

A cryptic elapid snake persists in the wake of catastrophic wildfires

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Abstract The increased severity and frequency of bushfires accompanying human-induced global warming have dire implications for biodiversity conservation. Here we investigate the response of a cryptic, cool-climate elapid, the mustard-bellied snake *Drysdalia rhodogaster*, to the extensive Black Summer fires of 2019/2020 in south-eastern Australia. The species is categorized as Least Concern on the IUCN Red List (last assessed in 2017), but because a large part of its range was burnt during the Black Summer and little was known about its ecology, *D. rhodogaster* was identified as a priority species for post-fire impact assessment. We evaluated three lines of evidence to assess the impact of the Black Summer fires on *D. rhodogaster*. Habitat suitability modelling indicated that c. 46% of the predicted range of the species was affected by bushfire. Field surveys conducted 9–36 months post-fire and collation of records from public databases submitted 0–24 months post-fire indicated that *D. rhodogaster* persisted in burnt landscapes. Fire severity and proportion of the landscape that was burnt within a 1,000-m radius of survey sites were poor predictors of site occupancy by *D. rhodogaster*. Although conclusions regarding the effects of fire on *D. rhodogaster* are limited because of the lack of baseline data, it is evident that the species has persisted across the landscape in the wake of extensive bushfires. Our work highlights the need for baseline knowledge on cryptic species even when they are categorized as Least Concern, as otherwise assessments of the impacts of catastrophic events will be constrained.

Keywords Black Summer, bushfire, *Drysdalia rhodogaster*, habitat suitability model, mustard-bellied snake, occupancy, reptile, species distribution

The supplementary material for this article is available at doi.org/10.1017/S0030605324000048

Introduction

Fire is a natural process that has shaped landscapes globally for more than 420 million years (Bowman et al., 2009) and is crucial in maintaining the health of many ecosystems. Yet wildfires can lead to long-lasting changes in ecosystem structure, species distributions and species persistence (Haslem et al., 2011; Lovich et al., 2017; Merrick et al., 2021; Smith et al., 2021). At a regional scale, the extent, frequency and severity of fires can shift because of land-use changes such as human settlement (Spyratos et al., 2007) and logging (Lindenmayer et al., 2020). At a global scale, human-induced global warming is driving shifts in fire regimes, with forecasts and correlative studies predicting increases in the extent, frequency and severity of wildfires (Pitman et al., 2007; Canadell et al., 2021; van Oldenborgh et al., 2021). This increased prevalence of megafires has resulted in some authors referring to the contemporary period as the Pyrocene (Nimmo et al., 2021).

Determining how different fire regimes directly and indirectly affect species is a central research priority in contemporary conservation science (Driscoll et al., 2010). Although species in fire-prone landscapes have probably adapted to cope with the effects of fires, increased severity and frequency of fires could exceed the capacity of these adaptations to facilitate population persistence (Pausas & Parr, 2018; Nimmo et al., 2021). For example, in a fire-adapted landscape, a survey conducted 20 years after an extreme fire found only 7.9% of 1,630 shrubs showed any resprouting (Nicholson et al., 2017). Beyond direct mortality, fire can have species-specific effects on habitat structure (Costa et al., 2020), fecundity (Smith et al., 2012) and predation pressure (Leahy et al., 2016) that can cause shifts in ecosystem dynamics. Because these effects are species-specific, comprehensive information across a range of taxa is required to obtain a clear understanding of how ecosystems

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Received 19 April 2023. Revision requested 13 June 2023.

Accepted 5 January 2024. First published online 22 November 2024.

respond to fire, which is particularly important considering the increased risk of megafires (Canadell et al., 2021).

Mounting fears regarding the increased extent of wild-fires were realized in the 2019–2020 austral bushfire season (hereafter ‘Black Summer’), during which prolonged drought led to catastrophic bushfires in the forested landscapes of south-eastern Australia (van Oldenborgh et al., 2021). During the Black Summer c. 97,000 km² of vegetation on the Australian mainland burnt (Ward et al., 2020). Bushfires of such an extent and severity were historically unprecedented in the Australian landscape (Gibson et al., 2020; Ward et al., 2020). Understanding the conservation implications of these megafires has been a key concern for scientists and land managers, with estimates suggesting that 2.8 billion vertebrates were occupying areas affected by the fires (van Eeden & Dickman, 2023) and that the range of more than 13,000 species of invertebrates was affected (Marsh et al., 2022). Some field surveys have confirmed the dire predictions of the impacts of the Black Summer fires, with reports of adverse impacts on some species of lizards (Letnic et al., 2023), snails (Decker et al., 2023), birds (Lee et al., 2023), frogs (Beranek et al., 2023) and bats (Law et al., 2022a). However, the effects of the Black Summer appear to be species- and context-specific, with some frogs, invertebrates, lizards and snakes showing varying responses to the severity of the fires and some being relatively unaffected (Webb et al., 2021; Foon et al., 2022; Reid et al., 2022; Hartley et al., 2023; Letnic et al., 2023).

