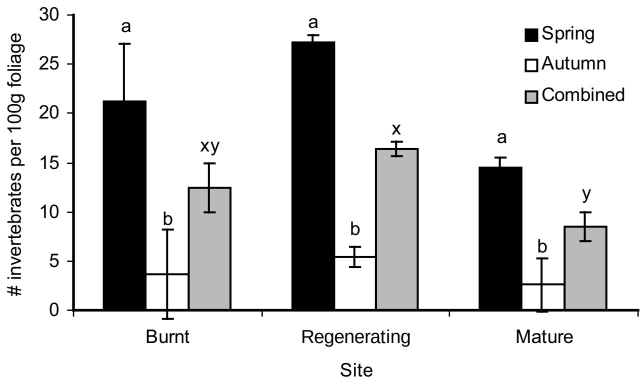

Fig. 5. Abundances of foliage insects (mean ± s.e.) for the burnt, regenerating and mature heath in Ngarkat Conservation Park in spring 2000, autumn 2001 and across both seasons (combined). Different labels within spring and autumn (a and b) and combined (x and y) indicate a significant difference at α = 0.05 (Tukey Honestly Significant Difference Test). For each habitat type n = 30 in each of spring and autumn, and n = 60 for combined data.

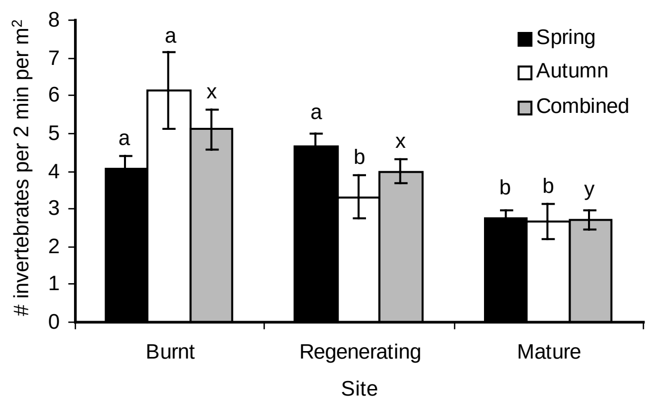

Fig. 6. Insect counts in the burnt, regenerating and mature heath in Ngarkat Conservation Park in spring 2000 and autumn 2001. Different labels within spring and autumn (a and b) and combined (x and y) indicate a significant difference at α = 0.05. For each habitat type, n = 50 in each of spring and autumn, and n = 100 for combined data.

each habitat type equally ($F = 4.3$, d.f. = 2,294, $P = 0.0132$). The only significant seasonal change in insect activity was a decrease between spring and autumn in the regenerating heath (Fig. 6).

Discussion

Densities of Slender-billed Thornbills found in Ngarkat confirm that Slender-billed Thornbills increase in abundance after fire. Comprehensive searches in 2000–01 indicated that within the burnt and regenerating heath, densities were at least three times higher than those in the mature heath. These estimates are consistent with, and provide replication of, the increases in winter densities following the fires in the summers of 1990–91, 1997–98 and 1998–99, documented from transect data between 1991 and 2002 (Fig. 2). The densities are also consistent with those estimated by Matthew (1994) and Woinarski (1989) for Slender-billed Thornbills in Ngarkat (0.2 birds ha^{-1}) and north-western Victoria (0.09 birds ha^{-1}), respectively.

A comparison of bird densities in the years immediately after the three fires between 1990 and 2002 suggests that recolonisation of burnt areas is dependent on the immigration of birds, presumably from adjacent areas of unburnt heath, and is strongly affected by the size of the area burnt. For example, in the two years after the large fires in the summers of 1990–91 and 1998–99 (Fig. 1), Slender-billed Thornbills occurred in relatively low densities in these areas. In contrast, bird densities in the burnt heath following the much smaller fire in the summer of 1997–98 (Fig. 1) increased more rapidly, suggesting that the immigration of a greater number of birds was facilitated by the smaller size of the burnt area.

The density of Slender-billed Thornbills in the 1991–2002 study period peaked (0.3 birds ha^{-1}) about seven years after the fire in the summer of 1990–91. This increase could be due to either ongoing immigration of birds from adjacent areas of unburnt heath, and/or an increased breeding output. However, the difference in Slender-billed Thornbill densities after the fire in the summer of 1997–98 indicates that the quantity and timing of this density peak is likely to vary with the quality and carrying capacity of different areas recovering from previous fires, and possibly also with the rainfall in the years immediately after fire.

In general, however, the higher densities in heaths that had been burnt probably resulted from these habitats being more productive and having greater food availability than the mature heath. Consistent with this, the abundances of foliage insects were higher in the regenerating heath than in the mature heath, and insect activity was higher in both the burnt and regenerating heath than in the mature heath.

This increase in insect activity and abundance is most likely a direct result of the mass post-fire regeneration of a wide range of plant species, which either germinate from seed (e.g. *Gyrostemon australasicus*) or regenerate from adaptive organs such as lignotubers (e.g. *A. pusilla*) (Specht *et al*. 1958; Gill 1981). Such regeneration provides abundant shoot growth and soft foliage upon which phytophagous insects in Ngarkat are dependent (Edmonds and Specht 1979). Even 10 years after fire, Ngarkat heaths are still relatively productive habitats in comparison with mature heaths (Specht *et al*. 1958). With age, however, many seeding shrubs present after the fire senesce (Ward and Paton 2004), decreasing habitat productivity and the diversity of shrubs present in the mature heaths (Specht *et al*. 1958).

