Monitoring indicates greater resilience for birds than for mammals in Kakadu National Park, northern Australia.

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Abstract

Context. A previous study reported major declines for native mammal species from Kakadu National Park, over the period 2001-2009. The extent to which this result may be symptomatic of more pervasive biodiversity decline was unknown.

Aims. Our primary aim was to describe trends in the abundance of birds in Kakadu over the period 2001-2009. We assessed whether any change in bird abundance was related to the arrival of invading cane toads (*Rhinella marina*), and to fire regimes.

Methods. Birds were monitored at 136 one hectare plots in Kakadu, during the period 2001-04 and again in 2007-09. This program complemented sampling of the same plots over the same period for native mammals.

Key results. In contrast to the decline reported for native mammals, the richness and total abundance of birds increased over this period, and far more individual bird species increased than decreased. Fire history in the between-sampling period had little influence on trends for individual species. Interpretation of the overall positive trends for bird species in Kakadu over this period should be tempered by recognition that most of the threatened bird species present in Kakadu were unrecorded in this monitoring program, and the two threatened species for which there were sufficient records to assess trends - partridge pigeon (*Geophaps smithii*) and white-throated grass-wren (*Amytornis woodwardi*) - both declined significantly.

Conclusions. The current decline of the mammal fauna in this region is not reflected in trends for the region's bird fauna. Some of the observed changes (mostly increases) in the abundance of bird species may be due to the arrival of cane toads, and some may be due to local or regional scale climatic variation or variation in the amount of flowering. This study provides no assurance about threatened bird species, given that most were inadequately recorded in this study (perhaps because their decline pre-dated this study).

Implications. These contrasting trends between mammals and birds demonstrate the need for biodiversity monitoring programs to be broadly-based. The declines of two threatened bird species over this period indicate the need for more management focus for these species.

Additional keywords: cane toad, conservation, fire, mammals, threatened species

Running head: monitoring birds in Kakadu National Park

Introduction

Kakadu National Park is one of the world's premier conservation reserves, and one of the largest and best-resourced national parks in Australia. Nonetheless, recent monitoring has demonstrated a rapid and severe decline in the small- and medium-sized native mammal fauna of the park, and probably across much of northern Australia (Woinarski *et al*. 2001, 2010, 2011). The available evidence cannot demonstrate unequivocally the main cause of this decline, but unfavourable fire regimes are implicated in part (Woinarski *et al*. 2010). This study considers whether a comparable level of decline is also occurring in the park's terrestrial bird fauna. This question is of inherent conservation interest, in part because Kakadu includes a major proportion of the range of several highly-restricted bird species, and is recognised as an important bird area (Dutson *et al*. 2009), and in part because previous research has indicated that broad swathes of the bird fauna of northern Australia may be in decline (Franklin 1999; Franklin *et al*. 2005). Furthermore, a comparative assessment of trends in the bird fauna may also provide some context for resolution of the causal factors involved in the current decline of mammals.

This study provides a direct counterpoint to our previous reporting of monitoring of mammals (Woinarski *et al*. 2010): a large number of permanently marked plots was sampled (and re-sampled) simultaneously for mammals and for birds over the period 1996 to 2009. As described in our assessment of the results of the mammal monitoring, the fire history between sampling and re-sampling episodes was chronicled for every plot, and changes in the fauna were related to this fire history. The park is situated in a region with very high fire frequency (with typical fire frequency for any site of 3-5 fires per decade: Gill *et al*. 2000; Andersen *et al*. 2005; Edwards and Russell-Smith 2005), and this current fire regime has caused significant recent detriment to some fire-sensitive plant species and environments (Russell-Smith *et al*. 1998, 2002; Edwards and Russell-Smith 2005; Russell-Smith 2006; Woinarski *et al*. 2009). However, the responses of birds to fire management in this region remain poorly defined. Several studies have reported immediate responses to single fire events, including attraction of some bird species to recently burnt areas (Woinarski 1990; Woinarski *et al*. 1999), poorly defined responses to fire regimes over periods of 2-10 years (Corbett *et al*. 2003; Woinarski *et al*. 2004a), but more marked responses to contrasting fire regimes imposed over longer periods (Woinarski 1990; Woinarski *et al*. 2004b). Moreover, inappropriate fire regime is considered to be a threatening factor for relatively many threatened bird species in this region (Woinarski *et al*.

2007). A detailed response study for one threatened species, the partridge pigeon (*Geophaps smithii*), in Kakadu National Park, suggested that particular features of the fire regime, especially fire patch size and heterogeneity, were critical for habitat suitability, and that extensive high intensity late dry season fires were particularly detrimental (Fraser *et al*. 2003).

The period of this study also coincided with the arrival and proliferation in Kakadu of the cane toad *Rhinella marina*, although the study timing was imperfect for a crisp assessment of toad impacts, with only a minority of the monitored plots first sampled before toad arrival. Some previous studies have reported dramatic impacts of toads on some reptile and mammal predator species (Burnett 1997; Griffiths and McKay 2007; Letnic *et al*. 2008; Doody *et al*. 2009; Ujvari and Madsen 2009; O'Donnell *et al*. 2010), but the few previous studies that have considered bird responses have reported few and subdued impacts (Catling *et al*. 1999). Cane toads may have many and complex impacts (Shine 2010), with potential beneficial and adverse consequences for bird populations through (i) direct poisoning of carnivorous bird species; (ii) reduction in predator pressure, particularly for ground-nesting and ground-feeding birds, as many native predators (goannas, elapid snakes, quolls) are killed by the toad's poison; (iii) reduction in food availability (particularly for terrestrial insectivores) due to voracious consumption of invertebrates by very high numbers of toads; (iv) reduced nesting success particularly for tunnel-nesting birds due to direct predation of nestlings or eggs by toads; (v) increased food availability for predatory birds that can safely consume toads; and (vi) increased food availability for predatory and carrion-feeding birds because of the toad-caused reduced abundance of competing mammal and reptile carnivores.