The variability in species’ responses to fire highlights that effects of such extreme disturbance events are complex and poorly understood (Ratnayake et al., 2019; Jolly et al., 2022). Further complications arise regarding species that are rare or elusive because of their low detectability (Bellemain et al., 2005). Similarly, for species or ecosystems for which baseline ecological knowledge is lacking, ecological shifts may not be detected because of shifting baselines (Mills et al., 2020). Snakes are a taxonomic group that is subject to these combined effects because they are generally under-represented in ecological research (Pyšek et al., 2008; Trimble & van Aarde, 2012) and often show cryptic behaviour, which makes them difficult to detect (Mazerolle et al., 2007). The lack of baseline information combined with generally low detectability hampers the conservation of snakes in the wake of events such as the Black Summer fires.

The mustard-bellied snake *Drysdalia rhodogaster*, also referred to as rose-bellied snake or Blue Mountains crowned snake, is a small (maximum total length c. 400 mm), diurnal, elapid snake (Plate 1) endemic to New South Wales in south-eastern Australia. Prior to the Black Summer bushfires, *D. rhodogaster* was considered abundant and was categorized as Least Concern on the IUCN Red List when it was last assessed in 2017 (Shea et al., 2018). However, because of its small size and cryptic habits, little is known about the species’



PLATE 1. One of the mustard-bellied snakes *Drysdalia rhodogaster* that we detected during the field surveys. Photo: M. J. Hodgson.

ecology (Shine, 1981; Scanlon, 2000). Previous studies indicate that *D. rhodogaster* is live-bearing, occurs in areas with mild to cool climates and primarily consumes small scincid lizards (Shine, 1981). Because of a lack of knowledge about its ecology and preliminary assessments estimating that more than 30% of its distribution had burnt, *D. rhodogaster* was provisionally listed as needing conservation assessment following the Black Summer bushfires (Legge et al., 2020).

Here we present a multifaceted investigation of the impacts of the Black Summer bushfires on *D. rhodogaster*. Firstly, we use habitat suitability models to predict the extent of bushfires across the range of *D. rhodogaster* during the Black Summer. Secondly, we report on the findings from field surveys and occupancy modelling evaluating the effects of fire severity and fire extent on the site occupancy and detectability of *D. rhodogaster*. Thirdly, to further evaluate whether *D. rhodogaster* continued to occur in areas burnt during the Black Summer bushfires, we extracted records of *D. rhodogaster* made after the fires from a publicly accessible database (Atlas of Living Australia, 2021) and intersected these with publicly available information on the severity of the Black Summer bushfires.

Study area

Drysdalia rhodogaster is found in dry sclerophyll forest, heath and woodlands across coastal regions of south-eastern Australia (Plate 1; Shine, 1981). Accordingly, we conducted surveys in burnt and unburnt forests in the Greater Sydney Basin of New South Wales. We established survey sites within forest dominated by *Eucalyptus* spp. in Morton National Park ($n = 27$), Blue Mountains National Park ($n = 15$) and Wollemi/Yengo National Park ($n = 19$; Fig. 1) in close proximity (within 5 km) to localities where *D. rhodogaster* had been recorded previously according to the Atlas of Living Australia (2021). Individual sites were at least 500 m apart.

