The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*)

Stephen A. Murphy[A,B,D], *Sarah M. Legge*[A,C], *Joanne Heathcote*[A] *and Eridani Mulder*[A]

[A]Australian Wildlife Conservancy, PO Box 8070, Subiaco East, WA 6008, Australia.

[B]School for Environmental Research, Institute of Advanced Studies, Charles Darwin University,
  Darwin, NT 0909, Australia.

[C]Botany and Zoology, Research School of Biology, Australian National University, Canberra,
  ACT 0200, Australia.

[D]Corresponding author. Email: steve.murphy@australianwildlife.org

Abstract

   Context. Mismanaged fire is one of the main processes threatening biodiversity in northern Australian savannas. While the suite of species adversely affected by fire has been quite well documented, empirical studies that seek to identify the ecological mechanisms that underpin these declines are rare. This dearth of mechanistic knowledge is hindering the refinement and development of conservation management practices and policy, such as early dry-season prescribed burning programmes.

   Aims. Our aim was to describe why red-backed fairy-wrens (RBWs; *Malurus melanocephalus*) decline after fire, as shown by previous studies.

   Methods. We examined the effects of early and late dry-season fire (and an unburnt control) on the mortality, dispersal, physiology and breeding of colour-marked RBWs. We also tested whether the early fire area became an important refuge after the late fire.

   Key results. Neither fire treatment caused a detectable increase in mortality. Individuals relocated short distances to unburnt habitat following both fires. Some individuals used the early fire area after the late fire, but only if they were already living nearby and most also relied on adjacent unburnt habitat. Blood-parasite infection and pectoral-muscle attrition were unaffected by the treatments. The early fire caused loss of body mass at a time when the control population gained mass after breeding, whereas the late fire had no effect on mass. Blood haemoglobin concentrations in birds affected by the late fire deviated from the levels observed in the control population, presumably because of disruption of behaviours associated with the onset of the breeding season. Mayfield estimations of daily egg-survival probability showed no difference among the treatments, whereas the daily probability of nestling survival was significantly lower in the late fire area. Pairs affected by the late fire also had a shorter breeding season and none attempted multiple broods after earlier successes.

   Conclusions. Our results suggest that the reproductive output of RBWs is low following late dry-season fire, and that this is the main mechanism that explains their decline.

   Implications. This study provides support for the value of using early dry-season prescribed burning to limit the effects of late dry-season wildfire. However, there are important caveats to this, such as the retention of near-by unburnt habitat, and the consideration of variable regeneration rates for different vegetation types.

Additional keywords: fire, land management, *Malurus melanocephalus*, northern Australia, prescribed burning, savanna.

Introduction

Evidence is mounting that north Australia is on the verge of a wave of vertebrate extinctions similar to that which occurred in the central deserts 50–100 years ago. Most notable are the precipitous guild-wide declines of small and medium-sized mammals (Woinarski *et al.* 2001) and seed-eating birds (Franklin 1999), although there are also other examples, such

as the grasswrens *Amytornis* spp. (Woinarski 1992), that together suggest landscape-scale dysfunction.

   Given the wide geographical and taxonomic scope of the problem, a broad structural and floristic change in northern habitats is normally inferred to be the principal cause of the loss in vertebrate biodiversity, and it is frequently suggested that fire is a key process causing this change (Andersen *et al.* 2003).

Other processes, such as predation, over-grazing or disease may be acting synergistically (Woinarski *et al*. 2001). Fire is an inevitable and natural process in savannas worldwide because of prolific wet-season growth (particularly grass) followed by dry-season curing (Andersen *et al*. 1998). However, there has been a dramatic increase in the frequency, scale and intensity of fires in northern Australia (Andersen *et al*. 1998). Half of the bioregions that constitute Australia's tropical savannas (as defined by the Interim Biogeographic Regionalisation of Australia, Version 6.1; Thackway and Cresswell 1995) have a mean fire-affected area of greater than 30% per year, with up to 57% per year for the Pine Creek Bioregion in the Northern Territory (on the basis of satellite data from 2003 to 2007 (NAFI 2008)). Rainfall, geology, land tenure and access also influence fire patterns (Russell-Smith *et al*. 1997; Edwards *et al*. 2001; Fisher *et al*. 2003; Yates and Russell-Smith 2003).

Fires that occur later in the dry season, when grassy fuel is most cured, are typically more intense and cover much larger areas than those that burn earlier (Andersen *et al*. 2003). For these reasons, late fires are perceived to be more threatening to biodiversity, infrastructure and livestock than those that burn earlier. Prescribed burning early in the dry season is widely practiced by land managers to reduce fuel loads, create refugia for biodiversity and livestock, and for generally creating the landscape heterogeneity that has long been thought important for maintaining biodiversity (Parr and Andersen 2006). Early fires also release fewer greenhouse gases (Russell-Smith *et al*. 2004).

Although the suite of species adversely affected by fire has been quite well documented (Woinarski 1999; Andersen *et al*. 2003; Legge *et al*. 2008), empirical studies that seek to identify the ecological mechanisms that underpin these declines are rare. Notable exceptions are those studies that have used individually marked or radio-tagged animals to elucidate autecological responses to fire. The value of such an autecological approach was well demonstrated by Brooker and Rowley (1991) in southern Western Australia, who showed that reductions in nesting material and food following fire caused poor breeding success in splendid fairy-wrens (*Malurus splendens*) and western thornbills (*Acanthiza inornata*). On the basis of this and similar studies on other birds, Woinarski (1999; p. 80) concluded that '*autecological studies are particularly valuable in that they can provide specific information on which to base carefully targeted fire management*'. Given the valuable insights proffered, it is surprising that autecological approaches have not been more widely applied when investigating the current extinction crisis facing northern Australia, or indeed fire-related conservation issues elsewhere in the world. This dearth of mechanistic knowledge is hindering the refinement and development of conservation management practices and policy.

Here, we present results of a study that employed an autecological approach to examine the effects of early and late fire on red-backed fairy-wrens, *M. melanocephalus* (RBWs). RBWs are small (6.6 g ± 0.5 s.d. *n* = 196) and weak-flying generalist insectivores that spend most of their time in the grass and shrub layers (Murphy *et al*. 2009). Although common, they are known to respond negatively to fire from three independent studies conducted in tropical savannas. Crawford (1979) showed that RBWs maintained only a

'tenuous hold' in swampy open forests and well drained open forests around Darwin, Northern Territory, where fire was frequent. Similarly, by using an experimental approach in the Victoria River District, NT, Woinarski *et al*. (1999) showed that RBWs were strongly associated with unburnt or infrequently burnt sites, especially in grasslands on cracking-clay soil. Near Townsville, northern Queensland, Valentine *et al*. (2007) imposed unburnt, dry-season and wet-season fire treatments in open eucalypt-woodland habitats and showed that RBWs were less abundant after burning, and indeed were never observed in dry-season fire treatments. All three of these studies suggested that the removal of dense grass and/or shrubs, on which RBWs depend, was the underlying cause. However, it remains uncertain whether individual RBWs were either incinerated or dispersed immediately after the fires, whether stressors imposed by the fires caused delayed mortality or morbidity, whether pairs suffered poor reproductive success in subsequent breeding seasons, or whether a combination of these factors was the ultimate cause of decline. In the present study, we examined the effects of three treatments (unburnt, early fire and late fire) on the mortality, dispersal, physiology and breeding of colour-marked individuals. We were also interested to see whether individuals affected by a late-season fire use areas burnt earlier in the same year as a refuge.

