Megafires attract avian scavenging but carcasses still persist

Thomas M. Newsome | Emma E. Spencer

Global Ecology Lab, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

Correspondence
Thomas M. Newsome, Global Ecology Lab, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
Email: thomas.newsome@sydney.edu.au

Funding information
Holsworth Wildlife Research Endowment; The Australia & Pacific Science Foundation

Abstract
Aim: The effects of fires on vertebrate scavengers have not been characterized despite the importance of scavenging in shaping food web dynamics. We assessed whether the 2019/2020 megafires in Australia shifted the species richness, carcass detection and feeding times of vertebrate scavengers, and whether the fire affected carcasses persistence times.

Location: Blue Mountains, south-eastern Australia.

Method: We monitored vertebrate scavengers via remote cameras on a total of 60 experimentally placed kangaroo carcasses for 30 days in two periods before the megafire (January 2018 and 2019) and one period after the megafire (March 2020) in both open and closed canopy habitats. We compared vertebrate species richness, carcass discovery and scavenging activity before and after the fire and between the two habitats. We also assessed carcass persistence (time to carcass removal) before and after the fire and between the two habitats.

Results: We collected more than 689,000 images of nine vertebrate scavengers including six avian, two mammal and one reptile species. We detected no decline in scavenger species richness following the fire, and rates of carcass detection for mammals and reptiles did not differ across pre- and post-fire periods. On the other hand, avian scavengers detected carcasses faster in the post-fire period and in open compared to closed canopy habitats. Overall, scavengers increased their feeding times in the post-fire period, especially avian scavengers, but carcasses persisted longer in the post-fire period when compared to the second pre-fire period.

Main conclusion: Our study identified that a widespread fire could influence avian scavenging dynamics, but that other factors such as habitat and possibly apex scavenger presence affected carcass persistence times over the study period in addition to fire. Future monitoring of carcasses following fires should focus on the responses by both vertebrate and insect scavengers to fully elucidate the effects of these major disturbance events on critical ecosystem processes linked to decomposition.

Keywords
carcass persistence, disturbance, fire, scavenging
INTRODUCTION

Extreme disturbance events can influence the patterns and processes that shape and drive ecosystem dynamics (Turner, 2010). They can lead to major shifts in resource availability for animal populations, in turn altering their movements and foraging behaviours (Doherty et al., 2021). Such effects have been well documented following fires (Nimmo et al., 2019). Fire causes direct animal mortality, but it also incinerates vegetation, altering plant communities and the availability of food and shelter for biota (Haslem et al., 2011; Smit et al., 2010). This can affect the distribution and abundance of animals, as, for example, they starve, move to find more optimal habitat or are left more vulnerable to predation. On the other hand, some animals may benefit from fires, changing their movement patterns to take advantage of fleeing prey and newly cleared landscapes (Nimmo et al., 2019). Indeed, avian predators including rock kestrels (Falco tinnunculus) and jackal buzzards (Buteo ruffuscus) have been observed selectively hovering over burnt patches in search of food (Barnard, 1987). Terrestrial vertebrate predators such as red foxes (Vulpes vulpes) and feral cats (Felinus catus) are also attracted to recently burnt areas (Geary et al., 2020; McGregor et al., 2016). But in addition to making prey easier to catch, fires could also provide foraging opportunities for vertebrate scavengers if fire-related deaths cause animal carcasses to be abundant.

The effects of fires on vertebrate scavenging dynamics are not well known. This is despite knowledge that scavengers can perform an important ecosystem service by removing dead animal matter from the landscape (Barton et al., 2013; Benbow et al., 2019; Cunningham et al., 2018). In post-fire environments, this may be critical to reduce the spread of diseases or pathogens that can proliferate on or around carcasses. For example, Clostridium botulinum proliferates in carcasses after death and produces botulinum toxin, which is lethal to vertebrates that ingest it (Espelund & Klaveness, 2014). Although obligate scavengers such as vultures are most well known for their ability to rapidly remove carcasses from the landscape, there is increasing awareness that facultative scavengers can rapidly consume and regularly take advantage of animal carcasses (Wirsing & Newsome, 2021). This reflects the conclusion that more energy is transferred within terrestrial food webs as a result of scavenging compared to predation (Wilson & Wolkovich, 2011) and that the role of carrion in nutrient cycling and community dynamics is disproportionately large compared with plant detritus (Barton et al., 2013; Benbow et al., 2019).