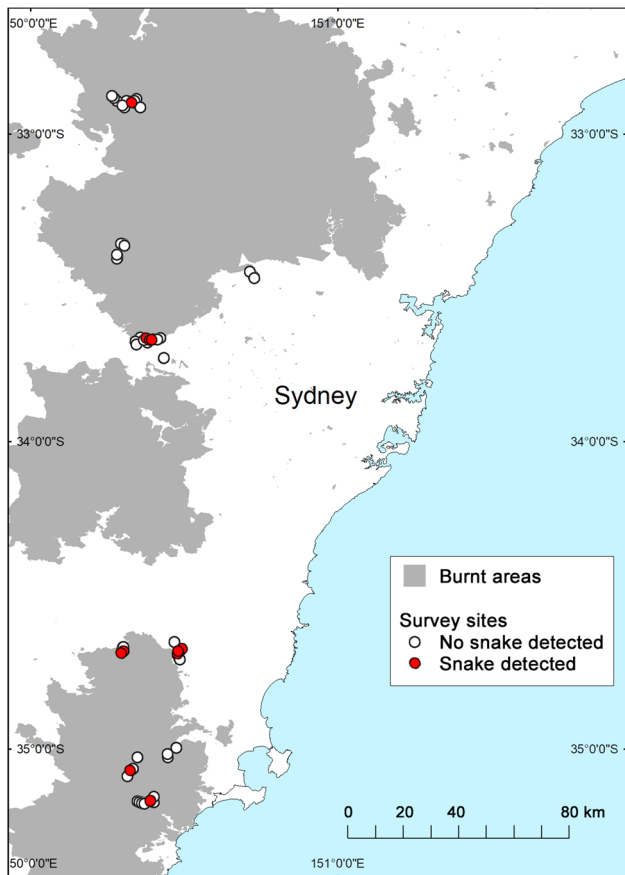


FIG. 1 The area surveyed for mustard-bellied snake *Drysdalia rhodogaster* occupancy in south-eastern Australia during October 2020–April 2021, September 2021–February 2022 and September 2022–December 2022, indicating survey sites with and without detections of the species, and the area burnt in the Black Summer bushfires (7 January 2019–24 March 2020).

Movement ecology studies of the Australian elapid *Hoplocephalus bungaroides* indicate that the maximum distance snakes travel in a month rarely exceeds c. 500 m (Webb & Shine, 1997), thus we assumed a distance of 500 m would ensure independence amongst sites for *D. rhodogaster*, which is a similarly sized elapid. Surveys were conducted in successive years following the Black Summer, during October 2020–April 2021, September 2021–February 2022 and September 2022–December 2022, in the warmer months when *D. rhodogaster* is most active (Shine, 1981).

Methods

Habitat suitability models

We constructed a habitat suitability model for *D. rhodogaster* using the maximum entropy (*MaxEnt*) algorithm in the package *dismo* (Hijmans et al., 2017) in R 4.1.2 (R Core Team, 2021). We downloaded occurrence records from the Atlas of Living Australia (2021) and New South Wales Bionet Atlas (New

South Wales Government, 2022). The Atlas of Living Australia is a biodiversity database that aggregates records from Australian institutions (museums, public sightings, citizen science projects and surveys). It also contains weekly integrations of Australian-based records from the global citizen science project iNaturalist (2024). Similarly, Bionet aggregates records from state-issued scientific datasets and surveys conducted by the environmental regulator. We cleaned the records from both sources and removed duplicates. This resulted in 271 occurrence records, further filtered to 198 unique records within 1 km² cells (reducing sample redundancy) that we input into the *MaxEnt* model algorithm along with 38,704 background records (Supplementary Material 1). We ran the models with 43 environmental variables that estimate climate, vegetation and soil conditions at those points (Supplementary Table 1). We chose these variables a priori to represent key determinants of habitat suitability for reptiles (Cabrelli et al., 2014; Cabrelli & Hughes, 2015).

Our model provided gridded estimates of habitat suitability at a spatial resolution of 280 m (the resolution of the gridded environmental variables). We then categorized these raw habitat suitability values into a binary representation of suitability (0 = no to low suitability, 1 = suitable) using a species-specific threshold: the 10th percentile training presence logistic threshold. This is based on the weighting of different model errors (commission errors, whereby a grid cell is classified as suitable when it is not suitable, vs omission errors, whereby a grid cell is classified as unsuitable when it is suitable).

To explore the effect of elevation on the distribution of *D. rhodogaster*, we plotted the latitude of database records and the centroids of grid cells generated by the habitat suitability model with a probability of occurrence > 0.5 against their elevation (in m). We extracted elevation data from the Australian Government's 3 second Shuttle Radar Topographic Mission Derived Digital Elevation Model Version 1.0 (Geoscience Australia, 2010).

To determine the approximate area of predicted habitat for *D. rhodogaster* that was burnt during the Black Summer, we intersected points from the suitability model with an aggregated layer of the fire extent from the Black Summer fires. A more detailed description of the methods used for environmental variable selection, data cleaning, model construction, calibration and evaluation is provided in Supplementary Material 1 and Supplementary Table 2, and the environmental layers used are in Supplementary Table 1. We treated our model predictions as hypotheses for the potential distribution of *D. rhodogaster* (Lee-Yaw et al., 2022), and therefore these hypotheses required independent testing through further field sampling.