Methods

Study site, experimental design and fire scar mapping

The study was conducted at Mornington Wildlife Sanctuary in the Central Kimberley, Western Australia (17.53°S, 126.14°E; Fig. 1), between December 2006 and March 2008. Three populations (unburnt, early burnt and late-burnt treatments) were identified in areas that had a common recent fire history, floristic and structural similarity, and wet-season access. On the basis of Landsat imagery (S. Murphy and S. Legge, unpubl. data), before our work no fires had affected any of the study area since 2003 when a non-contiguous area of 18 ha was burnt by July of that year. The three areas were located within a contiguous 400-ha patch of the same vegetation type, as defined by Hopkins *et al*. (2002). The dominant vegetation community is open woodland with *Eucalyptus brevifolia*, *Bauhinia cunninghamii* and *E. terminalis* in the canopy stratum, *Carissa lanceolata* and *Acacia lysiphloia* and *A. colei* in the mid-storey, and a diverse grass-layer dominated by *Dichanthium fecundum*, *Sehima nervosum*, *Triodia bitextura* and *Heteropogon contortus*. The terrain within each population comprised low slopes and hills, and small ephemeral creeks and soaks in low-lying areas.

The typical end-of-dry-season landscape in northern Australia is characterised by a relatively small total area of early prescribed burns intermingled with large areas burnt late, which work their way among the early burns (Price *et al*. 2007). To simulate this we juxtaposed the two experimental fires, whereas the edge of the unburnt control population was located ~550 m away (Fig. 1). We attempted to catch all RBWs within each population with mist-nets and each individual was colour-banded. No birds were observed moving between the control and treatment populations in over 5600 observations of 304 colour-banded individuals. We estimate
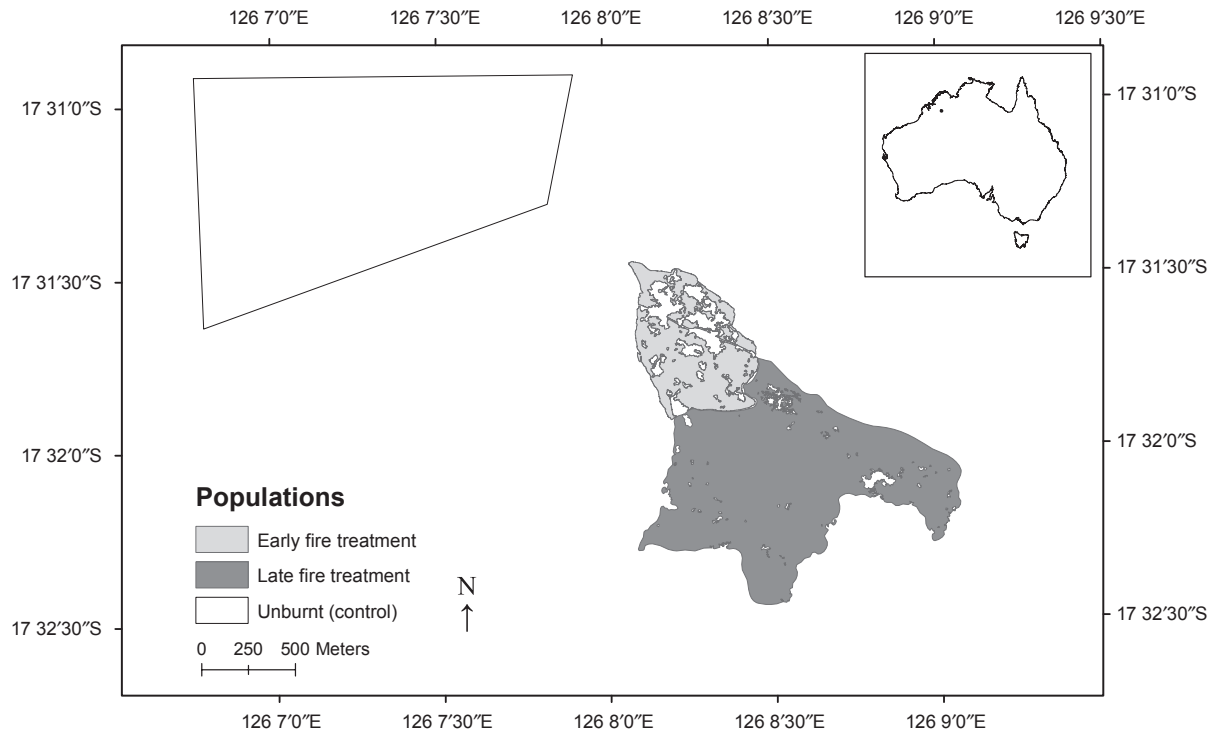
Fig. 1. Study site location and relative positions of the populations.

that >90% of the total study population was banded. The control, early fire and late fire populations covered ~105 ha, 38 ha and 108 ha, respectively. For our investigation into mortality, dispersal and physiology, we used a BACI (before–after control–impact) experimental design. Our comparison of breeding in the three areas included no pre-fire data.

To ensure that the experimental fires were contained, each area was prepared by grading parallel earth breaks around the perimeter (width range: 30–60 m) and burning the intervening fuel at night when the conditions were safe to do so. The early fire was lit mid-morning on 13 May 2007, at the eastern side, with a moderate easterly wind. Fuel moisture content was ~23.7% ($n = 13$; $\pm4.2\%$ s.d.) for *D. fecundum* and 23.5% ($n = 12$; $\pm4.7\%$ s.d.) for *T. bitextura*. The late fire was lit mid-morning on 4 October 2007, also along the eastern side, with a moderate to strong easterly. Fuel moisture content at that time was 4% ($n = 10$; $\pm1.7\%$ s.d.) in *D. fecundum* and 8.9% ($n = 10$; $\pm3.0\%$ s.d.) in *T. bitextura*. To calculate fuel moisture content, grass samples were weighed on digital scales to the nearest 0.1 g when fresh and after oven-drying for 36 h.

Accurate maps of the resultant fire scars were important to determine the extent to which all individual RBWs were affected. Aerial photographs were taken immediately after each burn with a 20-mm lens on 6.3-megapixel SLR digital camera mounted on a stablising jig. These were georeferenced against a geolocated DigitalGlobe image, with at least a second-order polynomial transformation. The images were mosaicked for a supervised classification based on user-identified burnt raster areas by using the computer program ER Mapper 7.2 (Erdas Inc., Norcross, GA, USA). The resultant maps were vectorised using ArcMap 9.3 (Environmental System Research

Institute Inc., Redlands, CA, USA) and then proofed by eye against the original photographs. Use of these images in the field showed that they were accurate to within 1–2 m.

The early fire burnt 71% of the pre-defined 38-ha area, which is typical of early dry-season prescribed burning regionally (S. Murphy and S. Legge, unpubl. data). In contrast, the late fire burnt 96% of the pre-defined 108-ha area, which is also typical of fires at that time of year. The late fire had a rate of spread ~3–5 times that of the early fire. Three years prior to this study, feral herbivores were removed from a large portion of Mornington and all populations were located in this area.

