Future of the Greater Glider (*Petauroides volans*) in the Blue Mountains, New South Wales

PETER SMITH AND JUDY SMITH

P & J Smith Ecological Consultants, 44 Hawkins Parade, Blaxland NSW 2774, smitheco@ozemail.com.au

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In a previous paper, we investigated whether the Greater Glider (*Petauroides volans*) is declining in Blue Mountains local government area and, if so, the factors responsible. In this paper, we reanalyse the data, replacing elevation (used as a proxy measure of climatic conditions) with temperature and rainfall estimates based on climatic modelling. The Greater Glider remains relatively common at higher elevations but has declined at lower elevations. In the 1980s, it occurred in similar abundance at all elevations, but in 2015-16 it was seven times more abundant above 500 m than below and could not be detected at 7 of 20 study sites in known habitat. Three variables accounted for most of the variation in abundance between sites: a negative relationship with mean annual temperature (31% of the variation) and positive relationships with mean annual rainfall (20%) and time since fire (14%), suggesting that the decline is linked to climate change, especially increasing temperature. We found no evidence that an alternative explanation, an increase in owl predation, was having a significant impact. The situation has worsened since our study, with a disastrous bushfire season in 2019-20 heralding a likely drastic change in the fire regime under climate change. The future prospects of the Greater Glider are looking increasingly bleak.

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KEYWORDS: climate change, fire, Greater Blue Mountains World Heritage Area, owl predation, population decline, rainfall, temperature.

INTRODUCTION

Human-mediated climate change (IPCC 2015) has been driving range shifts in many species of fauna and flora worldwide, typically involving range contractions and local extinctions at the 'warm edges' (lower latitudes and elevations) of their ranges (Chen et al. 2011, Lenoir and Svenning 2015, Wiens 2016), including multiple examples for mammals (Moritz et al. 2008, Myers et al. 2009, Rowe et al. 2010, Beever et al. 2011). Range shifts are a relatively well known response to climate change but the factors that cause variation in range shifts between species are complex and our ability to predict shifts is limited (MacLean and Beissinger 2017, Williams and Blois 2018).

One Australian mammal that has been predicted to undergo a contraction in range as a result of climate change is the Greater Glider (*Petauroides volans*) (Kearney et al. 2010). The Greater Glider (Fig. 1) is a cat-sized marsupial, weighing 1-1.5 kg, with an unusually long tail and long, thick fur (Fig. 1). There are two colour morphs – dark phase (black with a white chest and belly) and pale phase (pale grey to white) - which are often found together, plus intermediate forms. The Greater Glider is Australia's largest gliding possum and is capable of glides of up to 100 m, which may involve changes in direction of as much as 90° (Van Dyck and Strahan 2008). Like the Koala (Phascolarctos cinereus), the Greater Glider has a specialised diet consisting almost exclusively of eucalypt leaves. It has a patchy distribution in eucalypt forests along the coast and ranges of eastern mainland Australia, from central Victoria to northern Queensland. It is a sedentary, nocturnal species that shelters during the day in tree hollows and, except during the breeding season, is usually solitary, although because of its small home range (typically 1-3 ha, females overlapping but not males), it may occur at relatively high densities in suitable habitat (Lindenmayer 2002).



Figure 1. Greater Glider (*Petauroides volans*), dark phase

In 2016, the Greater Glider was listed as a vulnerable species under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* after the Threatened Species Scientific Committee (2016) concluded that the species has undergone a substantial overall reduction in numbers and that this decline, the cause of which is uncertain, is continuing.

Following indications that the Greater Glider was declining in the Blue Mountains local government area west of Sydney, we undertook a study in 2015-16 to confirm that the species was declining and to assess whether the decline was associated with climate change or with other factors. We concluded that the Greater Glider had declined at lower elevations in the Blue Mountains since the mid 1990s but remained relatively common at higher elevations. The most likely cause of the decline was the direct and indirect effects of a marked increase in temperature in the Blue Mountains in the last 20 years (Smith and Smith 2018). We found no evidence of a change in rainfall or fire regime that might explain the decline, nor any evidence that Greater Gliders have been impacted by increases in Powerful Owls (Ninox strenua), Sooty Owls (Tyto tenebricosa) or Sulphur-crested Cockatoos (Catatua galerita) since the 1980s.