Field surveys for *D. rhodogaster*

At each site on each survey occasion we searched a 100 × 50 m area for 1 person-hour (active search) to

standardize for the variable number of surveyors between sites. We deployed artificial refugia consisting of four roof tiles (42 × 33 cm) and two sheets of tin (c. 1 m²) at each site and checked these at the conclusion of the searches. Little is known about the activity periods of *D. rhodogaster*, with anecdotal evidence suggesting that the species is primarily diurnal; however, the species has also been found to be active at night (MJH, pers. obs., 2022). Because of the dearth of knowledge about *D. rhodogaster* activity patterns, we conducted the surveys under conditions assumed to maximize snake detection, avoiding excessively warm conditions or heavy rain. Searching included looking for surface active animals, turning over suitable refuges and raking litter. Where possible we minimized disturbance to the microhabitat and in all instances we replaced turned objects back to their original positions.

There was a minimum of 7 days between surveys at each site, with most sites having at least 14 days between surveys. The number of repeat surveys conducted within and across years varied between sites (1–8 surveys per site). We sampled only a subset of sites (Blue Mountains National Park, *n* = 14; Morton National Park, *n* = 21) 3 years post-fire. We sampled one Blue Mountains National Park site only 2 years post-fire.

Post-fire occurrences of *D. rhodogaster*

To complement our field surveys and further assess responses of *D. rhodogaster* across the species range, we analysed post-fire presence records from the Atlas of Living Australia (downloaded on 25 March 2022). We extracted records of *D. rhodogaster* that were observed in the 24 months following the end of the bushfires in the greater Sydney region (10 February 2020–1 March 2022). We excluded records of *D. rhodogaster* in the Atlas of Living Australia that were generated from the field surveys conducted for this study. We determined whether each record had been detected in a burnt or unburnt region by extracting burn severity values from a remote sensing dataset that was created after the Black Summer fires to quantify the extent and severity of fires in New South Wales (Fire Extent and Severity Mapping dataset; Department of Planning, Industry and Environment, 2020).

Covariates and statistical analysis

To determine site occupancy, we ran a single-species, single-season occupancy model in *R*. We built detection histories for each site by assigning a score of 'o' if we did not detect a snake, '1' if we did detect a snake and 'NA' for no survey. We ran the occupancy models in the *unmarked* package in *R*, using the *occu* function (Fiske & Chandler, 2011). As surveys occurred across multiple years, we included 'year' as a site-level covariate. We also included 'park' as an occupancy

covariate because the initial occupancies probably varied between the parks.

To assess the impacts of bushfire on *D. rhodogaster*, we calculated the extent of habitat burnt within a 1,000-m radius around each survey site using data extracted from the Fire Extent and Severity Mapping dataset in ArcGIS (Esri, USA) and estimated the fire severity at each site. We assessed fire severity based on evidence of scorching and canopy condition in the first round of surveys conducted in spring 2020 (Letnic et al., 2023). We classified sites as being burnt at low severity if their understorey showed evidence of recent burning (scorch marks on trees, burnt stumps and shrubs) but the canopy of *Eucalyptus* trees remained intact. We classified sites as being burnt at high severity if evidence of recent burning was observed in the understorey and in the canopy (i.e. leaves in the canopy were either absent or evident as epicormic buds).

To account for seasonality in the detectability of reptiles, we included an observation-level covariate of 'day of year', which we defined as the difference between the survey date and the start of the austral spring (1 September). Finally, because air temperature affects the detection of cryptic reptiles (Scroggie et al., 2019), we included 'daily maximum temperature' as an observational covariate. We extracted daily maximum temperature data from the SILO climate database (Jeffrey et al., 2001; Queensland Government, 2023), which provides interpolated daily temperature data at a 5 × 5 km grid resolution. Given that this method treats sites across years as different, if a site had no surveys in a given year, then we omitted that year from the final analysis (*n* = 27). We standardized fire extent, day of year and daily maximum temperature (mean = 0 ± SD 1) using the *scale* function in *R*. If daily temperature data could not be accurately assigned to a site visit, we removed it from the final occupancy analysis.

We constructed a global model, a null model and several candidate models (Table 1) to investigate our a priori hypotheses regarding *D. rhodogaster* occupancy. For all models excluding the null model we included daily maximum temperature and day of year as detection covariates. Our model hypotheses were: (1) site occupancy is constant, (2) occupancy will decrease with greater burn extent and decrease in the years following fire, (3) occupancy will decrease with greater burn extent, (4) occupancy will decrease with greater burn extent and greater burn severity, (5) occupancy will decrease with greater burn severity and in the years following fire and (6) occupancy will decrease with greater burn extent and differ across parks. We constructed the final global model with burn extent and severity as well as year and park predicting occupancy probability and daily maximum temperature and day of year predicting detection probability.