Coincidently, this monitoring program overlapped considerably in time with a recently reported assessment of changes in the bird fauna of another region in northern Australia, Cape York Peninsula, for which baseline sampling occurred in the period 1998 to 2001, and subsequent sampling occurred in 2008 (Perry *et al*. 2011). The Cape York Peninsula monitoring spanned a far larger area, and included more sites (418), but the Kakadu monitoring used a more tightly circumscribed monitoring plot and protocol, used repeated visits to the same plot during a monitoring event, and derived an abundance measure (rather than presence only) for every species in every plot. With due regard to these methodological differences, we make a limited comparison between the two monitoring programs, seeking to assess the extent of commonality in trends across these two significant portions of northern Australia. This study is also analogous to an ongoing monitoring program for terrestrial vertebrates in Litchfield National Park, about 300 km west of Kakadu. Monitoring results for that study for the period 1995-96 to 2001-02 were reported by

Woinarski *et al*. (2004a), and included an overall plot-level increase in bird species richness, and of eight individual bird species, over this period.

Note that the primary objective of this study is to examine and interpret monitoring results: we do not aim to describe habitat associations or other factors in this paper.

Methods

Study area

This study occurred in the 20,000 km^2 Kakadu National Park in the Northern Territory, Australia. The Park comprises a broad range of environments from heathlands on sandstone plateaux and escarpments through lowland woodlands and open forests to coastal floodplains. Monitoring plots were selected, prior to this study, to sample representatively across the park and its terrestrial environments: more detail of the overall monitoring program's design and history is provided in Edwards *et al*. (2003) and Russell-Smith *et al*. (2009).

The study area is characterised by a strongly season (monsoonal) climate, with most (ca. 80-90%) of the annual rainfall (mean 1547 mm for Jabiru airport – Bureau of Meteorology http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=139&p_display_type=dataFile&p_startYear=&p_c=&p_stn_num=014198) falling in the wet season from November to April. Temperatures are high year-round. Rainfall over the course of the study period was highly variable, with notably high tallies in 2006 (2100 mm) and 2007 (2623 mm) and low tallies in 2002 (1230 mm) and 2009 (1056 mm).

There were no marked management changes in Kakadu National Park over the course of this monitoring period, although park managers achieved some gradual reduction in the occurrence of extensive late dry season fires (Russell-Smith *et al*. 2009).

Bird monitoring

Bird sampling was conducted in a series of 1 ha (100 m x 100 m) plots, each encompassing the 50 m x 50 m quadrat used for sampling mammals. Every 1 ha plot was sampled for birds on eight occasions over a continuous 3-4 day period, with most sampling undertaken within 1-2 hr of dawn. All birds seen or heard within the plot were identified and counted in an instantaneous (“snapshot”) census. In practice, this could take up to 5 mins, but birds entering the plot during this period were not counted. Birds flying through or over the plot were not included, unless these were hawking or hunting. All plots were also sampled twice at night for a 10 min period, using spotlights. The total number of birds recorded across the ten samples was tallied as a measure of the abundance of every species in every plot. The total number of bird species across the ten samples was also tallied for every plot. Bird sampling was undertaken by a set of observers all with at least a decade of experience of sampling birds in this environment. This high level of observer experience, the repeated sampling of individual plots to derive a summed abundance measure, and the frequent use of more than one observer in that repeated sampling of individual plots is considered to have helped reduce some of the inherent “noise” in terrestrial bird sampling (Lindenmayer *et al*. 2009).

As designed initially (for plants), the monitoring program was based on a 5-year rotation, commencing in 1996. However, the logistics of fauna sampling proved more challenging than for plants. Sampling of fauna in monitoring plots commenced in 1996, but few plots were sampled in that year or the five years thereafter. For most plots initial sampling of fauna occurred in the period 2001 to 2004 (not all plots could be sampled within any single year). Sampling of plots was undertaken in most months, but in every case re-sampling of plots (typically five years after initial sampling, but in some cases up to seven years) occurred in the same month (or within one month) of the original sampling time. For this paper, we restrict consideration to the 136 plots that were sampled once in the period 2001-04 and again in the period 2007-09.

Fire and toads

The fire history of all plots was assessed in each year of the monitoring program through both satellite imagery and regular visits to the plots by Kakadu ranger staff (Russell-Smith *et al*. 2009). Here, we consider only two parameters in that history, the number of years in which the plot burned between the baseline and subsequent bird sampling, and the number of years in which the plot experienced a late dry season fire over this period. This latter parameter is of interest because such fires tend to burn at higher intensity and are more extensive and less patchy, and hence are presumed to have more serious impacts on many plant and animal species (Williams *et al*. 1998; Russell-Smith and Edwards 2006; Yates *et al*. 2008; Edwards and Russell-Smith 2009; Perry *et al*. 2011). Analyses relating these fire parameters to trends in bird numbers used both the number of years that the plot was burned and also the proportion of years in which the plot burned, recognising that the between-sampling period was typically five years but extended to seven years in a small proportion of plots.

Cane toads colonised the south-east of Kakadu National Park in 2001 (Watson and Woinarski 2003), and extended incrementally to encompass all of the mainland sections of the Park over the following 3-4 years. The timing of arrival of toads at any of our monitoring sites was not necessarily precisely determinable, as often a few "pioneer" toads arrived at a site one or several years before the main toad "front". With due regard to this imprecision, we attempted to categorise plots as already colonised by toads at the first sampling or not yet colonised by toads at the first sampling, based on information supplied by rangers and traditional Aboriginal land-owners, and our observations at the time of initial sampling. Cane toads were present at all plots at the time of our second sampling.