In our original analysis, we used elevation as a proxy measure of climatic conditions at our study sites. For the present paper, we have reanalysed the data, replacing elevation as an explanatory variable with temperature and rainfall estimates for each study site based on climatic modelling from the NARCliM (New South Wales/Australian Capital Territory Regional Climate Modelling) project (Olson et al. 2014, 2016). This has the advantage of replacing a proxy measure of general climatic conditions (elevation) with specific temperature and rainfall values for each site. The disadvantage is that the values are estimates from modelling and should be treated with caution. However, the modelling has a further advantage in that it provides predictions of future temperature and rainfall values for each study site, allowing us to assess how many of the sites are likely to support Greater Gliders in the future if climatic changes continue on their current trajectory.

METHODS

Study area

The Greater Blue Mountains region in the ranges west of Sydney is internationally renowned for its scenic grandeur and its unique and diverse natural habitats. Our specific study area, Blue Mountains local government area, forms part of this region and covers over 140 000 ha on the eastern side of the Great Dividing Range, 65-100 km west of the Sydney coastline (Fig. 2). Three-quarters of the local government area is reserved in Blue Mountains National Park, which is one of the eight conservation reserves that make up the Greater Blue Mountains World Heritage Area, recognised as having World Heritage significance because of its outstanding biodiversity values, including its faunal diversity (Smith et al. 2019).

Blue Mountains local government area increases in elevation east to west from 10 to 1100 m above sea level. The geology is chiefly Triassic sandstones, characterised by extensive rock outcrops and sandy, infertile soils. More fertile soils occur patchily in association with other geological formations. The dominant vegetation is eucalypt forest and woodland, mostly with a dense, shrubby, floristically diverse understorey, interspersed with small areas of rainforest, heath and swamp (Keith and Benson 1988, Benson 1992). The evolutionary adaptation and diversification of eucalypt vegetation in the Greater Blue Mountains is a central feature of its World Heritage significance.

Urban development in Blue Mountains local government area is restricted to a string of townships along the Great Western Highway. Rural and semirural development occurs on better soils in valleys in the west and basalt-capped mountains in the north. However, the majority of the area is natural vegetation.

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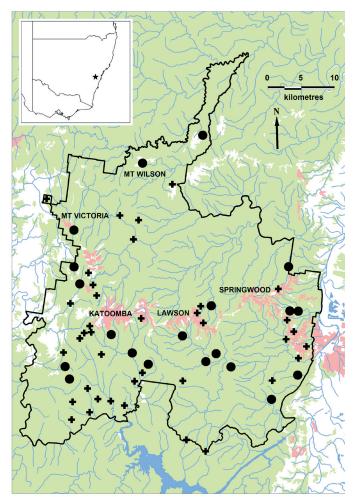


Figure 2. Map of Blue Mountains local government area showing the 58 sites where Greater Gliders have been recorded. $\bullet = 20$ sites resurveyed in 2015-16; + = other sites.

Greater Gliders were widespread in the Blue Mountains in the 1980s but with a patchy distribution associated with pockets of tall eucalypt forest on more fertile soils (Smith and Smith 1990, 2018). Common tree species in their local habitat include Mountain Blue Gum (*Eucalyptus deanei*), Sydney Peppermint (*E. piperita*), Monkey Gum (*E. cypellocarpa*), Turpentine (*Syncarpia glomulifera*) and Sydney Red Gum (*Angophora costata*) (Fig. 3).

Glider surveys

In a review of previous records, we identified 58 sites in Blue Mountains local government area where Greater Gliders have been recorded (Smith and Smith 2018). We selected 20 of these sites for resurvey in 2015-16 (Fig. 2). These were selected to sample the geographic spread of records across the study area and included 10 sites at elevations over 500 m and 10 sites below 500 m.



Figure 3. Example of Greater Glider habitat in the Blue Mountains: wet sclerophyll forest of Mountain Blue Gum, Turpentine and Sydney Red Gum at Murphys Glen.

Each site was surveyed on three nights between 17 March 2015 and 4 May 2016. Each survey consisted of a one-hour search by two people, each with a spotlight and binoculars, walking a transect along a road or track through eucalypt forest, counting the number of Greater Gliders detected and estimating the distance of each glider from

the transect centre-line. The mean transect length was 880 m but the transects varied in length, degree of contortion, and degree of fragmentation of the eucalypt forest by clearings and other habitats. Accordingly, we calculated the area of eucalypt forest sampled along each transect by mapping and measuring the area of eucalypt forest within 60 m of the transect centre-line (the maximum distance at which gliders were detected) using an aerial photography GIS layer. Survey results were expressed as the mean number of Greater Gliders detected per hectare of eucalypt forest over the three survey nights.