Mortality and dispersal

To determine fire-induced mortality and dispersal, we recorded the identity and location of individuals using spotting scopes and GPS units. This was done most mornings and afternoons for 1–2 months before and 1–2 months after each experimental fire, and was also done for the control population during the same periods.

For mortality analyses, we included only those birds that had been seen more than once before each of the fires and excluded those that had any part of their pre-fire home range outside the burn areas because we wanted to be sure that all birds were subjected to the fires. We compared pre- and post-fire resighting data to determine the number of birds that had disappeared from each population by the end of each post-fire period. The post-fire period was approximately 1 month after each fire. We tested the significance of the observed difference by using chi-square tests. We assumed that any differences between control and treatment populations could be attributed to the effect

of the fires, arising either through mortality or fire-induced dispersal.

We described the spatial response of fire-affected birds, hereafter referred to as either early fire or late fire refuges, by mapping their pre- and post-fire locations. Refugees were defined as those individuals that spent the majority of their time (on the basis of pre-fire observations) within the areas that were to be affected by either of the treatments. We only included individuals that had been seen four or more times pre- and post-fire. We were also interested in describing refugees' post-fire use of the burnt area relative to the proximity of unburnt habitat (either internal unburnt or the contiguous unburnt area outside the treatments). To do this, we calculated the mean distance between refuge post-fire locations and the nearest unburnt habitat, and compared this to the mean distance to unburnt habitat for 100 randomly placed points, by using simple *t*-tests.

For the late fire refuges, we were especially interested in what extent the early burnt area became an important refuge. We also examined whether pre-fire proximity to the early fire area (as defined by the distance between the mean centre point of each bird's pre-fire locations and the edge of the early fire area) explained whether or not a late fire refuge used the early fire area, by using logistic regression in JMP 8.0.1 (SAS Institute, Cary, NC, USA). All spatial manipulations were done using the extensions Hawth's Analysis Tools v3.27 (www.spatialecology. com, verified March 2010) and ET Geo Wizards (www.ian-ko. com, verified March 2010) in ArcMap 9.3 (Environmental System Research Institute Inc., Redlands, CA, USA).

Physiological assays

We caught a subset of individuals in the treatment populations before and after each fire for physiological analyses and compared the measurements to those from the control population. It is possible that the spatially contiguous arrangement of our fire treatments could make it difficult to interpret results from the late fire period for those individuals that straddled both areas. However, in reality refugees tended to avoid the early fire area until after the late fire (see Figs 2, 3). For all individuals, we measured the following four traits that describe physiological condition that we expected may respond to the fires: (1) body mass (measured with a 0.25-g-increment spring balance); (2) peripheral whole blood haemoglobin concentration (Hb) measured in g L^{-1} (± 3 g L^{-1}) with a Hb 201+ portable analyser (Hemocue, Ängelholm, Sweden). Hb has been shown to reflect condition in previous studies, and can be especially informative when used in a comparative way (Andersson and Gustafsson 1995; Box *et al.* 2002; Banbura *et al.* 2007); (3) pectoral-muscle attrition, measured on a qualitative scale from 0 (sharp keel) to 3 (large and bulging pectoral muscle; (Gosler *et al.* 1998)); and (4) presence/absence of blood parasites.

A small (<30 µL) blood sample was taken from the brachial vein and DNA was extracted by using an ammonium acetate protocol (details available on request). The presence of blood parasites was assayed using the polymerase chain reaction (PCR) technique, as described in Bensch *et al.* (2000), whereby birds testing positive produce a ~500 base-pair band

Fig. 2. Habitat use of late fire-treatment refuges before the late fire.
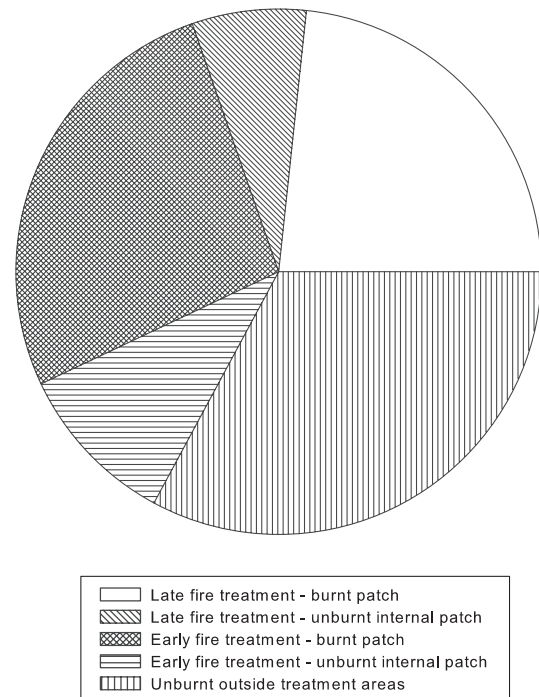

Fig. 3. Habitat use of late fire-treatment refuges after the late fire.

after electrophoresis. Note that this test provides information only about the presence or absence of infection, and not about the level of infection. We sequenced PCR products from three RBWs that tested positive to confirm that PCR protocols were amplifying *Haemoproteus* blood parasites, rather than a non-

specific RBW locus. Sequencing protocols are available on request. Knowledge of an individual's sex is important to accurately interpret physiological tests. In RBWs, young males and some non-breeding males exhibit brown plumage that is indistinguishable from females. We determined the sex of all birds displaying this brown monomorphic plumage by using the molecular sexing technique described in Griffiths *et al*. (1998).

We used population (i.e. control, early or late), time period (i.e. before or after fire) and sex as predictor terms in full-factorial regression models to explain the observed variation in body mass, haemoglobin, the presence or absence of parasites and pectoral score. Alternative models were assessed by using a backwards stepwise regression modelling approach in JMP 8.0.1 (SAS Institute, Cary, NC, USA). Interacting terms were included in models only if their precedent terms were also included as main effects. Terms not significant at $P = 0.1$ were removed in succession, starting from the least significant. Standard least-squares or ordinal logistic regression techniques were used to estimate terms in the model with the lowest Akaike's information criterion value (Akaike 1987). Residual plots were examined for each model to assess assumptions of normality.

Breeding

RBWs in our study area breed in the wet season. They incubate their clutch of up to 4 eggs for 12–13 days and nestlings remain in the nest for 11–12 days (Rowley and Russell 1997). Their dome-shaped nests are constructed of dry grass bound by cobwebs. Occasionally, breeding pairs are helped by one or more auxiliaries (Rowley and Russell 1997). However, we saw no evidence of co-operative breeding after hundreds of observations (including 75 h of video footage) spread over 52 active nests. Nests were found by following nest-building or attending colour-banded individuals, and search effort was equal among treatments. Breeding attempt number was recorded wherever possible. To minimise disturbance, nests were visited approximately weekly when clutch size, brood size and progress was recorded. The reason for the disappearance of eggs and nestlings was assumed to be predation. Eggs laid by Horsfield's bronze-cuckoos (*Chalcites basalis*) were easily identified by being more rounded and uniformly spotted. We assumed the loss of one egg whenever brood parasitism was observed (Langmore *et al*. 2007).