The role of carrion in shaping terrestrial food web dynamics is known to vary depending on its quantity and dispersion within an ecosystem (Barton et al., 2019), habitat context (Pardo-Barquin et al., 2019), season (Turner et al., 2017), climate (Barton & Bump, 2019), anthropogenic impacts (Sebastián-González et al., 2019) and scavenger community composition (Sebastián-González et al., 2016). However, scavenging dynamics could shift in unexpected ways following fires. For example, large apex scavengers may be impacted by fires if they cannot escape the burnt areas, in turn diminishing their influence on smaller mesosavengers (O’Bryan et al., 2019) or carcass persistence times (Hill et al., 2018). Habitat is also known to influence scavenging dynamics, with some scavengers preferring open habitats compared to more closed canopy habitats (Roen & Yahner, 2005). For example, monitoring of scavengers on carcass piles in south-central Spain identified that griffon vultures (Gyps fulvus) scavenged more in open habitats, while the red fox and wild boar (Sus scrofa) scavenged more in vegetation-covered habitats (Carrascos-Garcia et al., 2018). Fires could therefore influence carcass detection and feeding times if there is a shift in vegetation structure, with potentially more favourable conditions for avian scavengers if the fire-affected areas become more exposed.

Examining the effects of fires on scavenging dynamics ideally requires monitoring of scavenger populations and carcass persistence times before and after a fire. Such studies are difficult to plan in the absence of management burn scenarios. However, as part of a scavenging study on the edge of the Greater Blue Mountains National Park, in New South Wales south-eastern Australia, we were uniquely placed to study the impacts of a widespread fire event. Specifically, we were monitoring vertebrate scavengers using experimentally placed carcasses (Wirsing & Newsome, 2021). This reflects the conclusion that overall vertebrate scavenger densities declined post-fire, especially ground dwelling species. Carcass densities may have also increased because of fire-related deaths or starvation of animals following the fires. Understanding how this massive disturbance event influenced scavenger populations is critical in a world that is now experiencing increases in the intensity and frequency of natural disasters (Bradshaw et al., 2021; Ripple et al., 2020) that can result in mass animal mortality events and thus an influx of carcasses into the ecosystem (Fey et al., 2015).

Although Australia has no obligate scavengers, it does host a diverse suite of facultative scavengers (Cunningham et al., 2018; Forsyth et al., 2014). In our study site, the largest native/long-established vertebrate scavengers include the dingo (Canis dingo) and wedge-tailed eagle (Aquila audax). Both species have the potential to rapidly consume carcass biomass including bones and could feasibly exclude smaller mesosavengers from accessing carcasses through fear effects (Cunningham et al., 2018; O’Bryan et al., 2019). Native meso-savengers in the study site include ravens (Corvus spp.) and magpies (Gymnorhina tibicen), as well as goannas (Varanus spp.). The study site also has introduced facultative scavengers, namely the red fox and feral cat. The relative use of carcasses by the red fox and feral cat are not well documented in Australia, but red foxes fed on 60% of deer carcasses monitored in the state of Victoria in Australia,
and their scavenging patterns were consistent with the idea that red foxes avoid dingoes (Forsyth et al., 2014). Scavenging by feral cats in the same study was low (10% of carcasses) (Forsyth et al., 2014), but feral cats increased their scavenging rates in the absence of Tasmanian devils (Sarcophilus harrisii) on the island state of Tasmania (Cunningham et al., 2018). Whether red foxes and feral cats increase or decrease their scavenging rates after fires has implications for understanding if carcasses support their populations, and thus potentially exacerbate their impacts on native species (Newsome et al., 2015).