Analysis

To compare the results of this bird monitoring most directly with that already reported for mammal monitoring of these same plots, we largely follow the analyses described for the mammal monitoring (Woinarski *et al.* 2010).

For all bird species recorded from five or more plots (and bird richness and the total number of individual birds), we use Wilcoxon matched-pairs tests to compare abundance in the 2001-04 period with that in the re-sampling of the same plots during the 2007-09 period. Matched-pairs testing is relatively powerful in that it removes from consideration that variation associated with environmental differences between plots (Siegel 1956). This analysis was also repeated for two composite groups of birds, finches and quails (including button-quail), because these groups included several species that were recorded too infrequently to assess individually and because these groups may be particularly susceptible to several threatening factors (fire regimes, grassy weeds, feral herbivores and feral cats).

For every species in every plot in which it was recorded, we calculated a simple measure of change as $A_{T1} – A_{T0}$, where A_{T1} is the abundance of that species in that plot at the most recent sampling and A_{T0} is the abundance of that species in that plot at the previous sampling. Across the set of plots in which the species was recorded, this index was related to the percentage of years with fire and the percentage of years with late dry season fires in the between-sampling period, using Spearman correlation.

The extent of change in bird abundance was compared between the set of plots in which cane toads were already present at the "baseline" sampling and that set of plots in which toad arrival occurred between the baseline and subsequent sampling. Analysis used Mann-Whitney U tests on the change index described in the above paragraph.

Change in the richness and total abundance of birds was compared with that for mammals at the same plots over the same period, using Spearman correlation; and with change indices standardised to vary from -1 (individuals present at time T0 but no individuals present at time T1) to +1 (individuals present at time T1 but no individuals present at time T0), using the formula

$$(A_{T1} – A_{T0})/(A_{T1} + A_{T0}).$$

Results

A total of 138 bird species was recorded in plots across the monitoring program (Table 1). Of these, 91 species were recorded from at least five of those 136 plots sampled in the period 2001-04 and re-sampled in the period 2007-09.

Bird species richness, total abundance and the abundance of 17 species (pied imperial-pigeon (*Ducula bicolor*), nankeen night-heron (*Nycticorax caledonicus*), whistling kite (*Haliastur sphenurus*), black kite (*Milvus migrans*), brown goshawk (*Accipiter fasciatus*), rainbow lorikeet (*Trichoglossus haematodus*), varied lorikeet (*Psitteuteles versicolor*), barking owl (*Ninox connivens*), forest kingfisher (*Todiramphus macleayii*), black-tailed treecreeper (*Climacteris melanura*), striated pardalote (*Pardalotus striatus*), white-throated honeyeater (*Melithreptus albogularis*), silver-crowned friarbird (*Philemon argenticeps*), black-faced cuckoo-shrike (*Coracina novaehollandiae*), white-bellied cuckoo-shrike (*Coracina papuensis*), Torresian crown (*Corvus orru*) and mistletoebird (*Dicaeum hirundinaceum*)) increased significantly between the 2001-04 sampling and the 2007-09 sampling. The abundance of three species (partridge pigeon, red-backed fairy-wren (*Malurus melanocephalus*) and white-throated grass-wren (*Amytornis woodwardi*)) decreased significantly over this period.

There was relatively little relationship across plots between change in the abundance of individual species and the fire history of the plots between sampling events (Table 2). Grey butcherbird (*Cracticus torquatus*) was more likely to show increase in plots that were more frequently burnt, and rufous-banded honeyeater (*Conopophila albogularis*) was more likely to decrease in such plots; black-tailed treecreeper and magpie-lark (*Grallina cyanoleuca*) were more likely to increase in plots that had a higher proportion of late dry season fires, and varied lorikeet, long-tailed finch (*Poephila acuticauda*) and total finches were more likely to decrease in such plots. There was no significant correlation across plots between the extent of change in either bird species richness or the total number of birds and the frequency of fires or late dry season fires (Table 2). Change in the number of individual bird species showed a humped relationship with the number of fires, but the relationship was not significant (Fig. 2).

The number of bird species was significantly more likely to increase in those plots for which the monitoring period included the arrival of cane toads than in those plots for which initial sampling was subsequent to cane toad arrival (Table 3). This pattern was also evident for eight individual bird species, and the reverse was the case for four species.

There was no significant correlation across plots in the trends for mammals and for birds, either for species richness (r_s=0.10, p=0.36) or for the total number of individuals (r_s=0.07, p=0.40).

There was little commonality in the trends observed in Kakadu and those reported for Cape York Peninsula (Table 4). In contrast to the Kakadu trends, for terrestrial birds, more species declined (15) than increased (9) over the monitoring period in Cape York Peninsula. For individual species there was little similarity in trends: forest kingfisher, white-throated honeyeater and white-bellied cuckoo-shrike increased in both areas; no species declined significantly in both areas; black kite, rainbow lorikeet and striated pardalote declined in Cape York Peninsula but increased in Kakadu; and many species changed significantly in one area but showed no significant trend in the other.

Likewise, there was little commonality in trends for individual bird species reported for Kakadu during this monitoring period and those for Litchfield National Park for the 1995-96 to 2001-02 period. For Litchfield, nine species increased significantly in abundance, and no species showed significant decrease. Of the nine species showing significant increase in Litchfield over this period, only one (whistling kite) also showed significant increase in Kakadu in the somewhat later monitoring period reported here.

Discussion

The most striking result of this study was that the monitoring results for birds showed remarkably little similarity to the overwhelmingly negative trends reported for mammals across the same set of sites and the same time frame. Indeed, the per-plot species richness and total abundance of birds increased significantly over this monitoring period and far more individual bird species increased than decreased. This affords some level of conservation relief, indicating that the reported declines of native mammals are not symptomatic of a pervasive ecological collapse affecting the area's biodiversity, but rather are a consequence of some factor(s) that are far more narrowly specific in their impact.

