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Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape

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Abstract

Where threatened species persist in multiple use landscapes, management activities, such as prescribed burning, may influence the availability of resources for those species. We examined how time since fire can influence food resources for the endangered Carnaby's cockatoo (*Calyptorhynchus latirostris*) in banksia woodlands of southwestern Australia. Tree density and cone productivity of dominant plant species, *Banksia attenuata* and *B. menziesii*, were compared across 44 sites of varying post-fire aged vegetation. The number of Carnaby's cockatoos that could be supported in banksia woodlands was estimated using the bird's energetic requirements and seed energy content. *Banksia attenuata* produced more cones at sites aged 10–30 years since fire in both survey years, while cone productivity for *B. menziesii* was highest in very old sites (>35 years since fire) in one year only. Higher numbers of Carnaby's cockatoos were predicted to be supported in vegetation aged between 14-30 years since fire, peaking in vegetation aged 20–25 years. The current distribution of post-fire aged vegetation within this area (>60% burnt within the last 7 years) is predicted to support ~2725 Carnaby's cockatoos, representing 25–35% of the estimated birds reliant on the area. Our results indicate that food resources are influenced by time since fire and, consequently, if optimising food resources was an objective, may be manipulated by altering burning patterns. While human and asset protection is a priority for prescribed burning, management of landscapes for improved persistence of threatened species is also important and complex trade-offs will have to be considered.

Key words: fire; prescribed burn; fire management; resource availability; threatened species; banksia woodland; bird conservation; Carnaby's cockatoo

1. Introduction

Species distribution patterns are generally influenced by the spatial availability of resources required for persistence (Mortelliti et al., 2010), and the abundance and distribution of these resources can be altered or manipulated by landscape management activities (Lindenmayer et al., 2013; Nappi and Drapeau, 2009; Valentine et al., 2012a). Where landscapes have undergone extensive habitat loss, the continued existence of threatened fauna may be dependent on high resource availability in remaining vegetation (e.g. adequate food, water, refuge resources and facilitation of movement patterns). Understanding how management actions affect resource availability for threatened species will therefore assist with more informed conservation decision-making, especially in landscapes with multiple-management objectives. In this paper, we examine how time since fire influences food resource availability for an endangered bird in a fragmented fire-prone landscape.

Fire plays a major role in maintaining the structure and function of ecosystems and is a broadly utilised management tool, implemented by humans for a variety of purposes (Burrows and McCaw, 2013; Fernandes and Botelho, 2003). Fire can substantially alter vegetation structure and diversity, in turn altering resource availability for fauna (Brawn et al., 2001; Haslem et al., 2012; Valentine et al., 2012b). Where fire influences the reproductive outputs of plants, it is also likely to influence the availability of food for species that feed upon these elements, such as nectar, fruits and seeds (Brawn et al., 2001; Valentine et al., 2012b). All aspects of a fire regime (e.g. frequency, intensity, season and type as well as the spatial and temporal arrangement of fires) are likely to influence the availability of resources for fauna. The fire-free period has been demonstrated to be a key component structuring faunal communities; with species predicted to reside when appropriate habitat and resources occur in the post-fire environment (Fox, 1982; Valentine et al., 2012a).

Fire management practices will influence resource availability for fauna, requiring an understanding of the individual requirements of target species and community dynamics (Clarke, 2008; Penman et al., 2011). Habitat quality for species and the impacts of management actions on resources are strongly driven by species-specific determinants (Fox, 1982; Mortelliti et al., 2010). For example, the red-cockaded woodpecker (*Picoides borealis*) in the south-eastern United States requires regular fires to enhance the availability of suitable nesting hollows (James et al., 2001; U.S. Fish and Wildlife Service, 2003). By contrast, the endangered Australian Leadbeater's possum (*Gymnobelideus leadbeateri*) predominantly nests in hollows formed in long-unburnt, mature montane ash forests, which are a scarce commodity under current burning regimes (both wildfire and prescribed burning; Lindenmayer et al., 2013). Consequently, a critical element for successful fauna management in fire prone-ecosystems is to understand how management actions affect resource availability.

Fire and conservation management is particularly complex in fragmented peri-urban areas, where there are multiple, often conflicting, objectives to fire management (Burrows and McCaw, 2013; Driscoll et al., 2010; Penman et al., 2011). Southwestern Australia has been occupied by humans for at least 30 000 years, and Aboriginal burning patterns, that are predicted to have created a patchy mosaic of post-fire vegetation, are thought to have been in place for the past 5000 – 7000 years (Hassell and Dodson, 2003). Fire is regularly used as a contemporary landscape management tool to reduce wildfires, although the application of prescribed burning is debated (Burrows and McCaw, 2013; Enright and Fontaine, 2014). Southwestern Australia is a global biodiversity hotspot that has undergone extensive habitat loss associated with agricultural and urban development, with <30% of the original vegetation remaining (Hobbs, 1993; Mittermeier et al., 2004; Saunders, 1989). As a consequence of this habitat loss, the endemic Carnaby's cockatoo (*Calyptorhynchus latirostris*) has experienced widespread loss of nesting and feeding habitat (Saunders, 1980, 1990) and is considered Endangered (~40 000 individuals) under the IUCN redlist (BirdLife International, 2012), and

Australian federal and state legislation (Department of Environment and Conservation, 2012). Since the 1950s, the species abundance has declined by >50%, the range has contracted by >30%, and birds have disappeared from more than a third of the former breeding areas (Garnett et al., 2011; Saunders, 1990; Saunders and Ingram, 1997, 1998). Understanding how fire alters food resource availability for Carnaby's cockatoo in remnant vegetation is essential for informed conservation decisions.

Carnaby's cockatoo is a gregarious species that forages predominantly upon seeds in coastal areas during the non-breeding season (January – June), with most adults migrating to the inland wheatbelt during the Austral winter to breed (Saunders, 1980). Foraging resources are limited in both the breeding and non-breeding range for this species (Saunders, 1980, 1990). The largest population of birds during the non-breeding season occurs north of Perth (Western Australia's capital city) (Department of Environment and Conservation, 2012; Kabat et al., 2012; Saunders, 1980, 1990), one of the most rapidly growing cities in Australia. In this fragmented peri-urban and rural environment, birds feed on seed from dominant native species *Banksia attenuata* and *B. menziesii* in remnant native vegetation, the introduced maritime pine *Pinus pinaster* in plantations and other species (Finn et al., 2009; Perry, 1948; Saunders, 1980; Stock et al., 2013; Valentine and Stock, 2008). Where they occur, the plantations replaced native vegetation, and Carnaby's cockatoos have a strong ecological association with this introduced food source (explored in more detail in Stock et al., 2013). Currently, the pine plantations are being harvested and their removal will reduce food availability (Finn et al., 2009; Stock et al., 2013; Valentine and Stock, 2008) increasing the reliance on native species in this increasingly fragmented landscape. To understand how fire influences food availability in the banksia woodlands, we i) examined how time since fire influences plant and cone densities of the two dominant native woodland food species, *B. attenuata* and *B. menziesii*; ii) estimated the number of Carnaby's cockatoo that would be supported in different post-fire aged banksia woodlands, and iii) estimated the number of Carnaby's cockatoo that could be supported with the current distribution of post-fire banksia woodland habitat.