We confirmed model fit by performing a Mackenzie–Bailey goodness-of-fit test using the function *mb.gof.test* in the *R* package *AICcmodavg* (Mazerolle, 2023) on the global

TABLE 1 Candidate model structures and model selection to investigate hypotheses regarding the detection $p(\cdot)$ and occupancy $\psi(\cdot)$ of the mustard-bellied snake *Drysdalia rhodogaster* in south-eastern Australia (Fig. 1). Models are ranked by quasi-likelihood Akaike information criterion corrected for small sample size (QAICc), which was used because of the small sample sizes and model variances being inflated by a global modal $\hat{c}$ value of 2.14. Models used in model averaging are marked with an asterisk (*).

Hypothesis/model	Model parameters ¹	QAICc	Δ QAICc	Model weight
Null model*	n/a	119.04	0.00	0.48
1*	$p(\text{temp} + \text{day})$	120.66	1.62	0.21
3*	$p(\text{temp} + \text{day}) \psi(\text{ext})$	120.98	1.94	0.18
4	$p(\text{temp} + \text{day}) \psi(\text{sev} + \text{ext})$	123.16	4.12	0.06
2	$p(\text{temp} + \text{day}) \psi(\text{ext} + \text{year})$	124.81	5.77	0.03
6	$p(\text{temp} + \text{day}) \psi(\text{park} + \text{ext})$	124.94	5.90	0.03
5	$p(\text{temp} + \text{day}) \psi(\text{sev} + \text{year})$	127.08	8.04	0.01
Global model	$p(\text{temp} + \text{day}) \psi(\text{sev} + \text{park} + \text{ext} + \text{year})$	131.03	11.99	0.00

¹day, day of year (difference between the survey date and the start of the austral spring on 1 September); ext, fire extent; park, location (national park in which the survey took place); sev, fire severity; temp, air temperature; year, survey year

model. We ran goodness-of-fit tests with 10,000 iterations. χ^2 test results returned non-significant values ($\chi^2 = 1,423.24$, $P = 0.07$), indicating that our global model fit the data; however, we found the models to have mild overdispersion ($\hat{c} = 2.14$). To account for this overdispersion, we inflated the variances of the candidate model covariates by the value of $\hat{c}$ prior to model selection. We assessed model suitability using the quasi-likelihood Akaike information criterion corrected for small sample size (QAICc) and considered model structures suitable if they had the lowest QAICc value or Δ QAICc < 2 compared to the leading model. To provide inferences on covariate impacts on detection and occupancy, we used model averaging with shrinkage on the supported models to generate beta estimates and confidence intervals using the *modavgShrink* function of *AICcmodavg* with an adjusted $\hat{c}$ (Mazerolle, 2023). We generated site occupancy and detection estimates for the most parsimonious model using the *predict* function in R.

Results

Habitat suitability models

Our model predicted the range of *D. rhodogaster* to be considerably larger than current presence records indicate. We predict that the range of *D. rhodogaster* extends north of Hunter Valley along the Great Dividing Range towards the border with Queensland (Fig. 2b). North of 34 °S the predicted distribution of *D. rhodogaster* is restricted to areas > 250 m elevation (Fig. 3c). When intersected with fire extent mapping, c. 46% of the predicted range of *D. rhodogaster* was burnt during the Black Summer.

Field detections and occupancy models

Across the three parks we surveyed 61 sites, representing a total effort of 542 person-hours. Of the 61 sites, we classified

24 as burnt at high severity, 19 as burnt at low severity and 18 as unburnt. We recorded 41 detections of *D. rhodogaster*, with 20 individuals recorded under tin sheets, seven under roof tiles and 14 found during active searches.

We detected *D. rhodogaster* at 16 sites: 11 observations in five sites classified as unburnt, 10 snakes in three sites burnt at low severity and 20 snakes in eight sites burnt at high severity. In the first 12 months after the Black Summer bushfires, 80% of the snakes detected were in burnt areas.