In this study, we compared vertebrate scavenger species richness, carcass detection, feeding times and carcass persistence times before and after a fire. The data were derived from monitoring vertebrate scavengers on experimentally placed eastern grey kangaroo (Macropus giganteus) carcasses, which were on average 30 kg in mass. Because of the potential effects of habitat on scavenging dynamics (Roen & Yahner, 2005), we monitored carcasses in both open and closed canopy habitats before and after the fire. We tested the following predictions: (1) species composition of vertebrates utilizing carcasses will differ as a function of the fire, with decreased scavenger species richness anticipated following the fire event (due to the possible decline in animal numbers; van Eeden et al., 2020); (2) carcass discovery time by vertebrates will differ as a function of fire and habitat type, with carcasses in pre-fire environments (where animal numbers are expected to be higher; van Eeden et al., 2020) and in open habitats (where carcasses are more conspicuous; Roen & Yahner, 2005) having shorter detection times; (3) vertebrate scavenging activity will decrease post-fire for mammals and reptiles (due to their possible decline post-fire; van Eeden et al., 2020) but less so for birds (who are mobile and can typically escape fires; Woinarski & Recher, 1997); and (4) carcass persistence (time to carcass removal) will increase post-fire (due to an overall decline in carcass visitations by scavengers, especially large mammalian scavengers such as dingoes; Spencer & Newsome, 2021). Our results provide the first assessment of how vertebrate scavenger dynamics and carcass persistence times change in relation to a fire event.

2 | METHODS

2.1 | Study site and timing of the fire

Our study was conducted in the Wolgan Valley in the Blue Mountains, south-eastern New South Wales (Figure 1a). The site is approximately 50 km² in size (altitude: 540–680 m) and is positioned on the edge of the Greater Blue Mountains National Park. This site contains a mix of open woodland and grassland habitats, with various Eucalyptus species (e.g. Eucalyptus viminalis and E. haemastoma) and a mix of native (e.g. Austrodanthonia sp. and Themeda triandra) and introduced (e.g. Microlaena stipoides) grasses. The climate is temperate, with average maximum temperatures of 27°C recorded in January and 11°C in July (nearest station 30 km away at Lithgow, records from 1878 to 2020; Bureau of Meteorology, 2021).

The fire reached the study site in December 2019. It was connected to a larger mega-fire in the Blue Mountains world heritage area (i.e. the Gospers’ Mountain fire, which burnt more than 510,000 ha in total; Boer et al., 2020). The fire burned approximately 90% of the entire study site (which comprised woodland and grassland habitat) over a period of one and a half months (between the 16th of November and the 22nd of December, although spot fires were present before and after these dates). There was virtually no unburnt ground cover left in the woodland or grassland habitats after the fires, although subsequent rains approximately one month (in February 2020) after the fire did result in the grassland habitats re-growing quickly (See Figure 1b–e for habitat comparisons in pre- and post-fire study periods). [Correction added on 20 November 2021, after first online publication: year has been updated in the first and last sentence of this paragraph.]

2.2 | Carcass monitoring

Carcass monitoring was conducted over three 1-month periods in the warm seasons of summer and autumn. The first two monitoring periods were conducted before the fire, in January 2018 and 2019, and the third was conducted in March of 2020, which was the first possible opportunity (due to study site access restrictions) to conduct follow-up research after the fire. Temperatures are similar between January and March (Bureau of Meteorology, 2021), and no major shifts in scavenger activity are likely. Comparisons between the two periods before the fire and one period after fire allowed for an assessment of whether the fire drove larger differences in scavenging dynamics than those observed between years before the fire. This approach reflects the fact that scavenging rates and species interactions around carcasses are influenced by anthropogenic impacts (Sebastián-González et al., 2019) and/or scavenger community composition (Sebastián-González et al., 2016), which can vary from year-to-year irrespective of background environmental conditions. Indeed, there was active poison baiting and shooting programmes targeting dingoes in the study site before the study began. Thus, our approach of including data from two monitoring periods before the fire allows us to capture and assess any variability in scavenging dynamics before the fire. This is arguably more robust than only including one monitoring period before the fire or lumping the two monitoring periods before the fire together.

During each monitoring period, we distributed 20 adult eastern grey kangaroo carcasses in an equal mix of open grassland (hereafter “open canopy”; n = 10 sites) and forest (hereafter “closed canopy”; n = 10 sites) habitat (Figure 1). Open canopy sites were at least 50 m from any stands of trees. The closed canopy sites had more than 20% canopy cover before the fire, and in the post-fire period carcasses were placed in forested locations where there was previously canopy cover of more than 20%. Estimated tree canopy cover within the closed canopy sites differed across periods, with the greatest variation occurring between the post-fire period (mean ± SE; 31.1 ± 4.6%...
coverage) and the pre-fire periods (first pre-fire period: 56.4 ± 3.1% coverage, second pre-fire period: 48.8 ± 2.9% coverage). Within monitoring periods, carcasses were separated by at least 1 km to mitigate scent travel between carcasses. Between monitoring periods, however, carcasses were positioned at least 100 m from any previous carcass placement. Carcasses from previous placements were not expected to influence animal behaviour, as they all were removed by scavengers within weeks of their placement and carcasses are generally common across this landscape. We used dead kangaroos sourced from nearby management culls, so no animals were killed for the purpose of this study. Any carcass displaying evidence of disease (e.g. heavy parasite loads) was not used. All carcasses were placed into the field without freezing within 24 hr of collection (i.e. all at the same time, with 24 hr being the longest time between the first and last carcass placement; January 2018; 9:00–23:00, January 2019; 8:00–13:00, and March 2020; 23:00–6:00). Scientific licences/permits were obtained to relocate the kangaroo carcasses (SL 101901), and research was approved by the University of Sydney Animal Ethics Committee (Project number: 2017/1173).