Habitat variables

For this paper, the variation in detection density of Greater Gliders between sites was analysed in relation to nine habitat variables:

Temperature and rainfall. Estimates of mean annual temperature and mean annual rainfall at



Figure 4. Powerful Owl preying on pale phase Greater Glider.

each survey site were obtained from climatic modelling by the NARCliM project. The values were estimated means for 1990-2009 at a geographic resolution of about 10 km, derived from downscaling of the CCCMA Global Climate Model using the R3 configuration of the WRF Regional Climate Model (Olson et al. 2016). This climate model was selected as it provides intermediate values compared with the other NARCliM model options (Olson et al. 2014).

- Time since fire. The date of the last fire at each survey site was obtained from GIS fire maps provided by the then NSW Office of Environment and Heritage. The fire maps show both wildfires and hazard reduction burns but do not show the severity of the fire. Both types of fire may vary widely in severity, although the more severe fires are usually wildfires.
- Habitat extent. The area of Greater Glider habitat (tall eucalypt forest) within 2 km of each transect centre-line was mapped and measured using an aerial photography GIS layer.
- Food trees. Greater Gliders are folivores and were observed in 15 different tree species during the surveys, but four species (*Eucalyptus cypellocarpa*, *E. deanei*, *E. piperita* and *E. viminalis*) accounted for 67% of all records (64 of 95 records) and appear to be the favoured local food trees. The combined abundance of these

four species at each survey site was measured as the number of live trees in a sample of 50 trees per transect (the 10 nearest live or dead trees at each of five sample points along the transect, excluding trees that were less than a third the height of the tallest trees).

- Hollow trees. Greater Gliders use hollows in both live and dead trees for shelter and breeding. The abundance of hollow-bearing trees at each survey site was measured as the number of live or dead trees with apparently suitable hollows in the sample of 50 trees per transect.
- Powerful Owl and Sooty Owl. Powerful Owls and Sooty Owls are known predators of Greater Gliders (Fig. 4) and both species have increased markedly in the Blue Mountains since the 1980s (Smith and Smith 2018). Their presence/absence in the vicinity of each survey site was recorded by searching and listening for owls during the glider surveys and by seeking records from other local naturalists during the study period. Male Powerful Owl calls were also broadcast with a megaphone after each glider survey, trying to elicit a response.
- Sulphur-crested Cockatoo. Several Greater Glider sites in the Blue Mountains have recently become regular roosts for large numbers of Sulphur-crested Cockatoos, whose activities could potentially disrupt the gliders. The number of roosting Sulphur-crested Cockatoos was recorded during each survey and the maximum count over the three surveys per site was used as a measure of cockatoo abundance.

Statistical analysis

Hierarchical partitioning (Chevan and Sutherland 1991) was used to assess the relative importance of the nine habitat variables in explaining the variation in detection density of Greater Gliders between sites. Hierarchical partitioning is a multiple regression method that assesses the relative importance of each explanatory variable, while alleviating problems associated with correlations between variables (Mac Nally 2002). Collinearity problems are reduced by estimating the independent contribution of each explanatory variable and separating it from the joint contribution resulting from correlation with other variables, thus isolating the amount of variance attributable to each explanatory variable.

The analysis was restricted to nine variables because of bias associated with variable order in models with more than nine explanatory variables (Olea et al. 2010). As recommended by Johnson

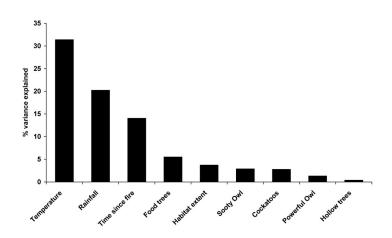


Figure 5. Independent contribution of each habitat variable to explaining variation in Greater Glider detection density (hierarchical partitioning analysis). Total variance explained 82%.