Do the results observed here for birds provide any inference on the factors that caused the decline of mammals in Kakadu over the period of this monitoring program? Almost inevitably, such comparison can provide only weak inference. In this case, the marked contrast between bird and mammal trends offers some support for a taxonomically-specific primary cause (such as disease), less support for predation (such as by feral cats), and even less support for environmental change associated with fire regimes, weeds or feral herbivores, because the latter factors would be more likely to also subvert bird assemblages. However, we note that this study reported declines for some ground-dwelling and/or granivorous species (such as partridge pigeon and white-throated grass-wren) that may be ecologically analogous to some declining mammal species, and are likely to be susceptible to changes in fire regime, weed invasion and predation by feral cats.

While far more bird species increased than decreased during this monitoring period, we note the important caveat that two of those three decreasing species (partridge pigeon, white-throated grass-wren) were the only threatened species for which we had sufficient records for analysis.

Indeed, a weakness of this study is that so few of Kakadu's threatened bird species were recorded with sufficient frequency to provide evidence of trends. Of bird species listed as threatened under Australian or Northern Territory legislation, and known to occur in Kakadu (Woinarski *et al*. 2007), we did not record gouldian finch (*Erythrura gouldiae*), red goshawk (*Erythrotriorchis radiatus*), crested shrike-tit (*Falcunculus frontatus whitei*), masked owl (*Tyto novaehollandiae kimberli*), yellow chat (*Ephthianura crocea tunneyi*) or Australian bustard (*Ardeotis australis*) in any plots, and we recorded emu (*Dromaius novaehollandiae*) from only one plot. For some of these species, significant decline may have preceded the initiation of the monitoring period described here (e.g. Franklin 1999; Franklin *et al*. 2005), with that earlier decline causing the sparsity of records that obscured our analysis of current trends for these species. The significant decline for the two most frequently recorded threatened species is of concern, and suggests that while there was an overall increase in the terrestrial bird fauna of Kakadu over this monitoring period, this does not necessarily equate to increase in conservation value, nor progress towards the biodiversity objectives set in the Park's Plan of Management (Director of National Parks 2007). The lack of, or insufficient, records for the other threatened bird species is also of some conservation concern. It suggests, at least, that the "ambient" monitoring program described here needs to be complemented by more targeted monitoring designed specifically to assess trends in these individual threatened species.

The set of species that increased over this monitoring period is heterogeneous, and no single factor is likely to have caused such observed increase across this diverse set. With the due caveat that this is a correlative study, we can offer plausible explanations for some of the observed changes. Several nectarivorous species (notably rainbow lorikeet, varied lorikeet, white-throated honeyeater and silver-crowned friarbird) increased in abundance over the monitoring period. This is most likely due to episodes of prolific flowering in the sampled area during one or more years of the re-sampling period, with regional influxes of nectarivores (notably including varied lorikeet) being a reported feature of monsoonal Australia in some years (Woinarski and Tidemann 1991; Franklin 1996; Franklin and Noske 1999). However we note that no such significant changes were observed for other nectarivorous species in this study (Table 1): in some cases, this may be because etheir pattern of movement and population fluctuation operates over a spatial scale that is more localised than regional (Morton and Brennan 1991; Franklin and Noske 1999). We have no plausible explanation for the observed marked increase in the mistletoebird.

The timing of this monitoring program provided an imperfect setting for an assessment of the short-term responses of birds to the arrival and proliferation of cane toads in Kakadu. For some plots, our baseline sampling occurred shortly (two years) before the arrival of cane toads, and in other plots the baseline sampling occurred shortly after the arrival of cane toads. We attempted to seek differences in the trends from these two plot categories, but the observed differences between these categories in the responses by bird species (Table 3) seem to make little ecological sense. Given that bird populations are likely to take several years to respond (if at all) to the establishment of toads, we consider that the distinction we sought was blurred, with both plot types essentially measuring short-term (<10 years) response to cane toad arrival. Notwithstanding the lack of insight from this particular analysis, we consider that overall trends for some bird species across the set of monitoring sites over the span of this monitoring period are most likely to be responses to the colonisation of Kakadu by cane toads. A series of carnivorous species and scavengers (including nankeen night-heron, whistling kite, black kite, brown goshawk, forest kingfisher and Torresian crow) increased over the monitoring period. We speculate that this may be a response to the invasion of the Kakadu area by the cane toad, manifested either by the additional food resource provided directly by the superabundance of toads (for those species that could "safely" consume toads), increase in carrion arising from the poisoning of other vertebrate taxa affected by toads (such as carnivorous mammals, varanid lizards and some snakes), or increase in carrion availability due to marked reduction in those competitors poisoned by toads. In contrast, there was little signal in our results that ground-nesting and ground-foraging birds may have benefited from predator reduction caused by the arrival of toads: for example, the partridge pigeon, red-backed fairy-wren and white-throated grass-wren decreased significantly over this monitoring period, although the ground (tunnel)-nesting striated pardalote increased.

We note that this study offers no proof that the observed increase in carrion-feeding and carnivorous bird species is a consequence of the arrival of cane toads: just as the observed increase in nectarivorous birds is probably due to particular climate characteristics and phenological conditions between years, so too may the increase in carrion-feeding and carnivorous bird species be due to influxes associated with weather conditions in the region or beyond it.

There was little commonality in the results of this study and a comparably-timed monitoring study of birds in Cape York Peninsula (Perry *et al*. 2011). This may suggest that bird trends are highly influenced by local-scale factors, for example with tendency for bird populations to increase in well-managed conservation reserves but not in land tenures managed for other outcomes (Watson *et al*. 2011). Alternatively, it may simply reflect that the monitoring period (for both studies) is too brief to detect longer-term changes, instead simply picking up more chaotic short-term responses to climatic variations or other transient factors.