2. Methods

2.1. Study area

Our study was undertaken on the Swan Coastal Plain, north of Perth, south-western Western Australia. Sites were located on the Gnangara Groundwater System, a distinct water catchment area of approximately 220 000 ha (Fig.A.1). The area experiences a Mediterranean-type climate, with hot dry summers (December – February) and cool wet winters (June – August), with a 100 year rainfall average (1912–2012) of 801 mm (Bureau of Meteorology), although rainfall has declined significantly in the last 30 years. While loss of remnant vegetation is continuing due to urban development, large tracts of remnant vegetation (> 100 000 ha) remain on the northern outskirts of the city, ~65% of which is protected under legislation of the Western Australia Department of Parks and Wildlife (DPaW; Fig.A.1).

The majority of protected remnant vegetation is low (~5–8 m) banksia woodland (~51 914 ha; Wilson et al., in press), dominated by a mixed overstorey of *B. attenuata* and *B. menziesii*, with a diverse understorey. This vegetation is considered critical habitat for Carnaby's cockatoo, due to the potential food sources (Department of Environment and Conservation, 2012). Threats to the biodiversity values of this habitat include further habitat loss, dieback from the introduced plant pathogen *Phytophthora cinnamomi* and inappropriate fire regimes (Davis et al., 2014; Wilson et al., in press). The banksia woodlands are considered some of the most flammable in Australia (Burrows and Abbott, 2003). Within 4 years of a fire, fine fuel accumulates rapidly within banksia woodlands (stabilising at ~6 years since fire) and is sufficient to support an intense and fast moving wildfire in extreme fire weather conditions (Burrows and McCaw, 1990). To reduce the risk of wildfires to human settlements, infrastructure and pine plantations, prescribed burning is undertaken, with a median interval of ~9 years between fires (Wilson et al., in press). Due to a dense understorey, very few unburnt patches remain following a fire, and average burn sizes are ~212 ha for prescribed burns and ~383 ha for wildfires (Wilson et al., in press).

We examined the food resources provided by *B. attenuata* and *B. menziesii*, which both resprout following fire. Forty-four sites were established across a range of post-fire aged vegetation (1–40 years since fire). Fire history records, involving spatially digitising hard copy records and using Landsat imagery to accurately depict fire boundaries, over the last 39 years have been collated for the study area (Wilson et al., in press). The most recent fire events were further validated for a 1-ha polygon around each site using VegMachine (Behn et al., 2009; Wallace et al., 2006) which uses Multispectral Landsat TM imagery to detect changes in reflectance which are correlated to change in vegetation cover over time. The majority (n=28) of sites were last burnt by prescribed fires (mostly during spring), with the remainder being burnt by wildfires (n=13) or of unknown origin. Study sites were spread across the two dominant landform systems (Spearwood Dunes in the west and Bassendean Dunes in the east), aiming to cover a range of post-fire vegetation where possible. Sites established on the Bassendean landform ranged from 2–40 years since fire while sites on the Spearwood landform ranged from 1–25 years since fire. Each site was surveyed once and represents an independent replicate; 27 sites were surveyed for food availability in 2008 (Bassendean n=17; Spearwood n=10) and 17 sites were surveyed in 2010 (Bassendean n=12; Spearwood n=5).

2.2 Assessing food availability for Carnaby's cockatoos

2.2.1. Banksia density and cone production

Both *B. attenuata* and *B. menziesii* produce conspicuous terminal inflorescences, a small number of which develop into woody fruits (infructescence; hereafter "cones") following pollination (George, 1984). These cones house several follicles that contain ~2 seeds each, and take 1–2 years to mature (George, 1984). Although both species are serotinous in the northern part of their range (Enright and Lamont, 1989), neither species rely on fire for recruitment in our study area and follicles can spontaneously release seeds with or without fire (Cowling and Lamont, 1985; Hobbs and Atkins, 1990). To determine food availability at each site, we established a 25 x 25 m plot and recorded the density (plants ha^{-1}) of adult (>2 m) *B. attenuata* and *B. menziesii* plants and cone productivity (average number of cones per plant per site). Cone production was determined by counting the number of cones containing unopened follicles on five adult plants of each species.

2.2.2. How many Carnaby's cockatoos can be supported in banksia woodlands?

Based on calculations of basal metabolic rate from captive birds in a respiratory chamber, the daily energy expenditure (field metabolic rate) for Carnaby's cockatoos is estimated as 726 kJ day^{-1} (Cooper et al., 2002). Energetic and nutrient analyses of *B. attenuata* seeds indicate that Carnaby's cockatoo require ~567 seeds to meet their estimated daily field metabolic rate (Stock et al., 2013). Data on the energetics provided by seeds of *B. menziesii* were unavailable and we assumed the energetic content of *B. menziesii* to be equivalent of *B. attenuata*, although *B. menziesii* seeds are lighter (~87 mg) compared to *B. attenuata* (~105 mg) seeds (Cowling et al., 1987). To determine the average amount of seeds on a cone, we collected ~5 cones (range: 0–11, median 5 cones per site) per species from each site surveyed in 2008, and counted the number of follicles present on each cone, assuming that each follicle contained two seeds (George, 1984). From this we estimated the number of cones Carnaby's cockatoo need to meet their daily field metabolic rate for *B. attenuata* (J) and *B. menziesii* (K) based on the mean follicle number per cone for each species. For each site, we derived a response variable (Y) that estimates the number of Carnaby's cockatoo that could meet their field metabolic requirements for a year (365 days) over 100 ha of vegetation using the following equation:

Y = [[*B. attenuata* Density x Cones / J x 365 days] + [*B. menziesii* Density x Cones / K x 365 days]] x 100 ha