The most parsimonious occupancy model was the null model. However, two additional models were supported. One included detection covariates of daily maximum temperature and day of year and the other contained these detection covariates and also fire extent (Table 1). Park and year were poorly supported (Table 1). Model averaging of the top models found no support for temperature ($\beta = -0.29$, 95% CI: $-1.14, 0.55$) or day of year ($\beta = -0.1$, 95% CI: $-0.39, 0.59$) influencing detection or of fire extent influencing occupancy ($\beta = -0.11$, 95% CI: $-0.66, 0.45$). When only considering the detection covariate model, detection decreased with higher daily maximum temperature ($\beta = -0.64$, 95% CI: $-1.21, -0.07$), and there was no effect of day of year ($\beta = 0.19$, 95% CI: $-0.26, 0.65$). Similarly, the model including fire extent found decreased detection with higher maximum temperature ($\beta = -0.66$, 95% CI: $-1.22, -0.10$) as well as no effects of day of year ($\beta = 0.23$, 95% CI: $-0.21, 0.69$) or fire extent ($\beta = -0.53$, 95% CI: $-1.07, 0.01$). However, we refrain from making inferences regarding these findings based on the low weight of this model relative to the null. Hereafter, we only present data from the most parsimonious (null) model. *D. rhodogaster* showed a low mean site occupancy ($0.3 \pm \text{SD } 0$) as well as low detectability ($0.2 \pm \text{SD } 0$).

Post-fire presence records

Excluding snakes observed by our survey team, a total of 38 records of *D. rhodogaster* were recorded in the Atlas of

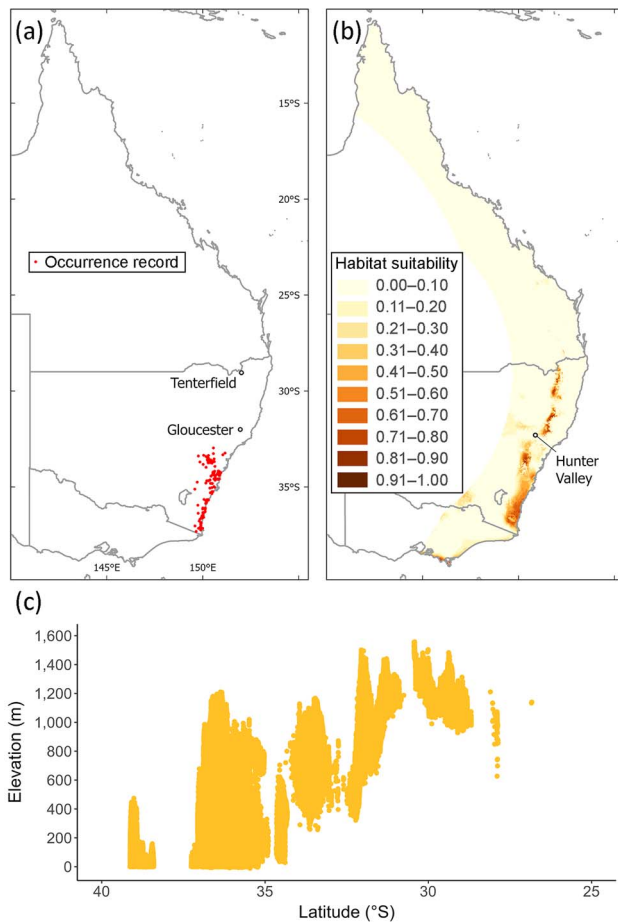


FIG. 2 (a) Occurrence records used for the habitat suitability model of *D. rhodogaster* across the eastern seaboard of Australia. Approximate locations of reliable *D. rhodogaster* records not recorded in the Atlas of Living Australia (2021) near the towns of Gloucester and Tenterfield are indicated. (b) Probability of suitable habitat generated by the habitat suitability model: values closer to 0 represent a low suitability and values closer to 1 represent high suitability. The location of Hunter Valley is indicated. (c) Plot of latitude vs elevation (m) of the locations for which the habitat suitability model for *D. rhodogaster* predicted a probability of suitable habitat > 0.5.

Living Australia in the 2 years after the Black Summer bushfires. Of these, 28 records were from unburnt areas and 10 records were from burnt areas (Fig. 3). Notably, in the first year after the fires all five snakes recorded in the Atlas of Living Australia were detected in areas that had been burnt.

Discussion

Our results show that c. 46% of the predicted distribution of *D. rhodogaster* was burnt during the Black Summer bushfires. However, our field surveys suggest that fire severity and burn extent at the site level probably had negligible impacts on the occupancy of *D. rhodogaster*. Similarly,