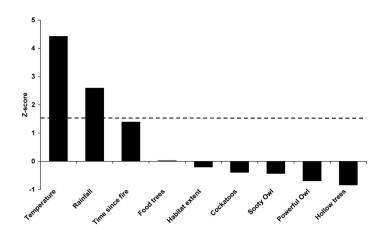


Figure 6. Z-scores showing the significance of each habitat variable in explaining variation in Greater Glider detection density. Based on 1000 randomisations of the data matrix. The dashed horizontal line represents the upper 95% confidence value.

and Lebreton (2004) and Grömping (2006), the LMG metric (Lindeman et al. 1980) was used to measure, for each variable, the average increase in the coefficient of determination R^2 across all possible linear regression models. The statistical significance of the explanatory variables was tested by randomising the data matrix (1000 replicates) and calculating Z-scores for each variable. Statistical significance was based on the upper 95% confidence limit ($Z \ge 1.65$). Analyses were carried out with the R statistical package version 3.4.3 (Venables et al. 2017), using the hier.part extension package version 1.0-4 (Walsh and Mac Nally 2015) and the relaimpo extension package version 2.2-2 (Grömping 2015).

RESULTS

Detection densities of Greater Gliders varied widely among the 20 survey sites. We failed to detect gliders at seven sites, despite all sites being in locations where Greater Gliders had been recorded previously. Five of the sites where no Greater Gliders were recorded were under 500 m elevation and two were over 500 m. The mean detection density in the 10 survey sites over 500 m (0.349 ± SE 0.097 gliders detected per ha) was about seven times greater than in the 10 survey sites below 500 m (0.053 \pm 0.024).

The nine habitat variables considered in the hierarchical partitioning analysis accounted for 82% of the variation in Greater Glider detection density between sites (Fig. 5). The largest independent contributions were from a negative relationship with mean annual temperature (31% of the variation), a positive relationship with mean annual rainfall (20%) positive relationship and а with time since fire (14%). The relationships with temperature and rainfall were statistically significant and the relationship with fire was close to significant (Fig. 6). The contributions of the other six variables were minor.

DISCUSSION

The glider surveys in 2015-16 showed a pattern of Greater Gliders being much more abundant (seven times more) in known habitat above 500 m than in known habitat below 500 m. Greater Gliders were not detected at half of the survey sites under 500 m even though all were known to have supported Greater Gliders in the past. Our review of previous records (Smith and Smith 2018) indicated that prior to the mid 1990s, Greater Gliders occurred in similar abundance in suitable habitat across all elevations in Blue Mountains local government area but have since declined at lower elevations while remaining relatively common at higher elevations.

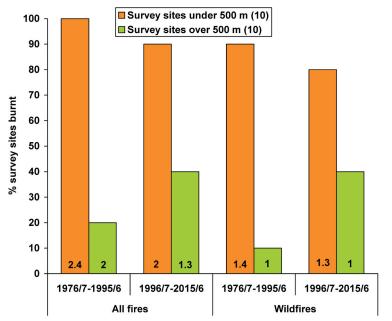


Figure 7. Comparison of the fire regime in survey sites above and below 500 m in the 20 fire seasons before this study and the previous 20 fire seasons. Figures in the columns are the mean number of fires per burnt site. 'All fires' includes hazard reduction burns. Data from NSW Office of Environment and Heritage GIS fire maps.

Our original analysis of habitat relationships (Smith and Smith 2018) explained a high proportion (84%) of the variation in Greater Glider abundance between sites, with the largest independent contributions coming from a positive relationship with elevation, used as a proxy for climatic conditions (37% of the variation), and a positive relationship with time since fire (23%). The present analysis, in which elevation has been replaced by modelled temperature and rainfall values, explains a similarly high proportion (82%) of the variation in Greater Glider abundance. The largest independent contributions were from a negative relationship with temperature (31%), a positive relationship with rainfall (20%) and a positive relationship with time since fire (14%).

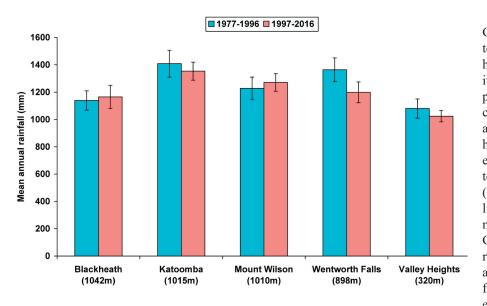
The other habitat variables included in the analyses made only minor contributions. All of the survey sites supported Greater Gliders in the past and thus all can be considered to be suitable habitat for the species. This probably explains why factors found to be important predictors of Greater Glider abundance in previous studies, particularly availability of tree hollows (Lindenmayer et al. 1990, Eyre 2006, Smith et al. 2007) and presence of favoured food trees (Kavanagh 2000), were not important in this study

(i.e. because all of the areas sampled had sufficient tree hollows and food trees).