Breeding success was calculated for all nests by the Mayfield method of estimating the daily probability of survival for eggs and nestlings (Mayfield 1975). Because we had some instances of clutch and brood reduction, we calculated 'exposure' on the basis of egg-days and nestling-days, rather than nest-days. We assumed that failure occurred mid-way between two visits if the exact failure date was unknown (Mayfield 1975). Hatching failure was recorded as egg loss. Differences among populations in the daily probabilities of survival for each stage (incubation and nestling) were examined by using standard analysis of variance.

To examine differences in the duration of breeding among the populations, we recorded when nest building started and how many nests were being built in each week of the breeding season (Week 1 being the week we first detected nest building).

We also recorded nest height above ground (in cm) and substrate, grouped as grass, forb (e.g. *Pterocaulon serrulatum*, *Crotalaria* spp.), shrub or tree. We also collected, oven-dried and weighed (in grams) a subset of complete nests where clutches or broods were observed. We assessed whether population could explain variation in these attributes, by using logistic or standard least-squares regression. We also used nest height, mass and substrate, along with population, as predictors of egg- and nestling-survival probabilities. We used JMP 8.0.1 (SAS Institute, Cary, NC, USA) for analyses.

Results

Mortality and dispersal

There was no difference in the number of birds that disappeared after either fire compared with the control population. Two individuals disappeared in the post-early fire period from both control and treatment populations ($n = 14$ and 28, respectively; early *v*. control, contingency analysis: $\chi^2_1 = 0.55$, $P = 0.46$). Four individuals disappeared from the control population in the post-late fire period ($n = 43$), whereas two disappeared from the treatment in the same period ($n = 56$; late *v*. control, contingency analysis: $\chi^2_1 = 1.4$, $P = 0.24$).

Thirty-two individuals were classified as early fire refugees and were seen 218 times before the early fire treatment: 200 times in the area to be burnt and 18 times in adjacent habitat. After the early fire, we made 175 observations of the early refugees, 66 times in adjacent unburnt habitat within 100 m of the fire, 64 times in internal unburnt patches and 45 times within the burnt area. For birds seen in burnt habitat, the mean distance to unburnt habitat was 11 m and this distance was significantly smaller than the 100 randomly allocated points ($n = 45$, $t_{143} = -2.37$, $P = 0.02$). This showed that individuals remained near unburnt cover when using the burnt area.

Forty-four individuals fulfilled the criteria of being late fire refugees. In the 33 days before the late fire treatment, refugees were observed 298 times, mainly within the unburnt habitat that was soon to be burnt (260 times). During this period, late refugees were seen in the early fire area only 17 times, including observations in internal unburnt patches (Fig. 2). In the 24 days after the late fire, refugees were located 356 times, shared roughly among the area unburnt area adjacent to both treatments within 200 m (117), and within the early burnt area (131 times). Figure 3 shows the break-down of where late fire refugees spent their time after the fire. Fourteen refugees were seen at least once in the early fire area in the post-late fire period. All but one of these individuals were also recorded in the unburnt habitat adjacent to both treatments. Individuals used the early fire area if they lived nearby in the pre-late fire period (logistic fit: $\chi^2_1 = 41.9$, $P < 0.0001$). For refugees seen in either burnt area in the post-late fire period, the mean distance to unburnt habitat of any size (both internal and external unburnt) was 24 m, and this distance was significantly smaller than the 100 randomly allocated points ($n = 229$, $t_{143} = -7.68$, $P < 0.0001$). As before, this showed that individuals remained near unburnt cover when using the burnt area.

Physiological effects

After the early fire, control birds gained body mass, whereas it decreased in treatment birds, irrespective of sex ($n = 145$; time period × population: $F_{3,141} = 3.8$, $P = 0.05$). Hb in control birds tended to decline in the post-fire period, whereas in the treatment birds it remained stable; however, this difference was not significant ($n = 112$; time period × population: $F_{4,107} = 3.7$, $P = 0.06$; Fig. 4). The incidence of parasite infection was higher in the post-early fire period compared with the pre-fire period for both populations, irrespective of sex, suggesting that the fire itself had no effect ($n = 44$; time period: $\chi^2_1 = 7.1$, $P = 0.008$). No model significantly explained variation in pectoral-muscle score.

For the late fire treatment, backwards stepwise regression retained sex as the only significant predictor of body mass ($n = 114$; sex: $F_{1,112} = 21.8$, $P < 0.0001$), suggesting that the late fire had no effect on body mass. Hb in the control population in the post-late fire period increased, whereas in treatment birds it did not change ($n = 85$; time period × population: $F_{3,81} = 4.2$, $P = 0.04$; Fig. 4). No models involving the late fire significantly explained variation in parasite infection or pectoral-muscle score.

Breeding

We calculated daily survival probabilities for 52 nests that had either eggs or chicks. Survival probability was equal among treatments during the incubation stage ($n = 627$ egg days; $F_{2,30} = 0.61$, $P = 0.55$). In contrast, the probability of nestling survival was significantly lower for the late fire treatment than either the unburnt or early fire treatment ($n = 511$ nestling days; $F_{2,25} = 3.67$, $P = 0.04$; Fig. 5).

Multiple nesting up to three times was recorded in each population, although there were differences among populations in whether pairs renested after successfully fledging young. Four pairs attempted a second brood after earlier success in the unburnt population (for two of these pairs, the second attempt was also successful). One pair in the early fire treatment managed two successful attempts. In contrast, none of the late fire-treatment pairs renested after successfully fledging young.

We observed 66 pairs build 89 nests across all populations. We were certain that 39 of these were first nests of the season, because of detailed daily observations of those pairs in the 2 weeks leading up to breeding activity. The mean start date (by week number) for these nests in the late fire treatment area was 2 weeks later than that in the control or early fire treatment ($n = 39$; $F_{2,36} = 7.01$, $P = 0.003$). When all nest-building was tallied, it was clear that late fire-treatment pairs did not extend their breeding seasons to compensate for this delayed start (Fig. 6); in other words, they had a shorter breeding season.

There were significant differences in the substrate, height and mass of nests among the populations. Pairs in the unburnt population nested more frequently in forbs and never in trees ($n = 89$; $\chi^2_6 = 24.3$, $P = 0.0005$; Fig. 7). Nests in the late fire area were higher than those in the unburnt area, whereas nest height in the early fire area was intermediate ($n = 52$; $F_{2,49} = 4.2$, $P = 0.02$; Fig. 8). Nests in the unburnt area were significantly heavier than nests in the early fire area, whereas nests in the late fire area were intermediate in mass ($n = 40$; $F_{2,37} = 5.0$, $P = 0.01$; Fig. 8). Nest height, mass and site were not significant main effects in any models predicting egg- or nestling-survival probabilities.