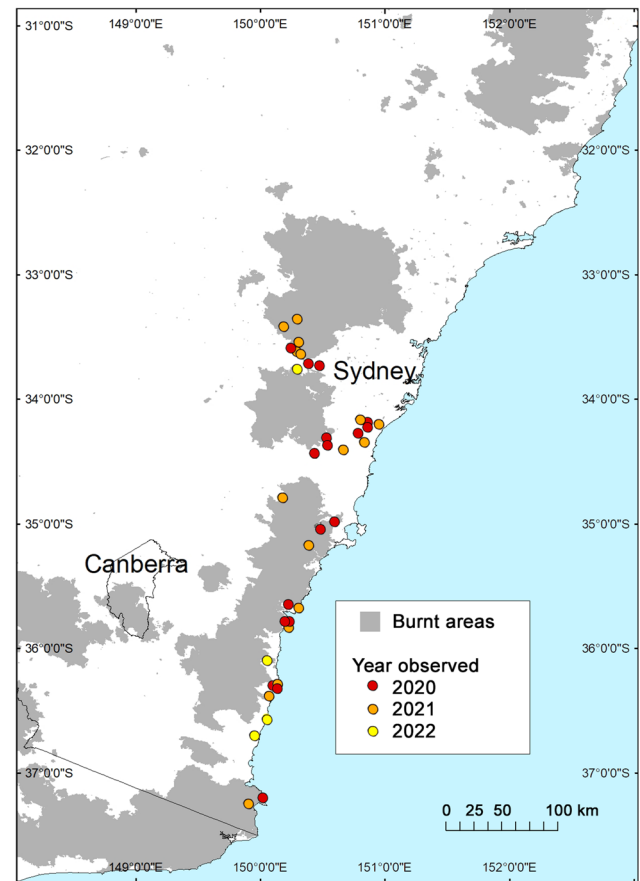


FIG. 3 Records of *D. rhodogaster* used to assess occurrence across the species distribution in south-eastern Australia in the years following the Black Summer bushfires. We obtained locality records from the Atlas of Living Australia (extracted 25 March 2022) and field surveys reported in this study. The shaded area represents areas burnt during the Black Summer bushfires.

occurrence records reported in public databases show that *D. rhodogaster* was recorded in areas that had been burnt during the Black Summer bushfires, with many of these snakes being observed during the first 12 months following the fires. Collectively, the results of our surveys and citizen science records indicate that *D. rhodogaster* has continued to occur in areas burnt by the Black Summer fires, suggesting that the fires had limited effects on the distribution and occupancy of *D. rhodogaster* within forest habitats.

During and immediately following the Black Summer there was significant concern regarding the effects of the fires on wildlife populations. Consequently, understanding the environmental conditions and life histories predisposing taxa to declines or persistence after severe fires is currently a strong focus of research in Australia (Ensby et al., 2023). Several studies have found that rainforest species appear to have been adversely affected by the Black Summer fires (Law et al., 2022a; Beranek et al., 2023), yet for grassland and dry forest species evidence of adverse effects is mixed (Webb et al., 2021; Hartley et al., 2023). However, for some

forest species fire severity appears to be an important factor, with the effects of fire being greatest in areas burnt at high severity (Law et al., 2022a,b; Letnic et al., 2023). Our occupancy models support emerging insights suggesting that the effects of the Black Summer fires have varied markedly between species, as fire severity and burn extent had little effect on the occupancy of forest habitat by *D. rhodogaster*.

The occurrence of *D. rhodogaster* across the landscape post-fire is not unexpected given that the long and narrow bodies of these snakes are well suited to seeking thermally buffered refugia to avoid mortality during wildfires (Pausas, 2019). Soil is an effective buffer against lethal temperatures, with depths as shallow as 6 cm being sufficient to reduce temperatures to c. 30 °C during surface fires (Bradstock & Auld, 1995), which is significantly below lethal temperatures for several closely related elapid snakes (Heatwole & Taylor, 1987). Given that *D. rhodogaster* is a terrestrial snake that often shelters under debris, it is plausible that the animals may have persisted in situ in buffered microsites rather than recolonizing from adjacent unburnt areas (Pausas, 2019). Post-fire composition of reptile communities has previously been found to be better explained by in situ persistence than by recolonization for adjacent unburnt regions (Santos et al., 2022).

Similarly, the post-fire occurrence of *D. rhodogaster* is likely to have been assisted by the low metabolic rates and energy demands that *D. rhodogaster* shares with other reptiles (Else & Hulbert, 1981). These low energetic demands are complemented by the availability of the small skinks on which the snakes prey (Shine, 1981), which are often abundant in post-fire environments (Lunney et al., 1991). Although we did not quantify prey availability, we frequently observed small skinks (e.g. *Lampropholis* spp. and *Saproscincus mustelinus*) at burnt sites, suggesting that food was amply available for snakes after the fires. Understanding the role of prey species in driving the occurrence of snakes post-fire could be an important focus of future research.