The presence of either or both Powerful Owls and Sooty Owls was found to have little effect on Greater Glider abundance. Increased owl predation is the most likely alternative to climate change as an explanation for the decline of Greater Gliders in the Blue Mountains. Powerful Owls often prey on Greater Gliders and have been implicated in localised population declines (Kavanagh 1988). Sooty Owls are also known to prey on Greater Gliders (Bilney et al. 2006), but are smaller birds and are likely to be a less important predator. Both owl species were rare in the Blue Mountains in the 1980s (Smith and Smith 1990) but have since undergone pronounced increases. Powerful Owls were recorded at 35% of our survey sites in 2015-16 and Sooty Owls at 50% of the sites. However, we found no evidence that either species was having a significant effect on Greater Gliders

The results of this study suggest that the decline of the Greater Glider in the lower Blue Mountains is linked to climate change, as predicted by Kearney et al. (2010). The next question is whether climate change has had an effect through a change in temperature, a change in rainfall, a change in the fire regime or a combination of these. To address this question, we have compared temperature, rainfall and fire regime in the 20-year period prior to the surveys (1997-2016), when Greater Gliders were declining at lower elevations, with the previous 20-year period (1977-1996), when Greater Gliders occurred in similar abundance across the Blue Mountains.

Greater Gliders are known to be impacted by fires, especially by major wildfires, which may result in the prolonged absence of the species from burnt areas (Lunney 1987, Lindenmayer et al. 2013, Andrew et al. 2014). Comparing the fire regime at survey sites above and below 500 m in the 20 fire seasons before this study and the previous 20 fire seasons, we found no evidence of an increase in fires at lower elevations that might explain the decline in Greater Gliders (Fig. 7). The number of sites burnt and the number of fires per burnt site both decreased at lower elevations in 1997-2016 compared with 1977-1996,



Glider is known to be sensitive to temperatures: high it is well adapted physiologically to cool conditions but poorly adapted to prolonged heat stress (Rübsamen et al. 1984). Extreme temperature events (heatwaves) are likely to cause high mortality of Greater Gliders, as has been reported for another arboreal marsupial folivore with a diet of eucalypt leaves, the Koala (Phascolarctos cinereus) (Lunney et al. 2012). Heatwaves also appear to impact

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Figure 8. Comparison of mean annual rainfall at Bureau of Meteorology weather stations in Blue Mountains local government area in 1997-2016 and 1977-1996. The stations shown are those with at least 10 years' data in each period. Error bars are standard errors.

whether considering all fires (wildfires plus hazard reduction burns) or just wildfires (which are likely to be the more severe fires). The number of sites burnt at higher elevations increased, but these were not the sites where Greater Gliders declined. Sites at lower elevations experienced much more fire than those at higher elevations over the entire 40-year period, which may make the lower Blue Mountains a more marginal habitat for the fire-sensitive Greater Glider. However, there was no obvious detrimental change in the fire regime to explain the decline in Greater Gliders at lower elevations.

There was also no evidence of a change in rainfall in 1997-2016 compared with 1977-1996. Annual rainfall at Bureau of Meteorology weather stations in Blue Mountains local government area is highly variable. For the five stations with sufficient data for analysis, the differences in mean annual rainfall between the two time periods were inconsistent in direction and were negligible in size compared with the year-to-year variability (Fig. 8). However, there has been a pronounced change in mean annual temperature. Temperatures at Katoomba (the only local weather station with long-term data) were on average 1°C warmer in 1997-2016 than in 1977-1996 (Fig. 9). The difference is highly significant (t-test, t = 6.52, df = 38, P << 0.001) and much higher than for Australia in general, for which the corresponding mean difference is 0.3°C warmer (Bureau of Meteorology ACORN-SAT dataset).