Discussion

Despite contemporary fire patterns being continually identified as a threatening process in northern Australian ecosystems, little empirical evidence exists to explain exactly why some species are negatively affected (Woinarski 1999; Andersen *et al.* 2005). Our results show that the absence or decline of RBWs following fire in tropical savanna, as demonstrated by at least three studies (Crawford 1979; Woinarski *et al.* 1999; Valentine *et al.* 2007), is likely to be explained by (1) short-distance dispersal away from burnt areas, which is likely to be a short-term effect of early and late fires, as described by Valentine *et al.* (2007), and (2) reduced reproductive output in subsequent breeding seasons after late dry-season fires. The latter effect could explain reduced densities of RBWs under a long-term
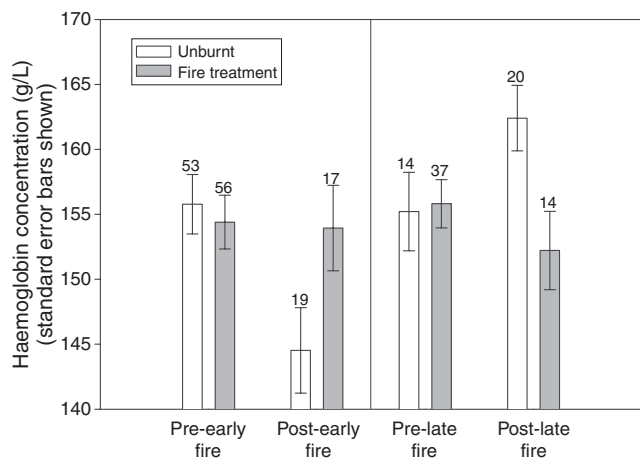

Fig. 4. The effect of the early and late fires on peripheral whole-blood haemoglobin concentration in red-backed fairy-wrens. Numbers above columns are sample sizes.
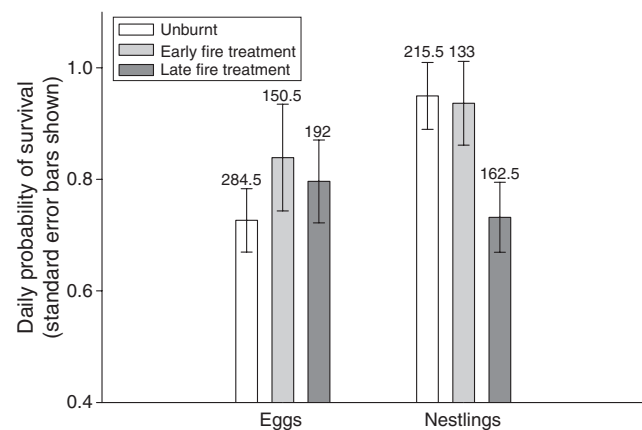

Fig. 5. Mayfield estimations of daily survival probabilities for red-backed fairy-wren eggs and nestlings in three populations. Numbers above bars indicate sample sizes in egg and nestling days.
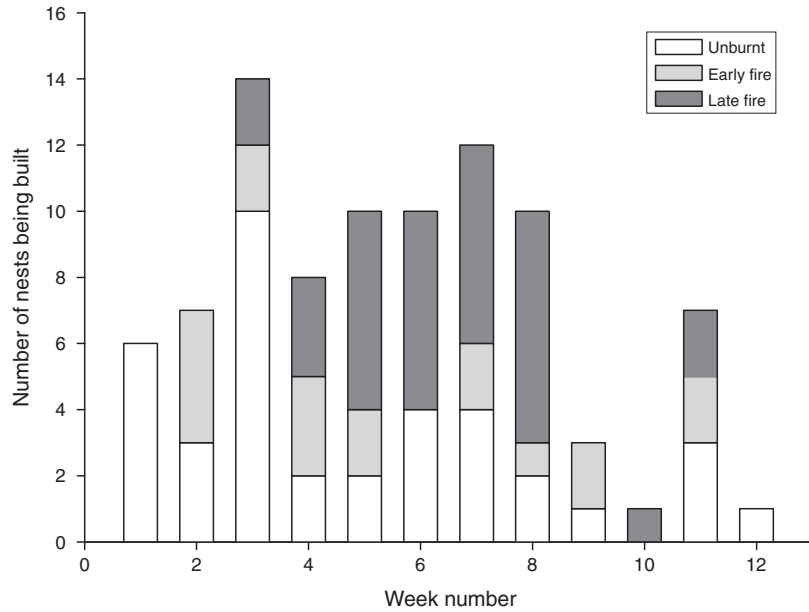
Fig. 6. The timing of nest initiation by red-backed fairy-wrens, grouped by week ($n = 89$).
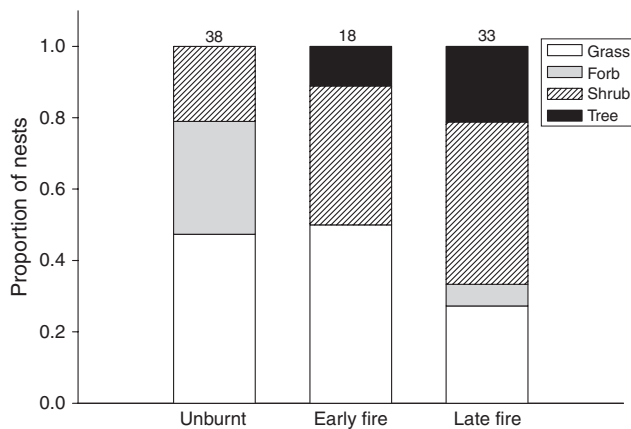

Fig. 7. Variation in the red-backed fairy-wren nest site among unburnt, early fire and late fire treatments. Numbers above columns are sample sizes.
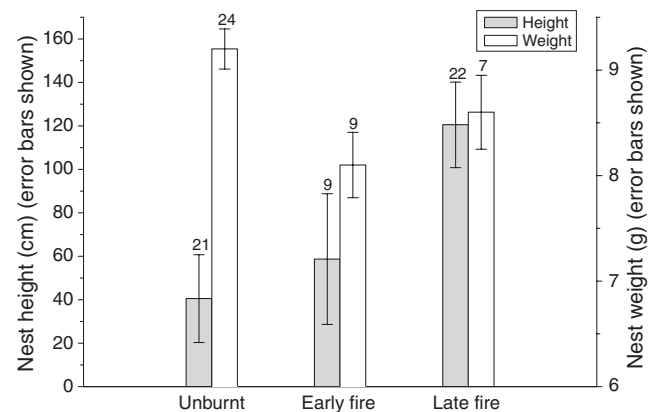

Fig. 8. The effect of unburnt, early fire and late fire treatments on nest weights and heights in red-backed fairy-wrens. Numbers above columns are sample sizes.

history of repeated late dry-season fires, as described by Crawford (1979) and Woinarski *et al.* (1999). We have also shown that RBWs visited the early fire area more regularly after the adjacent late fire, although we stress that the majority of individuals who did so also regularly visited adjacent unburnt habitat.

Before discussing these findings, we acknowledge three points about our experimental design. First, a limitation is our lack of treatment replication. However, given the dearth of experimentally derived knowledge about this important issue, we believe that our results make a considerable contribution to the field and demonstrate the value of taking an autecological approach. Second, on the issue of whether or not our experimental fires were realistic in terms of scale, RBWs have small home ranges of ~1–3 ha (S. Murphy and S. Legge, unpubl. data), and

this allowed us to conduct experimental fires at scales that were ecologically relevant while still being logistically possible and ethically acceptable (although see discussion below about the use of the early fire area after the late fire). Third, the present study is a response to a single fire, not a fire regime. The longer-term effects of repeated burning patterns may be more severe or at least different from those that we report here.