2.2.3. Incorporating foraging efficiency in resource use estimates

Observations indicated that Carnaby's cockatoo consume only a portion of each cone they feed upon, requiring the incorporation of foraging efficiency in our calculations to more accurately estimate the number of Carnaby's cockatoo an area could support. When feeding, Carnaby's cockatoo leave distinctive foraging trace, in the form of attacked, discarded cones, and torn flowers. During the 2008 survey, we recorded the presence of foraging trace at each site. To estimate foraging efficiency, we recorded the proportion of cone follicles removed from discarded cones. Using the equation above, we adjusted our estimates of the number of cones required to meet the field metabolic rate of Carnaby's cockatoos (J^F and K^F), deriving a new response variable that incorporates foraging efficiency (Y^F). Carnaby's cockatoo will nearly deplete the entire annual production of cones in pine plantations (Stock et al., 2013). Unfortunately there is no information on the proportion of cones per banksia tree that cockatoos forage upon, and our estimates assume the birds forage upon all available cones.

2.3. Statistical analyses

Data are presented as means with ±95% confidence interval (CI) throughout. Generalised Additive Models (GAM; Wood, 2006; Zuur et al., 2009) were used to examine the effect of time since fire, landform system and year of survey on our six response variables: *B. attenuata* density and cone productivity, *B. menziesii* density and cone productivity, the number of Carnaby's cockatoo supported in 100 ha of banksia woodland (*Y*), and the number of Carnaby's cockatoo supported in 100 ha of banksia woodland adjusted for foraging efficiency (Y^F). We used GAMs, rather than assuming linear fits, as scatterplots indicated there may be nonlinear relationships with the continuous time since fire variable. GAM models were fit using the gam function of the mgcv package in R (version 2.15.2, R Core Team, 2012).

The importance of time since fire (fitted as a penalized regression spline) and the two fixed predictor variables (year of survey and landform) was then explored by comparing all possible models of one, two, and three included predictors. Simplest models included a fixed predictor or a single smoother (across both years and landforms). More complex models included fixed effects for sampling year or landform (or both) and a smoother fitted to time since fire, and models representing the interaction between time since fire and either year of survey or landform (with a separate smoother for each year of survey or landform). We also included an 'intercept only' model (eleven models in total). All models were fitted using maximum likelihood (ML) estimation (Zuur et al., 2009). The set of alternative models were compared using the Bayesian Information Criterion (BIC) as well as Akaike's Information Criterion for small sample sizes (AICc; Burnham and Anderson, 2002). BIC is a measure of goodness of fit of the models similar to AICc but is more conservative (will favour simple models) than AICc as sample size increases, thereby having less tendency to 'overfit' (Burnham and Anderson, 2002). BIC/AICc values, their associated weights and adjusted R^2 values were used to select the optimal model (the most parsimonious according to AICc). BIC and AICc weights were calculated following Burnham and Anderson (2002). Observed values for each response variable were plotted against time since fire and predicted smoothers were plotted where time since fire was selected as the optimal model. All six response variables were square-root transformed, although we present the back-transformed data for the estimates of Carnaby's cockatoo that could be supported in banksia woodlands (Y and Y^F) to ease interpretation.

The distribution of post-fire ages of banksia woodlands within DPaW-managed estate (51 914 ha) in our study area was recently mapped (Wilson et al., in press). These data provide information on the actual extent of vegetation (ha) within each fire-age, and an idealised distribution of post-fire aged vegetation. Wilson et al. (in press) used the theoretical Weibull probability distribution, incorporating estimated minimum (8 – 16 years) and maximum (40 years) interfire periods, to derive an idealised distribution of post-fire aged vegetation based on plant life history attributes. Using the distribution of vegetation in each fire-age and the GAM-fit generated for response variable Y^F we estimated the total number of Carnaby's cockatoo that could be supported within the DPaW-managed banksia woodlands.

3. Results

3.1. Banksia density and cone production

All 44 sites contained *B. attenuata*, with an average density of ~248 (±37) plants ha^{-1}. Cones containing unopened follicles of *B. attenuata* were detected at every site, averaging 6.6 (±1.3) cones per plant. *Banksia menziesii* co-occurred with *B. attenuata* in all but one site, with an average density of ~187 (±30) plants ha^{-1}. We did not detect *B. menziesii* cones with unopened follicles at four sites, and sites averaged 2.8 (±1.0) cones per plant.

The density of *B. attenuata* was not well described by any of the models we examined (Table 1; Fig. 1a), with all models explaining ≤5% variation in the data, and the optimal model was the intercept-only model. In contrast, the number of cones per *B. attenuata* showed a curvilinear response (adjusted $R^2 = 0.38$) with time since fire (Table 1; Fig.1b). Fire was in all of the top ranking models of cone productivity (ΔAICc <2), and the only variable in the best model according BIC (Table 1, Fig.1b). The number of cones per plant increased with time since fire, with higher numbers detected at sites between 10 and 30 years since fire (9.7±1.8 cones per plant), before declining (Fig.1b). Sites that were <7 years since fire (3.40±1.23 cones per plant) or >35 years since fire (2.75±8.05 cones per plant) had the lowest amount of cone productivity (Fig.1b).

There was no obvious pattern in the density of *B. menziesii* with the predictors examined, and the most parsimonious model explained low amounts of variation in the data set (adjusted R^2 <10%; Table 1; Fig.1c). The best model according to BIC, also the most parsimonious according to AICc, included Landform, with sites located on the Bassendean landform (205.8±35.4 plants ha^{-1}) typically containing higher densities of *B. menziesii* than the Spearwood sites (151.5±54.8 plants ha^{-1}). According to both AICc and BIC, the best model describing the number of cones on *B. menziesii* plants included time since fire, landform and year of survey (Table 1; Fig.1d). This model described a strong (adjusted R^2 = 0.61) relationship between cone productivity and these three factors (Table 1, Fig.1d). In 2008, more cones were detected on trees in the Bassendean than Spearwood sites (Bassendean = 5.3±1.9; Spearwood = 1.6±0.6 cones per plant) and cone productivity was positively related to time since fire (Fig.1d): sites >10 years since fire typically had higher amounts of cones (5.13±1.87 cones per plant; Fig.1d). In contrast to the 2008 survey results (overall average: 4.0±1.4 cones per plant), few cones were detected in 2010 (0.8±0.4 cones per plant), and there appeared to be no relationship with time since fire (Fig.1d).