Between spring 2000 and autumn 2001, group sizes increased considerably only in the burnt heath. A similar pattern has been recorded for cooperatively breeding thornbills, including Buff-rumped Thornbills, *Acanthiza reguloides* (Bell 1985), Yellow-rumped Thornbills, *A. chrysorrhoa* (Ford 1963), and Western Thornbills, *A. inornata* (Recher and Davis 2000), which form pairs during the breeding season and larger groups outside of this period. Green and Cockburn (1999) suggested that cooperative breeding within birds is more likely to occur in higher-quality habitats. Furthermore, species living in dense habitat, such as Brown Thornbills, *A. apicalis* (Bell 1985), are more likely to breed in pairs (Cockburn 1996). It is therefore possible that the failure of Slender-billed Thornbills to form larger groups in the regenerating and mature heath in autumn may reflect the denser habitat structure of older heaths and a decline of quality compared to the burnt heath.

The spacing of Slender-billed Thornbills across the study site also provides an insight into habitat quality and the distribution of suitable resources. With increasing age of habitat, the degree of spacing of Slender-billed Thornbills increases. This suggests that as the heathland ages and becomes less productive and more senescent (Specht *et al*. 1958) the number of areas able to support sufficient food resources for Slender-billed Thornbills decreases and the remaining groups contract into the few remaining areas of better-quality habitat (Table 2, Fig. 3).

The pattern of repeated use of certain areas by Slender-billed Thornbills, as suggested by their clumped distribution and the short- and long-term site-fidelity data, supports this notion. Slender-billed Thornbills (but not necessarily the same groups), were more often found repeatedly in the same areas in the mature heath than they were in the regenerating and burnt heath. It is possible that with increasing age of habitat Slender-billed Thornbills become more reliant on widely spaced individual patches of habitat with suitable resources. The larger roaming groups of Slender-billed Thornbill in the burnt heath during autumn may have also contributed to lower site fidelity in this habitat.

Are frequent fires necessary?

Given the higher abundances of Slender-billed Thornbills in the years after fire, Slender-billed Thornbills initially seem reliant on frequent fires and heaths in earlier stages of post-fire succession. However, all other bird species of conservation significance in Ngarkat prefer habitat at later stages of post-fire succession (DCP, unpublished data), and the survival of many plant species in Ngarkat requires inter-fire periods longer than 10 years (Forward 1996). Therefore, focusing only on maintaining optimal habitat for Slender-billed Thornbills will conflict with the requirements of these other species.

A crucial question therefore is: Can Slender-billed Thornbills maintain populations in heath at later stages of post-fire succession? Ward and Paton (2004) suggest that the adaptable foraging behaviour of Slender-billed Thornbills allows them to occur in all three habitats. Furthermore, the current study has demonstrated that Slender-billed Thornbills can breed in mature heath. Although detailed studies of colour-banded populations are required to understand the sustainability of this breeding effort, it appears that small populations may be able to persist in the mature heath and frequent fires are not critical to conservation of Slender-billed Thornbills.

Furthermore, the heath in earlier stages of post-fire succession is just as prone as older senescent heaths to suffer from drought conditions. For example, the recovery of the regenerating heath after the fire in the summer of 1990–91 was severely impeded by drought (DCP, unpublished data), which may have contributed to the low Slender-billed Thornbill densities in 1991 and 1992, and there were declines in densities during 1994–1995 and 1997–98 after drought years in 1994 and 1997. Also, the very dry summer period of the 2000–01 study saw decreases in insect abundances in all habitats and decreases in bird densities in both the burnt and mature heath.

Therefore, although early successional heath may allow Slender-billed Thornbills to temporarily increase in abundance, mature heath is still able to support small populations from which dispersal into recently burnt areas can occur.

Ngarkat is currently dominated (~70%) by habitat in earlier stages of post-fire succession as a result of extensive fires in the summers of 1990–91, 1997–98, 1998–99 and 2002–03. This is not ideal given that recolonisation of burnt habitats takes longer when large areas are burnt, particularly when they abut areas in the early stages of recovery (Woinarski and Recher 1997).

The key for fire management in Ngarkat, therefore, is to identify and protect the areas of better-quality habitat in the mature heath, and to maintain a fine-scale spatial mosaic of heath at different stages of post-fire succession. This will protect ‘source’ areas of Slender-billed Thornbills, which facilitate recolonisation of burnt areas, while providing habitat for a full range of mallee- and heath-dependent flora and fauna. This proposed fine-scale mosaic is in keeping with recent plans for management of Ngarkat (Richards *et al*. 1999) and consistent with that proposed for other threatened Australian bird taxa (Woinarski and Recher 1997).

In order to clarify the details of dispersal and population increase after fire, more detailed long-term research is required with colour-banded birds and patches of burnt and unburnt heath as replicates and controls. However, the present study has provided a detailed account of the responses in densities, spacing and site fidelity of Slender-billed Thornbills to fire. The study also demonstrated that initial density estimates did not reflect the importance of mature heath to Slender-billed Thornbills, reinforcing that sensible management of fire for avifauna is dependent on detailed ecological research, and not simply measures of abundance in different post-fire habitats.

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