To allow for ongoing monitoring and detection of scavengers visiting and feeding on each carcass, we used a Reconyx PC800 Hyperfire™ camera trap (Professional Reconyx Inc., Holmen, WI, USA) attached to a free-standing star picket 3–4 m away from each carcass. The cameras were programmed to take continuous photographs when triggered by thermal movement around the carcass (rapidfire, no wait period). To prevent complete removal of the carcasses away from the remote camera monitoring frame, we secured carcasses to the ground by wire attaching the neck and achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. Cameras were used to monitor carcasses for 30 days to capture the main period of vertebrate scavenging activity and because the majority of carcass biomass (including meat, skin and bones) were removed from the environment in this time.
2.3 | Data collection

Camera images were tagged according to each new carcass visitation event by a different species, the number of individuals of a species present, whether any of the individual species fed on the carcass or not, and the date and time that the observation was recorded. A visitation event was considered new if it occurred ≥10 min from the previous visitation event by the same species. We defined scavenger species as species that were observed feeding on at least one carcass over the three study periods. All other animals captured on the remote cameras were excluded from our analyses. Finally, using a combination of in-person visual inspection of the carcasses and inspection of camera images, we determined the number of days until complete carcass consumption. A carcass was defined as completely consumed when less than 5% meat biomass and only skin, hair and/or bone remained.

2.4 | Statistical analysis

We analysed differences in species richness and composition, detection time, feeding time and carcass persistence across study periods and habitats. We conducted analyses on all vertebrate scavengers grouped together and then separately on all avian, mammal and reptile scavenger groups when assessing carcass discovery and feeding times. We conducted our analyses in R Version 4.0.2 (R Development Core Team, 2020).

We assessed scavenger species composition by (1) calculating the per cent occurrence for each vertebrate scavenger species documented visiting carcass sites (i.e. the number of carcasses where a species occurred divided by the total number of carcasses), and (2) by evaluating differences in overall vertebrate scavenger richness across different study periods and habitats. Scavenger species richness was calculated as the total number of scavenger species that visited a carcass. To determine whether scavenger species composition differed as a function of fire (Prediction 1), we used generalized linear models (GLMs) with Poisson distribution (Package: lme4; Bates et al., 2015) to compare the species richness of all vertebrate scavengers across each period (first pre-fire period, second pre-fire period and post-fire period) and habitat (open, closed). We therefore conducted a GLM with a negative binomial distribution using how long each species group fed in minutes (Package Mass; Ripley et al., 2021). We interpreted competitive models (ΔAICc < 2), which we selected from a suite of models fitted with all possible parameter and the interaction: habitat × period. To select models, we used a model selection procedure (Package MuMln; Bartoń, 2020) based on minimizing the Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). While data dredging may lead to the selection of biologically inappropriate models, all the models used during this process made biological sense. We visually assessed model predicted values against the residual values to confirm that each model met their necessary assumptions.