With a few exceptions, the trends reported here for birds showed no strong relationship with the fire history of plots between the baseline and subsequent sampling, again in contrast to the results reported for mammals (Woinarski *et al*. 2010), but consistent with the similar limited response of birds to between-sampling fire history in an analogous analysis of monitoring data at Litchfield National Park (Woinarski *et al*. 2004a). The subdued response for birds is consistent with some previous studies that have suggested relative resilience of this region's fauna to a broad range of fire regimes (e.g. Woinarski *et al*. 1999; Corbett *et al. 2003;* Andersen *et al*. 2005), but is inconsistent with other studies that have shown marked responses of some bird species to contrasting fire regimes (Woinarski 1990; Woinarski *et al*. 2004b). The disparity is due in part to the duration of studies, with studies relating to fire regimes imposed over longer periods (at least ten years) far more likely to detect significant fire-associated responses by bird species than those relating to shorter time spans, such as in this monitoring period. Of the few associations observed in this study, we note that the observed trend for increase of grey butcherbird in association with increased fire frequency is broadly consistent with results reported elsewhere in northern Australia (e.g. Woinarski and Ash 2002), and that decrease of long-tailed finch (and finches in general) with frequency of late dry season fires is consistent with some previous studies suggesting that such granivorous birds may be disadvantaged by frequent extensive and intense fires (e.g. Woinarski 1990; Fraser *et al*. 2003).

Many proponents assert that the species-group in which they are most interested provides the most ideal focus for environmental monitoring. The claim has been made frequently for birds (see e.g. Mac Nally *et al*. 2004). The comparison reported here suggests that single species-groups are unlikely to be representative of biodiversity more generally, and hence that the most robust foundations for any monitoring program will be provided when it represents biodiversity most comprehensively. The contrast reported here between birds and mammals should also serve to hone conservation management in this region to those aspects of biodiversity that are declining most severely, rather than attempting to smear conservation management effort across all taxonomic groups.

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Table 1. Trends in abundance of individual species between sampling in 2001-04 ("baseline") and re-sampling of the same plots in 2007-09. Z is z-score from Wilcoxon matched-pairs test; p is probability. Note that the body of the table only includes species recorded from five or more plots, and that mean abundance is calculated across all 136 sampled plots.

Scientific name	Common name	mean abundance		no. plots	Z	p
		baseline	re-sample			
Megapodius reinwardt	Orange-footed Scrubfowl	0.04	0.10	7	1.35	0.18
Coturnix ypsilophora	Brown Quail	0.09	0.04	7	0.25	0.80
Chalcophaps indica	Emerald Dove	0.04	0.01	5	0.94	0.35
Phaps chalcoptera	Common Bronzewing	0.07	0.10	10	0.07	0.94
Geophaps smithii	Partridge Pigeon	0.24	0.05	12	2.43	0.02
Petrophassa rufipennis	Chestnut-quilled Rock-Pigeon	0.34	0.23	25	0.83	0.40
Geopelia striata	Peaceful Dove	2.02	2.39	98	1.87	0.06
Geopelia humeralis	Bar-shouldered Dove	1.55	1.85	75	1.91	0.06
Ptilinopus cinctus	Banded Fruit-dove	0.05	0.08	12	0.59	0.56
Ducula bicolor	Pied Imperial Pigeon	0.01	0.12	6	2.02	0.04
Podargus strigoides	Tawny Frogmouth	0.06	0.05	14	0.22	0.83
Eurostopodus argus	Spotted Nightjar	0.01	0.08	5	1.62	0.11
Aegotheles cristatus	Australian Owlet-nightjar	0.05	0.07	15	0.60	0.55
Nycticorax caledonicus	Nankeen Night Heron	0.01	0.19	5	2.02	0.04
Haliastur sphenurus	Whistling Kite	0.19	0.52	42	3.16	0.002
Milvus migrans	Black Kite	0.01	0.32	12	2.71	0.007
Accipiter fasciatus	Brown Goshawk	0.01	0.08	11	1.96	0.05
Aquila audax	Wedge-tailed Eagle	0.01	0.05	6	1.36	0.17
Falco berigora	Brown Falcon	0.04	0.07	10	0.71	0.48
Burhinus grallarius	Bush Stone-curlew	0.02	0.02	6	0	1.00
Calyptorhynchus banksii	Red-tailed Black-cockatoo	0.14	0.10	10	0.89	0.37
Eulophus roseicapilla	Galah	0.25	0.17	10	0.10	0.92
Cacatua sanguinea	Little Corella	0.12	0.96	10	1.48	0.14
Cacatua galerita	Sulphur-crested Cockatoo	0.37	0.57	42	1.83	0.07
Trichoglossus haematodus	Rainbow Lorikeet	1.37	2.56	61	2.74	0.01
Psitteuteles versicolor	Varied Lorikeet	0.04	2.39	13	2.90	0.004
Aprosmictus erythropterus	Red-winged Parrot	0.51	0.57	51	0.60	0.55
Platycercus venustus	Northern Rosella	0.26	0.43	31	1.67	0.10
Centropus phasianinus	Pheasant Coucal	0.21	0.12	22	1.51	0.13
Eudynamys orientalis	Eastern Koel	0.01	0.06	5	1.08	0.28
Cacomantis variolosus	Brush Cuckoo	0.09	0.22	16	1.08	0.28
Ninox connivens	Barking Owl	0.01	0.07	6	2.20	0.03
Ninox novaeseelandiae	Southern Boobook	0.04	0.04	10	0.25	0.80
Ceyx azureus	Azure Kingfisher	0.06	0.02	6	1.48	0.14
Dacelo leachii	Blue-winged Kookaburra	0.40	0.47	54	0.63	0.53
Todiramphus macleayii	Forest Kingfisher	0.35	0.65	41	2.45	0.01