Mortality and dispersal

We found no evidence to suggest that the mortality of adults causes population decline in RBWs following fire. This was unexpected, not so much because we expected individuals to be incinerated by fire, a conclusion also reached by Lawrence (1966) and Braithwaite (1985), but more so because of the high

density of aerial predators attracted to the fires, both during and immediately afterwards. Such high predator densities are typical of savanna fires, which create easy foraging opportunities, including large numbers of winged insects fleeing the flames and dead animals lying in the resultant ash-bed (Crawford 1979; Press 1987; Woinarski 1990). RBWs are weak fliers and therefore may be expected to suffer from comparatively higher predation. In the few days immediately after both of our fires, alarm calling by RBWs was noticeably more common, and on two separate occasions, a collared sparrowhawk (*Accipiter cirrhocephalus*) and a pair of pied butcherbirds (*Cracticus nigrogularis*) were observed hunting RBWs (albeit unsuccessfully) by repeatedly flying through tiny unburnt habitat patches that were sheltering several of our colour-marked individuals. Nevertheless, if predation of RBWs does increase after fire, it occurred at an undetectably low level during our study.

Our census results showed that fire-affected individuals typically relocated short distances to adjacent unburnt habitat, and used unburnt patches within the burnt areas. Birds also used burnt habitat but remained close to unburnt patches while doing so. This was especially apparent in some large parts of the late fire area that had no unburnt patches where we failed to observe any birds at all. The early fire area provided a post-late fire refuge to RBWs whose pre-fire home range was nearby. However, it seemed that the early fire alone was insufficient as a refuge because all but one of the late fire refugees also frequently visited adjacent contiguous unburnt habitat. Behavioural observations (S. Murphy and S. Legge, unpubl. data) showed that our early burnt area was used only for foraging, with other behaviours, such as preening or resting being reserved for the adjacent unburnt habitat (and typically in the thorny shrub, *Carissa lanceolata*). It is important to note that early burnt areas may be used more by RBWs in the typical late-dry season fire-affected landscapes, where unburnt habitat is often very rare (Russell-Smith *et al.* 2003; Price *et al.* 2007). Such situations may expose RBWs to elevated predation.

Physiology

Our investigations failed to show that increased physiological stress alone explains why RBWs decline after fire. However, we did detect some physiological changes associated with the fires that are likely to relate to either the recovery from or the lead-up to the breeding season.

The mass of birds in the unburnt area during the post-early fire period increased, while there was a decrease in the mass in the treatment population. This effect was slight, but significant. Over the same period, Hb declined (although not significantly, possibly because of small sample sizes, see Box *et al.* (2002)) in the unburnt population whereas they were maintained in the individuals in the early fire treatment. It is likely that both of these effects relate directly to behavioural differences between the two populations. Physiological samples for both populations during the pre-early fire period were collected during the latter stages of the 2006/07 breeding season, when many adults were busily attending recently fledged young. In similar-sized passerines, it has been shown that such breeding behaviour is associated with a loss in the mass (Hõrak *et al.* 1998) and elevated Hb (Box *et al.* 2002). By the time of post-early fire sampling, individuals in the unburnt area had returned to a 'normal' non-breeding mass and Hb profile. In contrast, on the basis of the level of chasing and singing we observed after the early fire in adjacent unburnt habitat, it was our strong impression that early fire refugees were far more unsettled than their unburnt counterparts, and it was this behaviour that made them lose more mass while maintaining their high Hb.

The situation is somewhat similar for the late fire. Sampling for the pre-late fire period coincided with the early stages of breeding, which in RBWs involves oxygen-demanding within-territory activities such as territorial defence and courtship displays by both sexes (Rowley and Russell 1997). This pattern of behaviour increased further during the post-late fire period in the unburnt population, and is a likely explanation for the significant increase of Hb for these individuals, as shown by Box *et al.* (2002). In contrast, breeding preparations for late fire refugees were disrupted by the fire, and so the need for additional oxygen-carrying capacity was diminished.

Breeding

Our results showed that pairs nesting in the late fire-treatment area had a lower reproductive output for the season than did pairs nesting in unburnt and early burnt habitat. This was driven by a later start and overall shorter breeding season, lower daily survival probabilities of nestlings and the absence of multiple successful broods.

The difference in reproductive output is likely to be related to vegetative cover. Although we did not systematically collect data to show a difference in the rate of regeneration between the early and late treatments, we had four photo-monitoring points in each fire treatment that clearly showed that there was more cover in the early fire area than in the late fire area, especially in the first half of the breeding season (Fig. 9). Consequently, breeding in unburnt area and early burnt area started at roughly the same time, whereas pairs delayed breeding in the late fire area. Delayed breeding following fire has also been described for south-western Australian heathland birds (Brooker and Rowley 1991). It is important to note that if we had not excluded feral herbivores from the study area, the advantage conferred to pairs nesting in the early burnt area may have been significantly reduced (Rohrbaugh *et al.* 1999; Fondell and Ball 2004).

Our results showed that survival probabilities of eggs were equal among the three populations, although nestling survival was significantly lower in habitat burnt late. We suggest that reduced cover in the late fire area made visits to nests by attending parents more conspicuous to predators and that this explains lower nestling-survival rates. The idea that increased parental activity increases the rate of predation at the nestling stage was first proposed by Skutch (1949), and later refined by Martin *et al.* (2000). Humple and Holmes (2006) showed that daily nest survivorship (which combines incubation and nestling stages) in loggerhead shrikes (*Lanius ludovicianus*) was lower following fire, and suggested that it was because common ravens (*Corvus corax*) were able to find nests more easily. Pied butcherbirds and Torresian crows (*C. orru*)
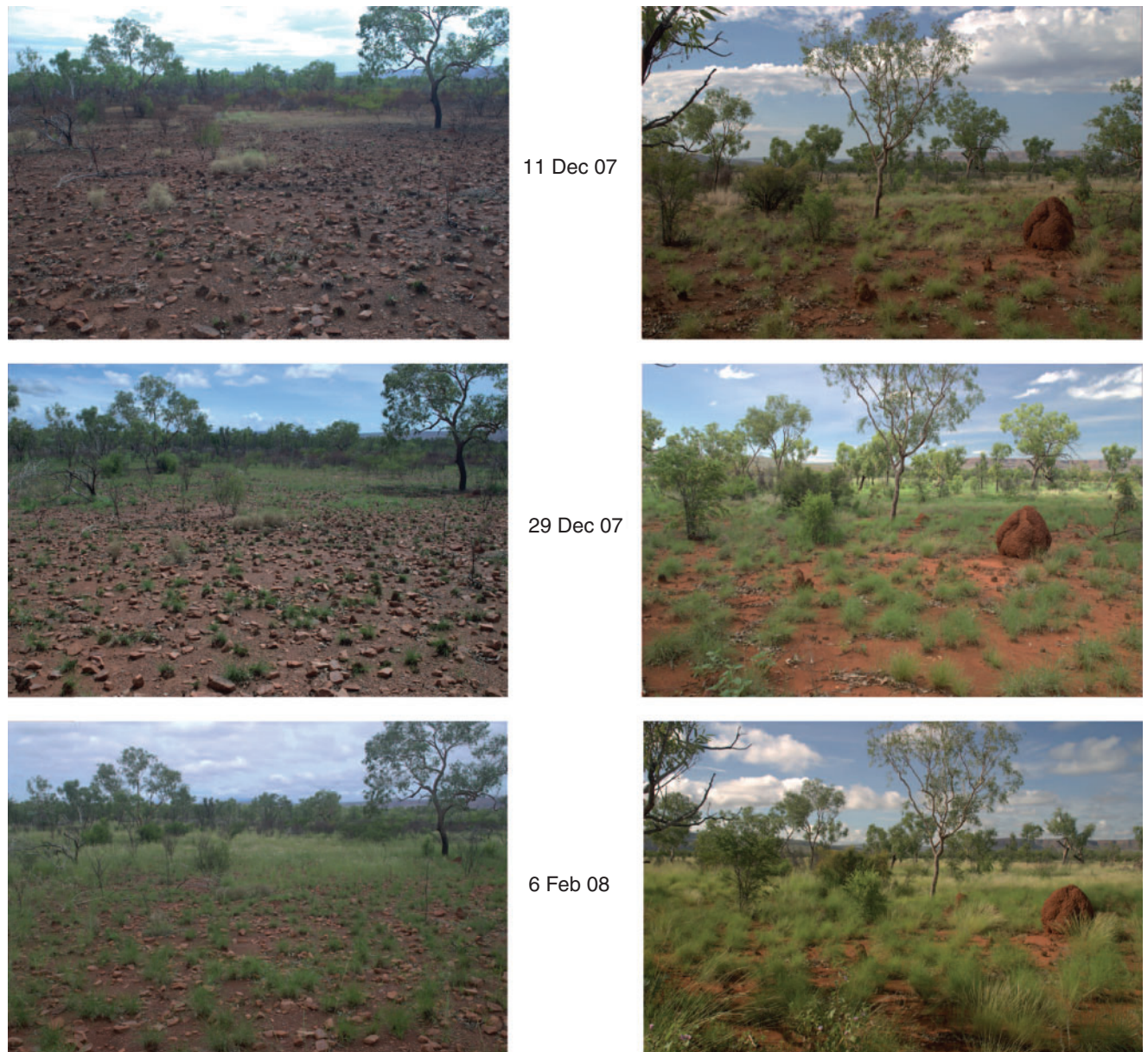
11 Dec 07