Discovery time was calculated in decimal hours as the time between when the carcass was first positioned and the arrival of the first visiting scavenger or visiting scavenger within a group. To determine whether carcass discovery time by vertebrates differed as a function of fire and habitat type (Prediction 2), we performed survival analyses using Cox proportional hazards models on the time taken for carcasses to be discovered in hours (Package Survival: Therneau, 2021). Survival analyses work well with censored data (Hosmer et al., 2008). Carcass discovery data were right-censored because some carcasses were not discovered by species groups by the end of monitoring periods. We ran three separate analyses investigating how long carcass discovery took for all scavenging vertebrates and then separately for the three scavenger groups (avian, mammalian and reptile). For all analyses, period (first pre-fire period, second pre-fire period and post-fire period) and habitat (open, closed) were used as the predictor variables. Again, we interpreted competitive models (ΔAICc < 2), which we selected from a suite of models fitted with all possible parameter and the interaction: habitat × period. Post hoc analyses were used to investigate differences in the total feeding times across the three different periods, and the interaction term habitat × period (if it was included in the model), and were calculated using Holm–Bonferroni log-rank tests for post hoc analysis (Package survminer; Kassambara et al., 2021). For all models, we tested the proportional hazards assumption by visualizing the survival curves and by testing the non-zero slope for the Schoenfeld residuals versus time (Therneau & Grambsch, 2000). To visualize the results, we separated data into carcasses monitored across the three different periods, and in open and closed canopy habitats and present the Kaplan–Meier estimates of the survival function comparing two survival curves for each scavenger group (Package ggplot; Wickham et al., 2020).

Total feeding time was calculated as the sum of all feeding events at a given carcass for each species, species group or for the combination of all species. We calculated the duration of a feeding event by subtracting the time at the start of the visit from the time at the end of the visit. We rounded all feeding visits to the closest minute; however, for visits less than 30 s, we considered the species present for 1 min rather than 0 min. To test if scavenging activity decreased post-fire (Prediction 3), we used three GLMs to evaluate foraging activity for all scavenger vertebrates and separately for each scavenger group, across different periods (first pre-fire period, second pre-fire period and post-fire period) and habitat (open, closed). Foraging data followed a Poisson distribution but were overdispersed (based on the global models: all: ϕ = 199.10; p < .001; bird: ϕ = 190.22; p < .001; mammal: ϕ = 112.90; p < .001; reptile: ϕ = 63.32; p < .001) and quasipoisson models did not produce acceptable residual versus fitted plots. We therefore conducted a GLM with a negative binomial distribution using how long each species group fed in minutes (Package Mass; Ripley et al., 2021). We interpreted competitive models (ΔQICc < 2), which we selected from a suite of models fitted with all possible parameters and the interaction: habitat × period. In this case, we used a model selection procedure based on minimizing the quasi-likelihood information criterion corrected for small sample sizes (QICc). QICc is a modification of AICc where the model parameters are estimated using quasi-likelihood and can be used to compare models with negative binomial distribution. We
visually assessed model predicted values against the residual values to confirm that each model met their necessary assumptions. We investigated differences in the total feeding times across the three different periods using Holm–Bonferroni tests for post hoc analysis (Package emmmeans; Russell et al., 2021).

We defined carcass persistence (time to removal) as the time elapsed between carcass placement and complete carcass consumption or decomposition where less than 5% meat biomass, and only skin, hair and/or bone remained. To determine whether carcass persistence increased post-fire (Prediction 4), we performed survival analyses using Cox proportional hazards models on data for the time taken in days for complete carcass decomposition. Period (first pre-fire period, second pre-fire period and first post-fire period) and habitat (open, closed) were used as the predictor variables. Competitive models (ΔAICc < 2) were interpreted and were selected from a suite of models fitted with all possible parameters and the interaction: habitat × period, using a model selection procedure (AICc). To visualize the results, we separated data into carcasses monitored over the three periods and across open and closed canopy habitats and presented Kaplan–Meier estimates of the survival function comparing survival curves. Differences in the total feeding times across the three different periods were investigated using Holm–Bonferroni log-rank tests for post hoc analysis.

3 | RESULTS

We monitored 60 kangaroo carcasses (including 40 kangaroo carcasses before and 20 carcasses after the fire event), resulting in a total of 1,800 observation days and more than 689,000 photo images taken between January 2018 and April 2020.

3.1 | Scavenger species composition

We recorded nine scavenger species during our study (Appendix S1). The species most frequently documented at carcass sites (i.e. visitation >60% of carcasses) included dingoes (Canis dingo; 90% of carcasses, n = 54), lace goannas (Varanus varius; 87% of carcasses, n = 52), Australian ravens (83% of carcasses, n = 50) and red foxes (62% of carcasses, n = 37) (Table 1). Overall, mean ± SE scavenger species richness was 3.9 ± 0.1 (range: 2–7). Two models of scavenger species richness were competitive (ΔAICc < 2) (Appendix S2). The first model included the intercept only (ΔAICc = 0.00) and the second model included habitat only (ΔAICc = 1.18) (Appendix S2). For the second model, mean species richness was similar between the open (4.2 ± 0.2) and closed (3.7 ± 0.2) canopy habitats (z = 0.98, p = .33) (Appendix S2).