Scientific name	Common name	mean abundance		no. plots	Z	p
		baseline	re-sample			
Todiramphus sanctus	Sacred Kingfisher	0.04	0.04	10	0.05	0.96
Merops ornatus	Rainbow Bee-eater	0.82	1.04	53	1.75	0.08
Eurystomus orientalis	Dollarbird	0.05	0.07	13	0.63	0.53
Climacteris melanura	Black-tailed Treecreeper	0.12	0.38	19	2.19	0.03
Ptilonorhynchus nuchalis	Great Bowerbird	0.40	0.33	46	0.61	0.54
Malurus melanocephalus	Red-backed Fairy-wren	0.90	0.54	33	2.20	0.03
Malurus lamberti	Variegated Fairy-wren	0.29	0.43	17	1.35	0.18
Amytornis woodwardi	White-throated Grasswren	0.09	0	6	2.20	0.03
Smicrornis brevirostris	Weebill	2.23	2.65	72	1.15	0.25
Gerygone chloronota	Green-backed Gerygone	0.09	0.25	11	0.80	0.42
Gerygone albogularis	White-throated Gerygone	0.01	0.07	6	1.78	0.07
Pardalotus striatus	Striated Pardalote	1.15	1.85	73	2.48	0.01
Meliphaga albilineata	White-lined Honeyeater	0.62	0.73	36	0.35	0.73
Lichenostomus unicolor	White-gaped Honeyeater	0.62	0.88	30	1.28	0.20
Manorina flavigula	Yellow-throated Miner	0.29	0.19	8	0.08	0.93
Conopophila albogularis	Rufous-banded Honeyeater	0.54	0.21	11	0.89	0.37
Myzomela obscura	Dusky Honeyeater	0.60	0.79	48	0.71	0.48
Cissomela pectoralis	Banded Honeyeater	0.04	0.26	8	1.12	0.26
Lichmera indistincta	Brown Honeyeater	3.99	3.43	86	0.47	0.64
Melithreptus albogularis	White-throated Honeyeater	1.88	3.03	79	2.99	0.002
Entomyzon cyanotis	Blue-faced Honeyeater	0.44	0.37	30	0.70	0.48
Philemon buceroides	Helmeted Friarbird	1.01	0.82	47	1.35	0.18
Philemon argenticeps	Silver-crowned Friarbird	1.36	2.17	79	2.39	0.02
Philemon citreogularis	Little Friarbird	0.74	0.76	39	1.24	0.22
Pomatostomus temporalis	Grey-crowned Babbler	0.54	0.29	18	1.35	0.18
Coracina novaehollandiae	Black-faced Cuckoo-shrike	0.23	0.58	38	1.99	0.05
Coracina papuensis	White-bellied Cuckoo-shrike	0.80	1.07	77	1.96	0.05
Coracina tenuirostris	Cicadabird	0.04	0.03	8	0.28	0.78
Lalage sueurii	White-winged Triller	0.15	0.40	20	1.74	0.08
Lalage leucomela	Varied Triller	0.37	0.29	28	0.31	0.76
Pachycephala rufiventris	Rufous Whistler	0.74	0.65	55	0.52	0.61
Colluricincla woodwardi	Sandstone Shrike-thrush	0.26	0.18	24	0.92	0.36
Colluricincla harmonica	Grey Shrike-thrush	0.10	0.07	16	0.57	0.57
Sphecotheres vieilloti	Australasian Figbird	0.19	0.04	7	0.68	0.50
Oriolus flavocinctus	Yellow Oriole	0.43	0.45	27	0.14	0.89
Oriolus sagittatus	Olive-backed Oriole	0.02	0.04	5	0.67	0.50
Artamus leucorynchus	White-breasted Woodswallow	0.11	0.38	20	1.27	0.20
Artamus minor	Little Woodswallow	0.20	0.56	18	1.50	0.13
Cracticus torquatus	Grey Butcherbird	0.23	0.15	7	0.68	0.50
Cracticus nigrogularis	Pied Butcherbird	0.37	0.35	32	0.83	0.40
Dicrurus bracteatus	Spangled Drongo	0.54	0.59	46	0.41	0.68
Rhipidura rufiventris	Northern Fantail	0.46	0.61	52	0.69	0.49

Scientific name	Common name	mean abundance		no. plots	Z	p
		baseline	re-sample			
Rhipidura leucophrys	Willie Wagtail	0.29	0.30	32	0.18	0.86
Corvus orru	Torresian Crow	0.40	0.92	51	2.53	0.01
Myiagra rubecula	Leaden Flycatcher	0.35	0.40	36	0.93	0.35
Myiagra alecto	Shining Flycatcher	0.05	0.09	7	1.15	0.25
Myiagra inquieta	Restless Flycatcher	0.13	0.18	15	0.75	0.45
Grallina cyanoleuca	Magpie-lark	0.21	0.13	15	0.80	0.43
Microeca flavigaster	Lemon-bellied Flycatcher	0.23	0.21	18	0.43	0.67
Cisticola exilis	Golden-headed Cisticola	0.35	0.53	17	0.28	0.78
Petrochelidon ariel	Fairy Martin	0.26	0.36	6	0.94	0.35
Dicaeum hirundinaceum	Mistletoebird	1.35	2.15	113	3.46	0.001
Taeniopygia bichenovii	Double-barred Finch	0.42	0.32	28	1.00	0.32
Poephila acuticauda	Long-tailed Finch	0.22	0.04	7	1.10	0.27
Neochmia phaeton	Crimson Finch	0.36	0.16	11	0.71	0.48
	bird species richness	11.7	13.1		2.01	0.04
	total individual birds	38.9	51.9		4.16	0.001
	total quails	0.13	0.05		0.56	0.58
	total finches	1.05	0.57		0.95	0.34