29 Dec 07

6 Feb 08

Fig. 9. Two photo-monitoring sites, one in the late fire area (left) and one in the early fire area (right), showing the lag in habitat regeneration in the late fire area. Each pair of photographs was taken on the same date.

were the likely visual predators of RBW nestlings in our study area.

Our results showed that pairs were seeking cover for nesting wherever they could find it, even if it meant nesting in trees, which also explains the significant difference in nest height between treatments. Brooker and Rowley (1991) also observed splendid fairy-wrens nesting in unusually high sites following fire in south-western Western Australia. These authors also demonstrated the subtle effects that fire can have on breeding success in birds (see Introduction). Although we describe similarly subtle effects on RBWs, we found that they did not negatively affect breeding success.

Conservation implications

Taken together, our results support the idea that prescribed burning early in the dry season to combat extensive late dry-season fire is likely to benefit RBWs and other species, but only if unburnt habitat is retained nearby. We do not suggest that complete fire exclusion is likely to benefit RBWs or other savanna birds, because as Woinarski *et al.* (2004) showed, such long-term fire exclusion may cause detrimental changes to habitats via woody thickening. Our results do not suggest that a landscape comprising only late- and early burnt habitat would be benign to RBWs. As discussed earlier, in addition to using the early fire area, the majority of late fire refuges rely on adjacent

unburnt habitat for specific behaviours, presumably to avoid potentially elevated predation risks. This highlights the need for land managers to use prescribed burning in a way that creates multiple well-spaced unburnt habitat patches that have a high chance of escaping from late dry-season fires, a theme echoed by Andersen *et al.* (2005).

Australian tropical savannas are a diverse mosaic of vegetation types, with different recovery rates after fire. In communities dominated by relatively slow-growing perennial grasses such as spinifex (*Triodia* spp.), reproductive output by birds after early fires may be more similar to areas burnt late than unburnt habitat. This could explain the extreme fire sensitivity in Australia's three species of tropical grasswren (*Amytornis dorotheae*, *A. housei* and *A. woodwardi*) that exclusively live and nest in areas of large, long-unburnt spinifex *Triodia* spp. (Rowley and Russell 1997; Higgins *et al.* 2001). Resolving this issue is an important area of future research that may benefit from taking an autecological approach as we have here. Until such time, it is critical that prescribed burning in these systems focus on burning to create unburnt patches that have a high chance of escaping late-season fires.

Acknowledgements

References

Akaike, H. (1987). Factor analysis and AIC. *Psychometrika* **52**, 317–332. doi:10.1007/BF02294359

Andersen, A., Braithwaite, R., Cook, G., Corbett, L., Williams, R., Douglas, M., Gill, A., Setterfield, S., and Muller, W. (1998). Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. *Australian Journal of Ecology* **23**, 95–110. doi:10.1111/j.1442-9993.1998.tb00708.x

Andersen, A. N., Cook, G. D., and Williams, R. J. (Eds) (2003). 'Fire in Tropical Savannas: The Kapalga Experiment.' Ecological Studies. (Springer-Verlag: New York.)

Andersen, A. N., Cook, G. D., Corbett, L. K., Douglas, M. M., Eager, R. W., Russell-Smith, J., Setterfield, S. A., Williams, R. J., and Woinarski, J. C. Z. (2005). Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* **30**, 155–167. doi:10.1111/j.1442-9993.2005.01441.x

Andersson, M. S., and Gustafsson, L. (1995). Glycosylated haemoglobin: a new measure of condition in birds. *Proceedings of the Royal Society of Biological Sciences Series B* **260**, 299–303. doi:10.1098/rspb.1995.0095

Banbura, J., Banbura, M., Kalinski, A., Skwarska, J., Slomczynski, R., Wawrzyniak, J., and Zielinski, P. (2007). Habitat and year-to-year variation in haemoglobin concentration in nestling blue tits *Cyanistes caeruleus*. *Comparative Biochemistry and Physiology* **148**, 572–577. doi:10.1016/j.cbpa.2007.07.008

Bensch, S., Stjernman, M., Hasselquist, D., Ostman, O., Hansson, B., Westerdahl, H., and Pinheiro, R. T. (2000). Host specificity in avian blood parasites: a study of *Plasmodium* and *Haemoproteus* mitochochondrial DNA amplified from birds. *Proceedings of the Royal Society of Biological Sciences Series B* **267**, 1583–1589. doi:10.1098/rspb.2000.1181

Box, J., Lill, A., and Baldwin, J. (2002). Seasonal variation in body mass and blood oxygen carrying capacity of the superb-fairy wren (*Malurus cyaneus*). *Australian Journal of Zoology* **50**, 313–323. doi:10.1071/ZO02033

Braithwaite, R. W. (1985). Fire and fauna. In 'Kakadu Fauna Survey. Final report to Australian National Parks and Wildlife Service'. (Ed. RW Braithwaite.) pp. 634–650. (CSIRO: Darwin, NT.)

Brooker, M. G., and Rowley, I. (1991). Impact of wildfire on the nesting behaviour of birds in heathland. *Wildlife Research* **18**, 249–263. doi:10.1071/WR9910249

Crawford, D. N. (1979). Effects of grass and fires on birds in the Darwin area, Northern Territory. *Emu* **79**, 150–152.