Our analysis of post-fire records showed c. threefold more *D. rhodogaster* observations in areas that were unburnt (Fig. 3). However, the presence of records in burnt areas during the 12 months immediately following the fires, including in areas burnt at high severity, suggests that these snakes survived the fires. The number of detections must be interpreted cautiously, as records from the databases used were collected in a non-systematic manner and are thus open to sampling bias. For example, after the Black Summer bushfires, many reserves were closed to the public for varying periods of time because of safety concerns and therefore would not have been accessible to citizen scientists. Covid-19 probably also decreased the input of records because of restrictions on the movements of citizen scientists (Stenhouse et al., 2022). Therefore, although most records of *D. rhodogaster* in the 2 years after the

fires were from unburnt areas, it is important to note that records from burnt areas may have been under-reported because citizen scientists had less access to these areas.

Our habitat suitability model (Fig. 2b) predicted a much broader potential distribution for *D. rhodogaster* than is evident from previous occurrence records (Fig. 2a). Our habitat suitability model predicted that the range of *D. rhodogaster* extends north of Hunter Valley at elevations > 250 m along the Great Dividing Range towards the border with Queensland (Fig. 2b,c). It is possible that our model overestimates the distribution of *D. rhodogaster* because it extends the range of the species into areas where there are no records in the Atlas of Living Australia. However, the reliability of our model is strengthened by published records of *D. rhodogaster* near Gloucester and Tenterfield in northern New South Wales (Fig. 2a), as well as by a specimen collected from the Tenterfield region in November 2020 (Australian Museum, R.188326; Goldingay et al., 1996; Daly & Lemckert, 2011), none of which are reported in the Atlas of Living Australia or included in our model. These populations north of Hunter Valley are probably genetically distinct as the valley is a dispersal barrier for many woodland reptiles (Chapple et al., 2011). Moreover, they may be heavily fragmented or patchily distributed. Further studies are warranted to confirm the relationship between populations separated by the valley and to confirm whether northern populations warrant additional conservation measures. This is particularly important as much of the predicted range of *D. rhodogaster* north of Hunter Valley was burnt in the Black Summer bushfires and because both published records from the region are from land used for recent or ongoing native forestry (Goldingay et al., 1996; Daly & Lemckert, 2011).

Given that the reptile fauna of north-eastern New South Wales has been extensively surveyed (e.g. Milledge 1993; Daly et al., 2011) and there are few reliable records of *D. rhodogaster* from the region, it is possible that biotic factors such as habitat type or competition may be restricting the species. However, because the literature records suggest that *D. rhodogaster* does occur in north-eastern New South Wales (Goldingay et al., 1996; Daly et al., 2011) and our suitability model suggests that the species will be geographically restricted to elevated areas with a cool climate, we believe it is more likely that survey efforts using methods appropriate to detect this cryptic species have been insufficient in climatically suitable habitats. Consequently, we recommend that targeted searches for *D. rhodogaster* are undertaken in areas of suitable habitat (e.g. high-altitude forest) in this region to better determine its status and how it is affected by fire.

Overall, the data on *D. rhodogaster* occupancy in post-fire environments that we have collated from our own surveys and the Atlas of Living Australia suggest that even though a considerable portion of the known and predicted

range of *D. rhodogaster* was burnt in the Black Summer bushfires, the species persists in areas affected by fires. Like many other species, *D. rhodogaster* was of low conservation concern prior to the fires, and little was known about its ecology or population status. Although our research provides some insight into the occurrence of *D. rhodogaster* after an extensive bushfire, the strength of our conclusions is limited by the absence of pre-fire information for this cryptic species. Moving forward, there is a need for a concerted effort to build baseline data on cryptic species categorized as Least Concern, so that more comprehensive comparisons can be made in the wake of future catastrophic events.

Author contributions Study conception: ML, with contributions from MJH; data collection: MJH, AKR, YL, SC, BR, OP, JW, NS, JL, SWL, ML; data analysis: MJH, SWL, HMB, FM, ML; writing: MJH, with contributions from HMB; revision: all authors; funding acquisition: JW, ML.

Acknowledgements We thank the many volunteers who assisted with the fieldwork; Tony Thorne for donating the roof tiles used in the field surveys; Marc Mazerolle for providing statistical advice; and two anonymous reviewers for their comments. This project was funded by the Bushfire Recovery Fund (BWHR-T2_GA-2000634). The University of Sydney has a publishing agreement with Cambridge University Press that facilitated the open access publication of this article.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. All fieldwork methods and animal handling were approved by the University of New South Wales Animal Ethics Committee (20/160B) and the University of Wollongong Animal Ethics Committee (AE1912). The field research was conducted with approval from New South Wales National Parks and Wildlife Service (SL102394).

Conflicts of interest None.

Data availability Occupancy data are available at doi.org/10.6084/m9.figshare.24804003. Pipelines for habitat suitability models are available at github.com/HMB3/habitatIntersect.

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