Species recorded from fewer than five plots: Arafura Fantail (2 plots), Australian Hobby (1), Australian Reed-warbler (2), Australian White Ibis (4), Bar-breasted Honeyeater (4), Black Bittern (1), Black-breasted Buzzard (1), Black-faced Wood-swallow (4), Brown Songlark (1), Buff-banded Rail (2), Chestnut-backed Button-quail (1), Chestnut-breasted Mannikin (2), Diamond Dove (1), Eastern Great Egret (1), Emu (1), Fork-tailed Swift (2), Grey Whistler (3), Hooded Robin (1), Intermediate egret (1), Jacky Winter (1), King Quail (1), Large-tailed Nightjar (1), Little Bronze-cuckoo (2), Little Egret (2), Little Shrike-thrush (2), Magpie Goose (1), Masked Finch (3), Nankeen Kestrel (4), Oriental cuckoo (1), Pacific Baza (2), Pallid Cuckoo (3), Peregrine Falcon (3), Pied Heron (1), Rainbow Pitta (2). Red-backed Button-quail (1), Red-backed Kingfisher (3), Rose-crowned Fruit-dove (2), Straw-necked Ibis (2), Tawny Grassbird (3), Tree Martin (3), Varied Sittella (1), White-breasted Sea-eagle (3), White-browed Crake (1), White-browed Robin (1), Yellow White-eye (2), Yellow-billed Spoonbill (1), Zitting Cisticola (1).

Table 2. Significant correlations across plots between the change in the abundance of individual species and the fire frequency in those plots in the years between baseline and subsequent sampling.

fire parameter	positive correlation		negative correlation	
	species	r	species	r
% of years with fire	grey butcherbird	0.85 *	rufous-banded honeyeater	-0.76 **
% of years with late dry season fire	black-tailed treecreeper	0.47 *	varied lorikeet	-0.66 **
	magpie-lark	0.52 *	long-tailed finch	-0.84 *
			total finches	-0.33 *

Table 3. Comparison between changes in mean abundance at plots in which toads were present at the initial sample and plots at which toads invaded between the initial and subsequent sample. Note that, except for species richness and the total number of birds, this tabulation only includes those species for which p<0.01.

Common name	change in abundance		z	p
	toads initially absent (N=58)	toads initially present (N=78)		
Australian Owlet-nightjar	0.86	-0.38	1.99	0.05
Red-winged Parrot	1.75	-0.57	2.74	0.006
Eastern Koel	0.33	3.00	1.78	0.08
Barking Owl	2.00	1.00	2.24	0.03
Dollarbird	-0.57	1.17	2.25	0.02
Great Bowerbird	0.50	-0.57	1.72	0.09
Dusky Honeyeater	2.35	-0.45	1.76	0.08
Brown Honeyeater	-5.09	2.00	3.84	0.0001
White-throated Honeyeater	2.98	0.86	1.88	0.06
Silver-crowned Friarbird	2.89	0.62	2.20	0.03
Grey-crowned Babbler	-3.62	2.60	2.47	0.01
Sandstone Shrike-thrush	1.67	-0.81	2.05	0.04
Grey Shrike-thrush	0.27	-1.40	2.43	0.01
White-breasted Woodswallow	6.25	-6.50	2.09	0.04
Grey Butcherbird	-5.20	8.00	1.94	0.05
Pied Butcherbird	1.08	-0.75	1.61	0.10
Double-barred Finch	0.67	-1.85	1.97	0.05
bird species richness	3.29	-0.08	3.29	0.001
total individual birds	14.2	12.2	0.97	0.33
total finches	-0.42	-3.67	2.23	0.03

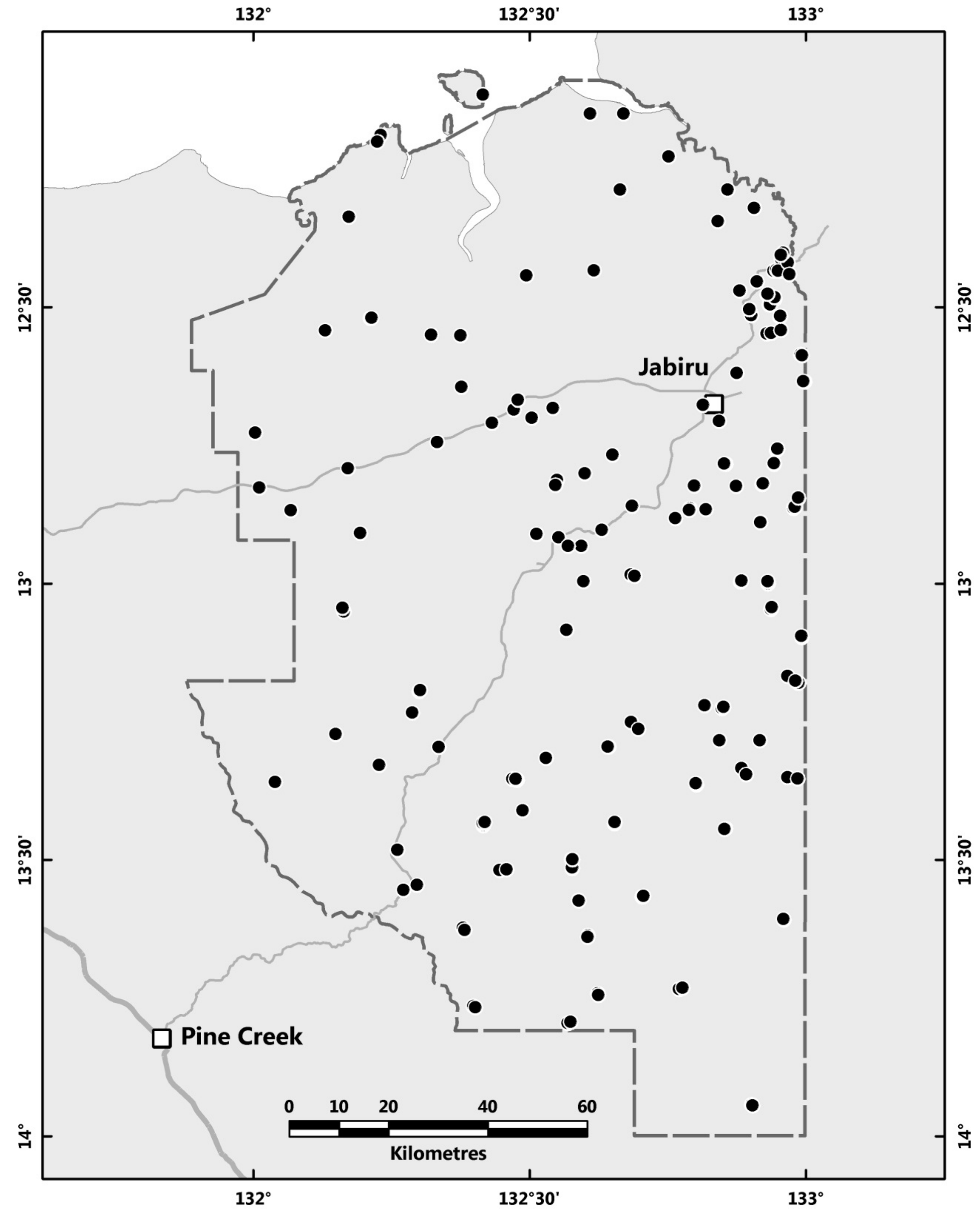
Table 4. Comparison of trends reported here with trends reported for comparable period for birds on Cape York Peninsula ["CYP"] (Perry *et al*. 2011). Note that this table only includes those terrestrial bird species that showed a significant change in one or more of the two areas.