Edwards, A., Hauser, P., Anderson, M., McCartney, J., Armstrong, M., Thackway, R., Allan, G., Hempel, C., and Russell-Smith, J. (2001). A tale of two parks: contemporary fire regimes of Litchfield and Nitmiluk National Parks, monsoonal northern Australia. *International Journal of Wildland Fire* **10**, 79–89. doi:10.1071/WF01002

Fisher, R., Vigilante, T., Yates, C., and Russell-Smith, J. (2003). Patterns of landscape fire and predicted vegetation response in the North Kimberley region of Western Australia. *International Journal of Wildland Fire* **12**, 369–379. doi:10.1071/WF03021

Fondell, T. F., and Ball, I. J. (2004). Density and success of bird nests relative to grazing on western Montana grasslands. *Biological Conservation* **117**, 203–213. doi:10.1016/S0006-3207(03)00293-3

Franklin, D. C. (1999). Evidence of disarray amongst granivorous birds assemblages in the savannas of northern Australia, a region of sparse human settlement. *Biological Conservation* **90**, 53–68. doi:10.1016/S0006-3207(99)00010-5

Gosler, A. G., Greenwood, J. J. D., Baker, J. K., and Davidson, N. C. (1998). The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* **45**, 92–103. doi:10.1080/00063659809461082

Griffiths, R., Double, M. C., Orr, K., and Dawson, R. J. G. (1998). A DNA test to sex most birds. *Molecular Ecology* **7**, 1071–1075. doi:10.1046/j.1365-294x.1998.00389.x

Higgins, P. J., Peter, J. M., and Steele, W. K. (Eds) (2001). 'Handbook of Australian, New Zealand and Antarctic birds. Vol. 5: Tyrant-flycatchers to Chats.' (Oxford University Press: Melbourne.)

Hopkins, A. J. M., Beeston, G. R., Harvey, J. M., Lemin, H., and Shepherd, D. P. (2002). A database on the vegetation of Western Australia stage 1. Department of Agriculture, Perth.

Hõrak, P., Jenni-Eirmann, S., Ots, I., and Tegelmann, L. (1998). Health and reproduction: the sex-specifc clinical profile of great tits (*Parus major*) in relation to breeding. *Canadian Journal of Zoology* **76**, 2235–2244. doi:10.1139/cjz-76-12-2235

Humple, D. L., and Holmes, A. L. (2006). Effects of fire on a breeding population of loggerhead shrikes in sagebrush steppe habitat. *Journal of Field Ornithology* **77**, 21–28. doi:10.1111/j.1557-9263.2006.00004.x

Langmore, N. E., Adcock, G. J., and Kilner, R. M. (2007). The spatial organization and mating system of Horsfield's bronze-cuckoos, *Chalcites basalis*. *Animal Behaviour* **74**, 403–412. doi:10.1016/j.anbehav.2006.09.019

Lawrence, G. E. (1966). Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* **47**, 278–291. doi:10.2307/1933775

Legge, S., Murphy, S., Heathcote, J., Flaxman, E., Augusteyn, J., and Crossman, M. (2008). The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research* **35**, 33–43. doi:10.1071/WR07016

Martin, T. E., Scott, J., and Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of Biological Sciences Series B* **267**, 2287–2293. doi:10.1098/rspb.2000.1281

Mayfield, H. (1975). Suggestions for calculating nest success. *The Wilson Bulletin* **73**, 456–466.

Murphy, S. A., Heathcote, J., Garcia, S., and Legge, S. M. (2009). Time partitioning and substrate use of red-backed fairy-wrens *Malurus melanocephalus. Corella* **33**, 39–42.

NAFI. (2008). North Australia fire Information. Available at www.firenorth. org.au [accessed 2 September 2008].

Parr, C. L., and Andersen, A. N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* **20**, 1610–1619. doi:10.1111/j.1523-1739.2006.00492.x

Press, A. J. (1987). Fire management in Kakadu National Park: the ecological basis for the active use of fire. *Search* **18**, 244–248.

Price, O. F., Edwards, A. C., and Russell-Smith, J. (2007). Efficacy of permanent firebreaks and aerial prescribed burning in western Arnhem Land, Northern Territory, Australia. *International Journal of Wildland Fire* **16**, 295–305. doi:10.1071/WF06039

Rohrbaugh, R. W., Reinking, D. L., Wolfe, D. H., Sherrod, S. K., and Jenkins, M. A. (1999). Effects of prescribed burning and grazing on nesting and reproductive success of three grassland passerine species in tallgrass prairie. *Studies in Avian Biology* **19**, 165–170.

Rowley, I., and Russell, E. (1997) 'Fairy-wrens and grasswrens.' (Oxford University Press: Oxford, UK.)

Russell-Smith, J., Ryan, P. G., and Durieu, R. (1997). A Landsat MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980–94 – seasonal extent, frequency and patchiness. *Journal of Applied Ecology* **34**, 748–766. doi:10.2307/2404920

Russell-Smith, J., Yates, C., Edwards, A., Allan, G. E., Cook, G. D., Cooke, P., Craig, R., Heath, B., and Smith, R. (2003). Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. *International Journal of Wildland Fire* **12**, 283–297. doi:10.1071/WF03015

Russell-Smith, J., Edwards, A., Cook, G. D., Brocklehurst, P., and Schatz, J. (2004). Improving greenhouse emission estimates associated with savanna burning in northern Australia: phase 1. Final Report to the Australian Greenhouse Office. Tropical Savannas CRC, Darwin, NT.

Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? *The Ibis* **91**, 430–455. doi:10.1111/j.1474-919X.1949.tb02293.x

Thackway, R., and Cresswell, I. D. (1995). An interim biogeographic regionalisation for Australia: a framework for establishing the national system of reserves. Australian Nature Conservation Agency, Canberra.

Valentine, L. E., Schwarzkopf, L., Johnson, C. N., and Grice, A. C. (2007). Burning season influences the responses of bird assemblages to fire in tropical savannas. *Biological Conservation* **137**, 90–101. doi:10.1016/j.biocon.2007.01.018

Woinarski, J. C. Z. (1990). Effects of fire on the bird communities of tropical woodlands and open forests in northern Australia. *Australian Journal of Ecology* **15**, 1–22. doi:10.1111/j.1442-9993.1990.tb01016.x

Woinarski, J. C. Z. (1992). The conservation status of the white-throated grasswren *Amytornis woodwardi*, an example of problems in status designation. *Northern Territory Naturalist* **13**, 1–5.

Woinarski, J. C. Z. (1999). Fire and Australian birds: a review. In 'Australia's Biodiversity – Responses to Fire: Plants, Birds and Invertebrates'. (Eds A. M. Gill, J. C. Z. Woinarski and A. York.) (Environment Australia: Canberra.)

Woinarski, J. C. Z., Brock, C., Fisher, A., Milne, D., and Oliver, B. (1999). Response of birds and reptiles to fire regimes on pastoral land in the Victoria River District, Northern Territory. *The Rangeland Journal* **21**, 24–38. doi:10.1071/RJ9990024

Woinarski, J. C. Z., Milne, D. J., and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscape of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* **26**, 360–370. doi:10.1046/j.1442-9993.2001.01121.x

Woinarski, J. C. Z., Risler, J., and Kean, L. (2004). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* **29**(2), 156–176. doi:10.1111/j.1442-9993.2004.01333.x

Yates, C., and Russell-Smith, J. (2003). Fire regimes and vegetation sensitivity analysis: an example from Bradshaw Station, monsoonal northern Australia. *International Journal of Wildland Fire* **12**, 349–358. doi:10.1071/WF03019