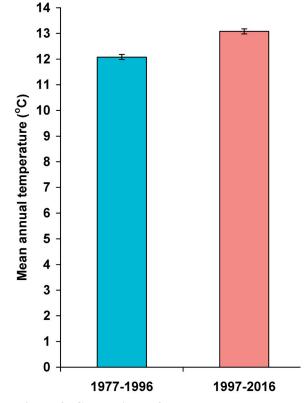


Figure 9. Comparison of mean annual temperature at the Bureau of Meteorology weather station at Katoomba (1015 m) in 1997-2016 and 1977-1996 (20 years' data in each period). Error bars are standard errors.

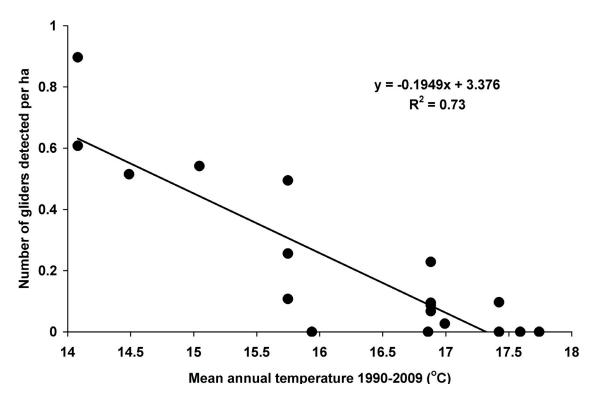


Figure 10. Relationship of Greater Glider detection density and mean annual temperature at our 20 survey sites based on the NARCliM CCCMA WRFR3 temperature model for 1990-2009.

on Koala fertility rates (Lunney et al. 2012) and may have a similar effect on Greater Gliders. Higher temperatures may also impact Greater Gliders indirectly through effects on the eucalypt foliage that is their source of both food (Kavanagh and Lambert 1990) and water (Rübsamen et al. 1984). Water stress from high temperatures coupled with drought can severely inhibit eucalypt growth and reduce the availability of young, softer, more nutritious foliage (Matusick et al. 2013), which is the Greater Glider's preferred food source (Kavanagh and Lambert 1990).

The effects of increasing temperatures on Greater Gliders are likely to be more severe in the hotter conditions of the lower Blue Mountains. The difference in mean annual temperature between Valley Heights (320 m) in the lower Blue Mountains and Katoomba (1015 m) in the upper Blue Mountains is 4.8°C (Bureau of Meteorology data). This would explain why the heat-sensitive Greater Glider has declined at lower elevations but not at higher elevations.

A linear regression of the relationship between Greater Glider detection density at our survey sites and the estimated mean annual temperature from the 1990-2009 NARCliM CCCMA WRFR3 model

suggests a tipping point at a mean annual temperature of 17.3°C, beyond which a site can no longer support Greater Gliders (Fig. 10). Using this figure and the NARCliM model predictions of future temperatures at the survey sites, we can estimate how many of the sites will be suitable for Greater Gliders as the effects of climate change intensify. Greater Gliders were present at all 20 survey sites in the 1980s but were recorded at only 13 sites (65%) in 2015-16. We predict that only seven sites (35%) will support Greater Gliders in 2030 and only four sites (20%) in 2070 (Fig. 11). Greater Gliders, once widespread across Blue Mountains local government area, will become increasingly restricted to the highest elevations and, if climate change continues on its current trajectory, will eventually become locally extinct.

As discussed above, we found no evidence of a major change in the fire regime in the Blue Mountains over the 40 year period before our 2015-16 study. However, the situation has now changed dramatically in the 2019-20 fire season, which saw the most extensive fires in Australia's temperate forests since European settlement, burning 21% of this biome, a globally unprecedented percentage burnt in a single fire season for any continental forest biome (Boer et al. 2020). The unusual scale of the fires has been

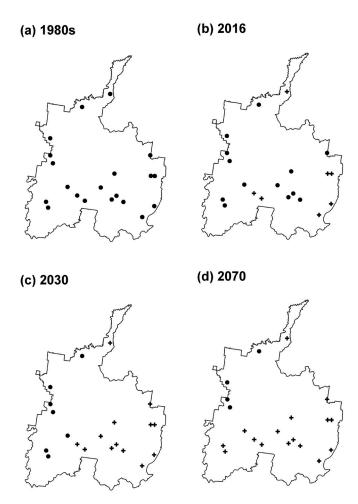


Figure 11. Presence of Greater Gliders at the 20 survey sites in the 1980s and 2016, and predictions for 2030 and 2070 (NARCliM CCCMA WRFR3 temperature model for 2020-39 and 2060-79). ● = present; + = absent.

attributed to climate change, with extreme drought conditions and high temperatures drying out the vegetation and fire fuels to an extraordinary degree (Nolan et al. 2020). The more flammable future predicted under climate change (Bradstock 2010, Hammill and Tasker 2010, Clarke and Evans 2019) has come earlier than anticipated (Boer et al. 2020).