		Kakadu			
		sig. increase	no change	sig. decrease	recorded from too few sites
	sig. increase	forest kingfisher, white-throated honeyeater, white-bellied cuckoo-shrike	peaceful dove, pheasant coucal, weebill, lemon-bellied flycatcher, spangled drongo, yellow oriole		
CYP	no change	pied imperial pigeon, whistling kite, brown goshawk, varied lorikeet, barking owl, black-tailed treecreeper, silver-crowned friarbird, black-faced cuckoo-shrike, Torresian crow, mistletoebird	*many species*	red-backed fairy-wren	
	sig. decrease	black kite, rainbow lorikeet, striated pardalote	bush stone-curlew, bar-shouldered dove, galah, sulphur-crested cockatoo, rainbow bee-eater, banded honeyeater, blue-faced honeyeater, magpie-lark		black-breasted buzzard, Australian bustard, pale-headed rosella, brown treecreeper
	recorded from too few sites			partridge pigeon, white-throated grass-wren	

Figure captions

Figure 1. Kakadu National Park, showing location of all monitoring plots.

Figure 2. Relationship between change in the total number of birds observed in a plot from the baseline to subsequent sampling and the fire history (number of years in which fire occurred) of that plot in the intervening period. Filled squares represent means, with whiskers denoting standard errors.



132°
132°30'
133°
12°30'
13°
13°30'
14°
Jabiru
Pine Creek
0
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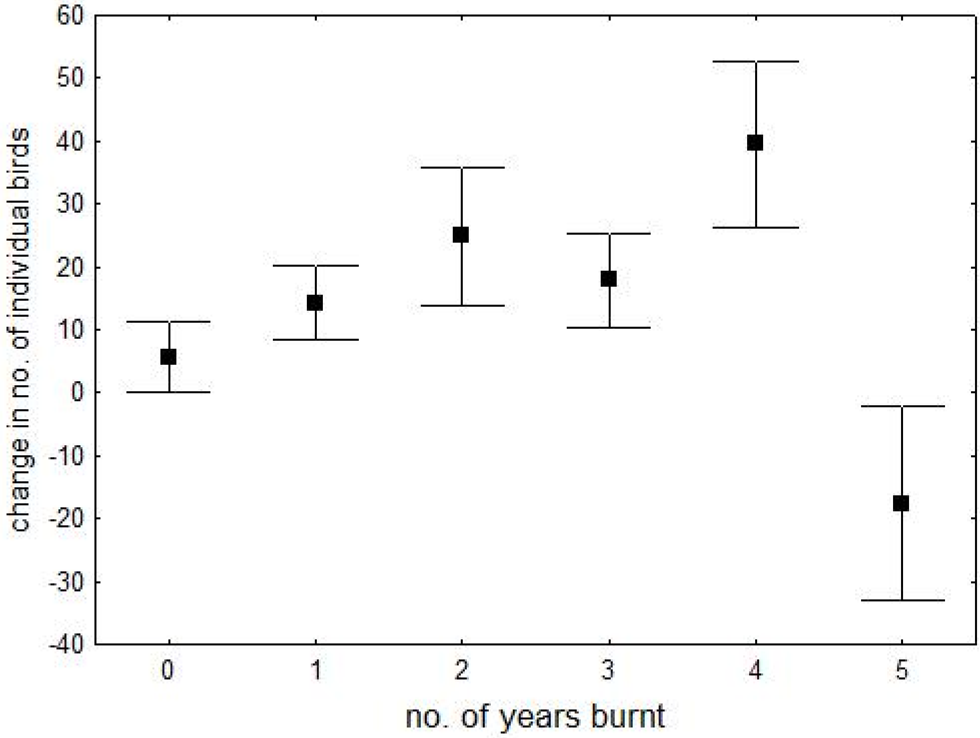
Kilometres



60
50
40
30
20
10
0
-10
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-40
change in no. of individual birds
0
1
2
3
4
5
no. of years burnt