3.2. How many Carnaby's cockatoos can be supported in banksia woodlands?

Cones of *B. attenuata* (144 cones from 27 sites) contained more than double the number of seed follicles than cones from *B. menziesii* (120 cones from 24 sites; Table 2). The number of cones required to meet the field metabolic rates of Carnaby's cockatoo is consequently lower for *B. attenuata* (~19) than for *B. menziesii* (~43) (Table 2).

The number of Carnaby's cockatoo estimated to be supported in 100 ha of banksia woodland (*Y*) showed a curvilinear response to time since fire (adjusted R^2 = 0.35; Table 1; Fig.2a). Although there was variability within a specific fire age at our sites, fewer (<20) Carnaby's cockatoo were estimated for very young (<7 years since fire) and very old sites (>35 years since fire) according to the GAM-fit. Most sites between 10–33 years since fire were estimated to support >25 Carnaby's cockatoos, with a peak of ~35–48 individuals predicted at 20–25 years since fire (Fig.2a). This response variable had one outlier (Fig.2a), which contained a high density of *B. attenuata* and *B. menziesii*, as well as a high amount of cones per *B. attenuata* plant. However, removal of this outlier did not alter the model output or pattern observed, except for increasing the weights of the best model (best model, Fire: df = 4.45, adjusted R^2 = 0.33, BIC weight = 0.56, AICc weight = 0.40).

3.2.1. Incorporating foraging efficiency in resource use estimates

Foraging trace was observed at 25 of the 27 sites surveyed in 2008, indicating that Carnaby's cockatoo were utilising the majority of areas visited. Of the 144 *B. attenuata* cones collected, 67 cones showed foraging evidence and ~30% of follicles had been attacked, while only 18 of the 120 *B. menziesii* cones showed evidence of foraging, with ~38% of follicles attacked (Table 2). Assuming that Carnaby's cockatoo only consume a proportion of seeds from each cone they attack (indicated by the number of follicles attacked, Table 2), the number of cones required to meet their daily field metabolic rates increases from ~19 to ~ 62 *B. attenuata* cones and ~43 to ~111 *B. menziesii* cones (Table 2). This subsequently reduces our estimate for the number of Carnaby's cockatoo potentially supported in 100 ha of banksia woodland (Fig.2b; response variable Y^F); though does not alter the model output (Table 2) and showed a similar curvilinear response with time since fire (Fig.2b). Very young (<7 years since fire) and very old sites (>35 years since fire) were estimated to support <6 Carnaby's cockatoo according to the GAM-fit. Sites between 14–30 years since fire were predicted to support >10 Carnaby's cockatoo, with a peak between 20–25 years since fire (Fig.2b). The outlier in this model was the same outlier described above (Fig.2a) and removal of the outlier did not alter the model output or pattern (best model, Fire: df = 4.43, adjusted R^2 = 0.33, BIC weight = 0.54, AICc weight = 0.38).

The distribution of post-fire ages within the banksia woodlands was highly skewed and the actual post-fire age distribution did not approximate the idealised distribution that was based on plant life history attributes (Fig. 3; Wilson et al., in press). The majority of vegetation (>60%) has been burned recently (within six years since fire) and is predicted to support a combined total of 1144 Carnaby's cockatoos (Y^F; Fig.3). Less than a third of vegetation was >10 years since fire, but because of the high yield of cones as a food source, this combined area was estimated to support 1338 Carnaby's cockatoos (Fig.3). Currently there is very little vegetation (~3.5%; 1707 ha) between 20–25 years since fire, when the predicted number of Carnaby's cockatoo supported by banksia woodland peaks (Fig.2). Overall, the post-fire age distribution of banksia woodlands is predicted to support a total of 2725 Carnaby's cockatoos (95%CI estimates = 2201–3313; Fig.3). Under an idealised post-fire distribution (see Fig.3), 3702–5352 Carnaby's cockatoos could potentially be supported.

4. Discussion

Our results show that the burning history of banksia woodlands has a significant influence on food availability for the endangered Carnaby's cockatoo, and highlight that fire may be an important factor in the effective management of habitat for this species; reinforcing previous research on plant and animal communities in this area (Valentine et al., 2012a; Wilson et al., in press). The time since fire was important in explaining variability in cone production of *B. attenuata* and *B. menziesii*, species that are critical food resources for this endangered bird. Cone production was highest for *B. attenuata* at sites aged 10–30 years since fire, but for *B. menziesii* increased with time since fire and was highest in the very old (>35 years since fire) sites. Time since fire was the principal variable when estimating the numbers of Carnaby's cockatoo that can be supported by banksia woodlands, with greater numbers of birds supported by vegetation that is 14-30 years since fire, with numbers peaking in 20–25 years post-fire aged vegetation.

4.1. Time since fire influences food availability for Carnaby's cockatoo

Compared to more arid regions where these species are shrubs and more reliant on fire for seed release, in the woodlands of the Swan Coastal Plain, both banksia species display limited serotiny, instead releasing seeds from cones shortly after maturation (Cowling and Lamont, 1985; Hobbs and Atkins, 1990). In our study area, *B. menziesii* cones released nearly all their seeds within two years of production, while *B. attenuata* cones shed ~40% within the first year and the majority of seeds have been released within 3 years (Cowling and Lamont, 1985). The low amount of canopy seed storage indicates that the high numbers of cones observed in the older-aged vegetation do not represent a build-up of food resources as time passes.

The fires in banksia woodlands are rarely stand-replacing, but scorching of adult plants during both prescribed burning and wildfires is likely, potentially eliciting vegetative regrowth, even under low-intensity burns. Both banksia species are resprouters following fire, and in the immediate post-fire environment, plants may invest in vegetative regrowth, reducing allocation to reproduction (Reekie and Bazzaz, 1987). Although inter-annual flowering may be variable (potentially rainfall dependent), there is often a time-lag following fire before the reproductive outputs of banksia resume. In the study area, it can take up to 8 years following fire for half of *B. attenuata* and *B. menziesii* plants present at a site to be flowering (Wilson et al., in press), indicating a potential time lag following fire in their reproductive outputs. We observed low numbers of cones per plant in most sites <7 years since fire; and for *B. attenuata*, the peak in number of cones per plant was observed ~20 years since fire. In more arid regions, where these species are more serotinous, resprouting adult *B. attenuata* resume seed production 2-3 years following fire, reaching a peak in seed production ~7 years after fire (Enright et al., 1998).