The Greater Blue Mountains World Heritage Area was one of the areas worst affected by the fires, with about 65% of the area burnt between October 2019 and February 2020 (Fig. 12, Smith 2020). About 34% of the World Heritage Area was burnt at high to extreme fire severity (canopy entirely burnt or scorched, Fig. 13), 26% at moderate severity (canopy partly burnt) and 5% at low severity (understorey burnt, canopy unburnt),

The impacts on the fire-sensitive Greater Glider are likely to have been severe. Many animals would have been killed by the fires or would have died in the aftermath because of the absence or shortage of the eucalypt foliage on which they feed, and because of the increased risk of predation after their habitat was opened out by fire. The severe and prolonged drought that preceded and accompanied the fires has also had an impact. Even in the unburnt parts of the Blue Mountains, we have had a number of reports of Greater Gliders being found dead, and an autopsy on one of these indicated that it had died from a combination of dehydration and starvation (Stephanie Chew and Peter Ridgeway, pers. comm.).

The ability of Greater Gliders to recolonise burnt areas depends on part of the population surviving in patches of unburnt forest, from which they spread out as the burnt areas become habitable again. The process is a slow one that is not helped by the low reproductive output of Greater Gliders (one young per year; Van Dyck and Strahan 2008). For example, Greater Gliders disappeared from Royal National Park, south of Sydney, after a major fire burnt 90% of the park in 1994. They were not seen again in the park until 2012, 18 years later (Andrew et al. 2014).

The unprecedented scale of the 2019-20 fires in the Greater Blue Mountains World Heritage Area means that there are fewer unburnt refuges than would normally be the case after a fire. It remains to be seen whether the Greater Glider can recover from this disastrous bushfire season, and whether it can survive what will likely be a drastic long-

term change in the fire regime. The future prospects of the Greater Glider are looking increasingly bleak in the Blue Mountains and elsewhere throughout its range.

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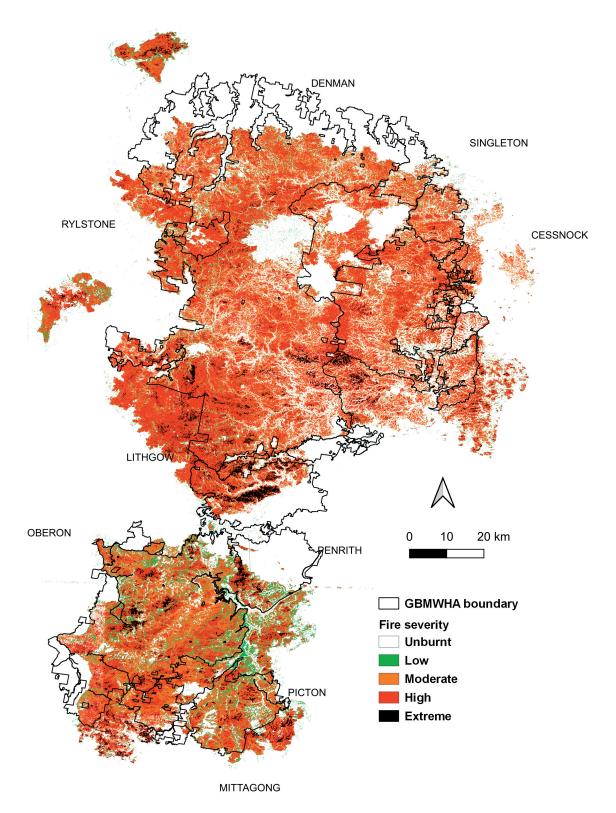


Figure 12. Areas burnt in and around the Greater Blue Mountains World Heritage Area in the 2019-20 bushfire season. Source: Smith (2020).

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Figure 13. Impact of the 2019-20 bushfires on Greater Glider habitat at Mount Wilson. Fire severity was high, with the entire canopy burnt or scorched, removing the gliders' food source. Photo taken about 11 weeks after the fire.

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