Low intensity fires that aim to promote floristic diversity in the understorey, but scorch the canopy, may reduce food resources for some species (Clarke, 2008). Like Carnaby's cockatoo, the endangered red-tailed black-cockatoo *Calyptorhynchus banksii graptogyne* of south-eastern Australia feed upon seeds and food resources may be limited by burning patterns (Koch, 2005). Low-intensity prescribed burns reduce food resources of key eucalypt species, by reducing the number of trees producing fruit and the quantity of fruit per tree, for up to 9 years post-fire (Koch, 2005). However, for some fire-associated species elsewhere, fire can increase short-term habitat resources. For example, nest density and reproductive success of black-backed woodpeckers (*P. arcticus*), a fire specialist consistently associated with severely burned forests (Hutto, 2008), is highest in recently burnt mature spruce forests (Nappi and Drapeau, 2009). Time since fire has also been linked with the availability of other critical resources for fauna, such as hollow-bearing trees (Haslem et al., 2012).

We detected differences between the two banksia species in their reproductive output and responses to time since fire. Similar to previous research (Enright and Lamont, 1989), we recorded more cones per plant for *B. attenuata*, with a greater number of follicles per cone, compared with *B. menziesii*. In our study, the cone productivity of *B. menziesii* was strongly influenced by year of survey, with a response to time since fire detected only in 2008. During the 2010 data collection, we detected very few unopened cones per plants. The winter prior to sampling (2009) was a dry year and annual rainfall (~608 mm; Bureau of Meteorology) below average; potentially reducing the reproductive output (either of flowering or cone production) of *B. menziesii*. In addition, we conducted our sampling following an unusually hot and dry summer, with both the lowest summer rainfall and the highest summer temperatures recorded for Perth to that date (Bureau of Meteorology), and these hot conditions may have elicited spontaneous release of seeds.

4.2. How many Carnaby's cockatoos can banksia woodlands support?

We noted evidence of Carnaby's cockatoo foraging at most sites (93%), suggesting that the majority of banksia woodlands on the Swan Coastal Plain can provide food resources for this endangered species. Hence, retention of remnant banksia woodlands will be important for future food supplies for Carnaby's cockatoos. Currently, the DPaW-managed banksia woodland in our study area is predicted to provide food resources for 2201–3313 birds, around one third (~25–35 %) of the numbers estimated visiting the Perth area (based on estimates by Kabat et al., 2012). This result indicates that these banksia woodlands represent an important food resource for this species. Thus, effective management of this habitat may be crucial for the persistence of Carnaby's cockatoo; and similar research is required in other forage habitat.

We have identified a strong relationship between seed availability and time since last fire. We acknowledge that the number of birds estimated in our analyses may vary as more information on foraging activity and behaviour of Carnaby's cockatoos emerges. Estimating the number of individuals an area can potentially support is challenging, especially for a highly mobile species, and the energetic estimates we used do not take into account the metabolic cost of feeding or handling of food (Cooper et al., 2002; Stock et al., 2013), nor do they incorporate alternative food resources (both native and introduced) that Carnaby's cockatoo may forage upon. Neither do these estimates allow for recruitment of the banksia species, assuming instead that Carnaby's cockatoos forage upon all available cones. However, they provide an indication of the potential carrying capacity of the banksia woodlands, an identified existing knowledge gap (Department of Environment and Conservation, 2012; Stock et al., 2013).

Our finding that time since fire can influence food availability for Carnaby's cockatoos suggests that altering burning patterns is a management action that could enhance the estimated carrying capacity for Carnaby's cockatoos in this region; with between 3702–5352 birds potentially supported under an idealised post-fire age distribution (Wilson et al., in press). This is especially relevant as little vegetation was within estimated peak in potential carrying capacity for Carnaby's cockatoo. Fire management aimed at maintaining or enhancing critical habitat features, such as nesting or food resources, has been recommended for the recovery of several threatened species elsewhere (e.g. red-cockaded woodpecker: James et al., 2001; U.S. Fish and Wildlife Service, 2003; and, Leadbeater's possum: Lindenmayer et al., 2013). These management actions can include restoring frequent burning patterns (James et al., 2001) or restricting burning to ensure the retention of older aged habitat (Lindenmayer et al., 2013). If optimising food resource availability for Carnaby's cockatoo was an objective, fire management would ideally incorporate a spatial and temporal element to burning patterns to ensure continuity in the older-aged banksia vegetation that provides peak food resources. The retention of older-aged vegetation has also been identified as important for other elements of biodiversity in banksia woodlands (Valentine et al., 2012a; Wilson et al., in press). Retaining older-aged vegetation would necessitate a change in current burning patterns. Although managing fire regimes has been recognised as a key activity under the Carnaby's cockatoo recovery plan (Department of Environment and Conservation, 2012), the implementation of this to enhance food resources for Carnaby's cockatoos may conflict with other management objectives in the area, such as fuel reduction burning.

Fire management in peri-urban areas is challenging, with managers conducting prescribed burns for multiple objectives, including human and asset protection and biodiversity conservation (Burrows and Abbott, 2003; Burrows and McCaw, 2013; Driscoll et al., 2010). In fire-prone landscapes where humans reside, community protection is the primary fire management goal (Burrows and McCaw, 2013); and there are potential conflicts with biodiversity conservation objectives (Driscoll et al., 2010; Penman et al., 2011). Resolving conflicts between burning objectives can be difficult due to the sometimes opposing outcomes of the objectives; the lack of information on specific biodiversity responses; and the lack of information on the effectiveness of prescribed burning for human and asset protection (Driscoll et al., 2010; Enright and Fontaine, 2014; Fernandes and Botelho, 2003; Penman et al., 2011). In addition, predicted changes to climate are likely to alter fire weather and potential prescribed burning regimes, further complicating fire management decisions and implementation (Enright and Fontaine, 2014).

Carnaby's cockatoo is a globally endangered species suffering from loss of breeding and foraging habitat. The banksia woodlands and pine plantations of our study area support one of the largest remaining populations of Carnaby's cockatoo, providing critical food resources for this species. Our research provides quantitative evidence of the impacts of fire on native food resources for this endangered species. This information, along with other research on the biodiversity responses (Valentine et al., 2012a) and the burning patterns in the study area (Wilson et al., in press) could be used in an adaptive decision theory framework (such as described by Driscoll et al., 2010) to assist making informed fire management decisions. There is a need to accurately estimate the risk of wildfire to humans and biodiversity assets across landscapes and assess the effectiveness of fuel reduction burning (Burrows and McCaw, 2013; Enright and Fontaine, 2014). If the retention of older-aged vegetation is considered too high a wildfire risk, there should be transparency regarding the decision to manage landscapes for human protection, and recognition that this may involve a trade-off in resources for endangered species. Alternatively, zoned management that involves different fire regimes can be employed such that the risk of wildfire damage to property is minimized while still retaining older-aged vegetation. Sacrifice zones around infrastructure coupled with increased householder awareness and education could improve both wildfire prevention and biodiversity outcomes. This type of situation is likely to become increasingly prevalent with ongoing urbanisation and rapid global environmental change.

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Tables

Table 1. Top-ranking generalised additive models (GAM) for *B. attenuata* and *B. menziesii* density and cone productivity, and the predicted number of Carnaby's cockatoos supported in 100 ha of banksia woodland. Models include different combinations of time since fire (Fire), landform type (Landform) and year of survey (Survey). Models included are the optimal BIC model for each response variable and the top-ranking AICc models (<2 ΔAICc). The most parsimonious model is highlighted in bold.

Response variable	Model[#]	df	R^2	ΔBIC	BIC weight	ΔAICc	AICc weight
B. attenuata density	**Intercept only**	**2.00**	**0.00**	**0.00**	**0.55**	**0.00**	**0.29**
	Survey	3.00	0.01	2.13	0.19	0.77	0.20
	Fire	3.65	0.02	3.61	0.09	1.44	0.14
	Fire + Survey	4.81	0.05	5.24	0.04	1.76	0.12
B. attenuata cones per plant	**Fire**	**4.60**	**0.38**	**0.00**	**0.42**	**0.00**	**0.27**
	Fire + Landform	5.56	0.39	1.71	0.18	0.74	0.19
	Fire * Landform	5.96	0.40	2.02	0.15	0.69	0.19
	Fire + Survey	5.59	0.38	2.25	0.14	1.26	0.15
B. menziesii density	**Landform**	**3.00**	**0.07**	**0.00**	**0.31**	**1.51**	**0.14**
	Fire * Survey + Landform	6.90	0.22	2.47	0.09	0.00	0.30
	Fire * Landform	6.36	0.18	3.69	0.05	1.62	0.13
B. menziesii cones per plant	**Fire * Year + Landform**	**6.00**	**0.61**	**0.00**	**0.56**	**0.00**	**0.67**
Carnaby's cockatoo supported by banksia woodland (*Y*)	**Fire**	**4.54**	**0.35**	**0.00**	**0.40**	**1.56**	**0.23**
	Fire * Landform	6.26	0.41	0.08	0.38	0.00	0.50
Carnaby's cockatoo supported by banksia woodland, adjusted for foraging (Y^F)	**Fire**	**4.52**	**0.35**	**0.00**	**0.43**	**1.29**	**0.25**
	Fire * Landform	6.25	0.41	0.37	0.35	0.00	0.48

[#] Interaction models also contain the main effects term within the model.

Table 2. The number of *B. attenuata* and *B. menziesii* seed follicles, the proportion of seed follicles attacked and the minimum number of cones required for Carnaby's cockatoo field metabolic requirements (FMR).

	Number of follicles per cone (±95%CI)	Percentage (%) of follicles attacked per cone (±95%CI)	Cones to meet FMR[1]	Cones to meet FMR[2] adjusted for foraging efficiency
B. attenuata	15.10 (±1.43)	30.2 (±4.12)	18.77	62.15
B. menziesii[3]	6.65 (±0.51)	38.3 (±14.11)	42.63	113.31

[1] Based on the estimated number of seeds required to meet a FMR of 726 kJ day^{-1} (Cooper et al 2002) as reported in Stock et al (2013). We have assumed that there are two seeds per follicle (George 1939).

[2] Based on the estimated number of seeds required to meet a FMR of 726 kJ day^{-1} (Cooper et al 2002) as reported in Stock et al (2013), but adjusted for foraging efficiency of Carnaby's cockatoo by incorporating the proportion of cone attacked.

[3] Assuming that the energetic content of *B. menziesii* seeds are equivalent to that of *B. attenuata*.

Figure Legends

Fig.1. Relationships for time since fire with a) square-root transformed density of *Banksia attenuata*, b) square-root transformed number of cones per *B. attenuata* and the GAM fit (±95%CI; adjusted r^2 = 0.38) for this relationship, c) square-root transformed density of *B. menziesii* and d) square-root transformed number of cones per *B. menziesii* and the GAM fit (±95%CI; adjusted r^2 = 0.61) for this relationship for the different combinations of landform type and year of survey. Symbols represent the different combinations of landform type (Bassendean or Spearwood) and year of survey (2008 or 2010).

Fig.2. GAM Relationships for the a) predicted number of Carnaby's cockatoos supported in 100 ha of banksia woodland (Y) with time since fire (±95%CI; adjusted r^2 = 0.35 for square-root transformed variable), and b) predicted number of Carnaby's cockatoo supported in 100 ha of banksia woodland, adjusted for foraging efficiency (Y*) with time since fire (±95%CI; adjusted r^2 = 0.35 for square-root transformed variable). Symbols as for Fig.1.

Fig.3. The actual (grey bars) and idealised (grey dash) post-fire age distribution (ha) of DPaW-managed remnant banksia woodland habitat sourced from Wilson et al. (in press) and the predicted number (±95%CI) of Carnaby's cockatoos supported by the actual amount of habitat within each fire interval (black circles; response variable Y*; predicted values based on GAM-fit shown in Fig.2b).

Figures

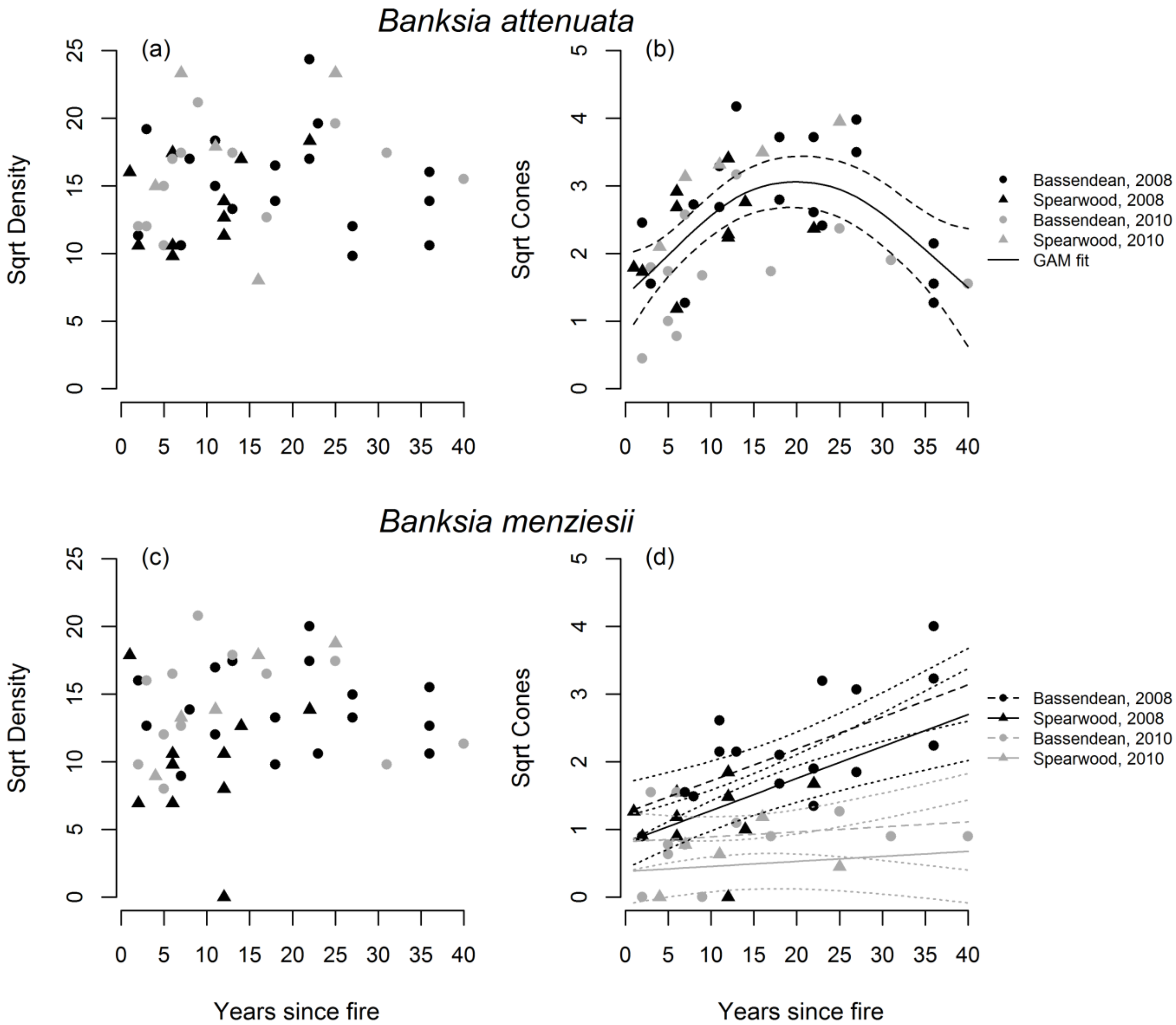
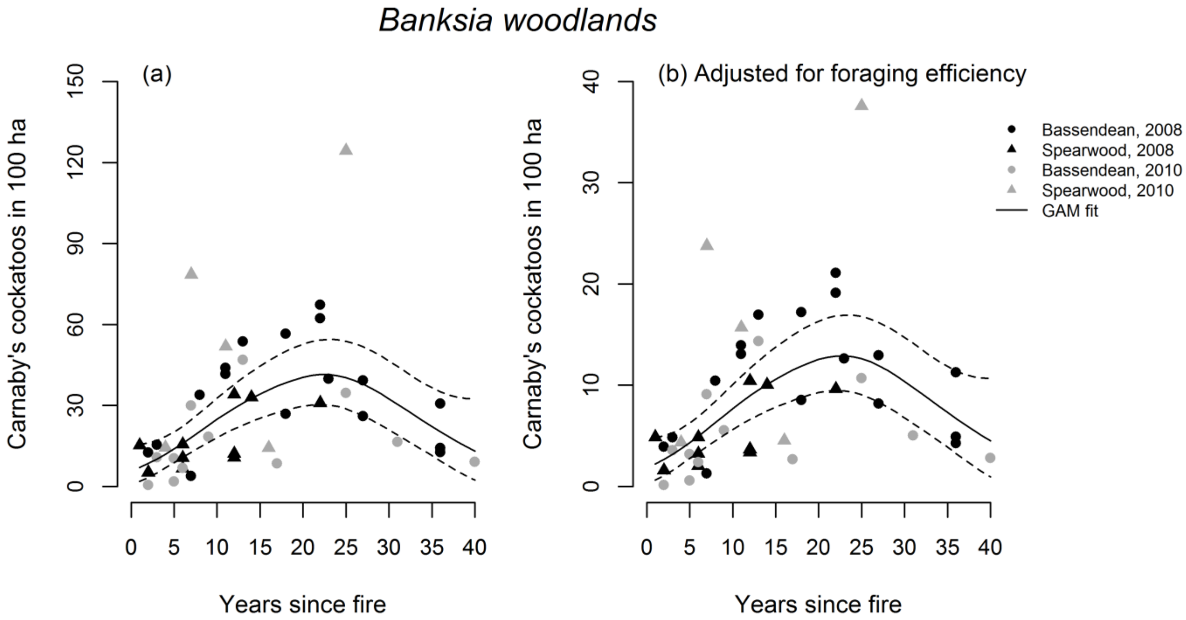


Fig.1.



Banksia woodlands
(a)
(b) Adjusted for foraging efficiency
Carnaby's cockatoos in 100 ha
Years since fire
Bassendean, 2008
Spearwood, 2008
Bassendean, 2010
Spearwood, 2010
GAM fit

Fig.2.

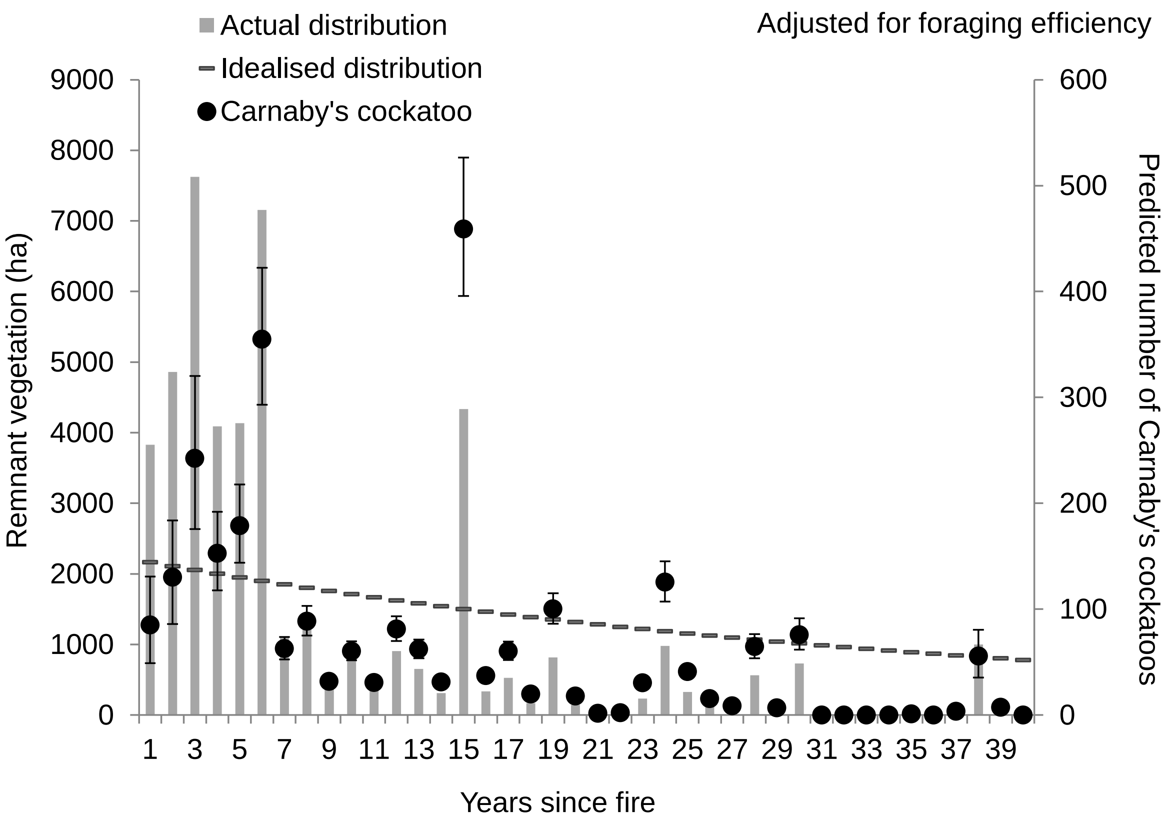

Actual distribution
Idealised distribution
Carnaby's cockatoo
Adjusted for foraging efficiency
Remnant vegetation (ha)
Predicted number of Carnaby's cockatoos
Years since fire
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
600
500
400
300
200
100
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39

Fig.3.

Appendix

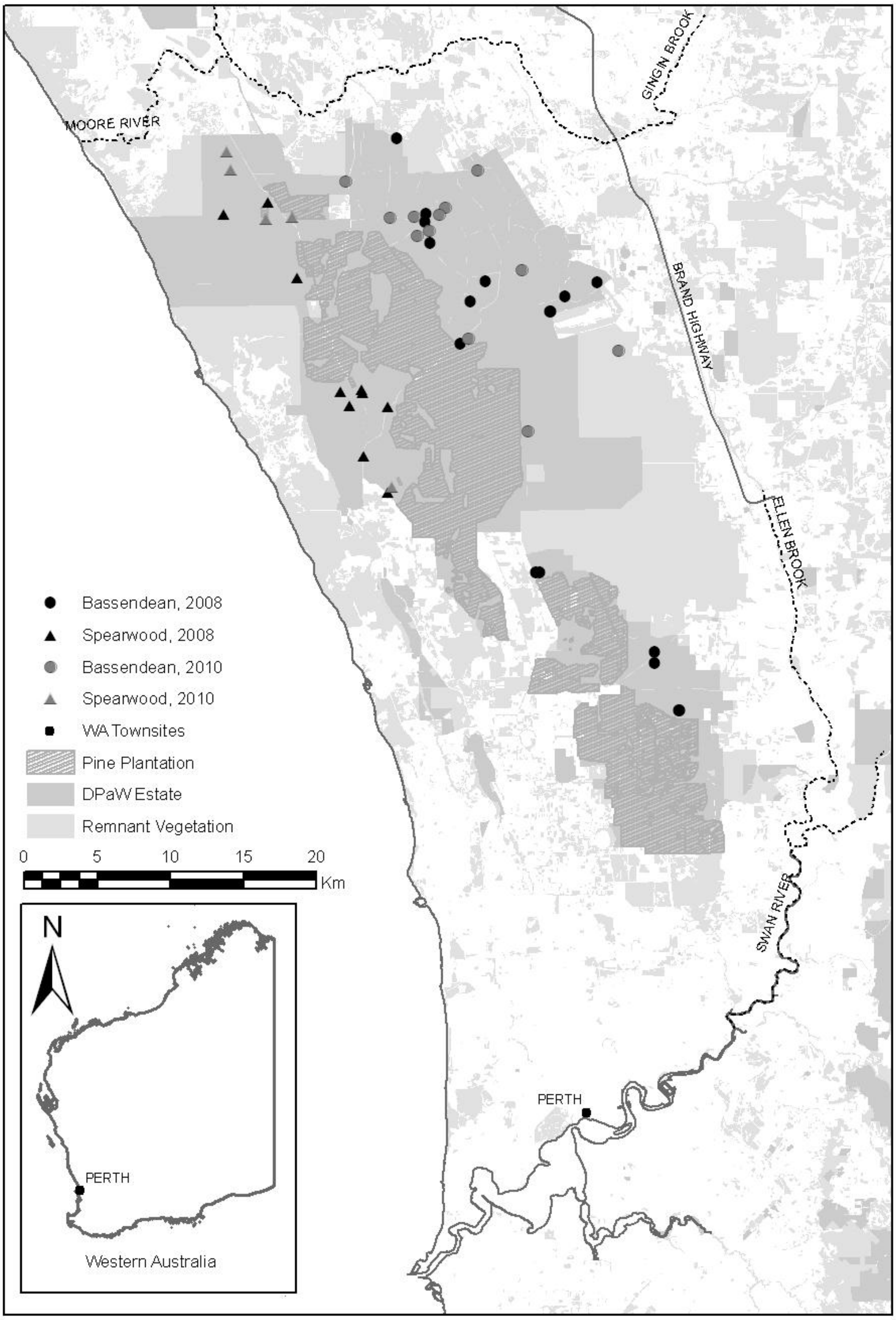


Fig.A.1. Survey sites located predominantly within the DPaW-managed remnant vegetation extent north of Perth.