| TABLE 1 | Per cent (%) frequency of occurrence of scavenger species detected at kangaroo carcasses across the three study periods and open (n = 10 carcasses per period) and closed (n = 10 carcasses per period) canopy habitat |
|----------|---------------------------------------------------------------------------------|---------------------------------------------------------------------------------|---------------------------------------------------------------------------------|---------------------------------------------------------------------------------|
| Scavenger species | January 2018 (First pre-fire period) | January 2019 (Second pre-fire period) | March 2020 (Post-fire period) | Overall % occurrence |
| | Closed | Open | Closed | Open | Closed | Open | Closed | Open |
| Mammal | | | | | |
| Dingo (Canis dingo) | 100 (90) | 100 (100) | 100 (80) | 100 (100) | 100 (90) | 80 (80) | 97 (90) |
| Red fox (Vulpes vulpes) | 80 (50) | 90 (80) | 100 (80) | 100 (100) | 90 (90) | 80 (80) | 90 (80) |
| Avian | | | | | |
| Australian raven (Corvus coronoides) | 90 (90) | 100 (100) | 60 (30) | 90 (80) | 100 (90) | 100 (100) | 90 (82) |
| Australian magpie (Gymnorhina tibicen) | 30 (0) | 10 (0) | 30 (10) | 60 (20) | 20 (10) | 60 (10) | 35 (8) |
| Wedge-tailed eagle (Aquila audax) | 10 (0) | 20 (10) | 0 (0) | 30 (30) | 30 (30) | 60 (50) | 25 (20) |
| Willie wagtail (Rhipidura leucophrys) | 0 (0) | 10 (0) | 0 (0) | 20 (10) | 0 (0) | 10 (0) | 7 (2) |
| Brown falcon (Falco berigora) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 10 (10) | 2 (2) |
| Indian miner (Acidotheres tristis) | 0 (0) | 0 (0) | 0 (0) | 10 (10) | 0 (0) | 0 (0) | 2 (2) |
| Reptile | | | | | |
| Lace goanna (Varanus varius) | 100 (100) | 80 (70) | 90 (80) | 90 (90) | 90 (90) | 70 (60) | 87 (82) |

Note: *Numbers in brackets are the per cent frequency of scavengers that consumed part of the carcasses.
3.2 Discovery time

All carcasses monitored were detected and fed upon by at least one vertebrate scavenger. The most common species to first detect carcasses were Australian ravens (45% of carcasses), then lace goannas (28% of carcasses), red foxes (12% of carcasses) and dingoes (10% of carcasses). The mean ± SE time to first detection was 26.4 ± 2.9 hr. Mammals detected 97% of carcasses and fed on 90%, with a mean detection time of 95.4 ± 17.2 hr. Avian scavenger species detected 90% of carcasses and fed on 82%, with a mean detection time of 62.6 ± 8.8 hr. See Appendix S1 for species-specific carcass detection times over the three study periods.

For all scavenger species, two models of discovery time were competitive (ΔAICc < 2) (Appendix S3). The first model only included habitat (ΔAICc = 0.00) and the second model included habitat and period (ΔAICc = 0.08) (Appendix S3). In both models, carcasses were detected faster in open compared to closed canopy habitats (Model 1/Model 2: z = 2.13, p = .03; Appendix S3) (Figure 2a). Post hoc tests and the Kaplan–Meir survival curves indicated that there were no significant differences between the first pre-fire period and the second pre-fire period (Holm-Bonferroni log-rank test: p = .09) and between the first pre-fire period and the post-fire period (p = .51), or the post-fire period and the second pre-fire period (p = .46) (Figure 2b).

For mammalian scavengers, only one model of discovery time was competitive (ΔAICc < 2) (Appendix S3). This model was the global model including habitat, period and the interaction between habitat and period (ΔAICc = 0.00; Appendix S3). There were no significant differences in detection time for mammals between habitats (z = −0.78, p = .44) (Appendix S3; Figure 3a). Post hoc tests and the Kaplan–Meir survival curves also indicated that there were no significant differences between the first pre-fire period and the second pre-fire period (Holm-Bonferroni log-rank test: p = .10) or the second pre-fire period and the post-fire period (p = .25), but there was a difference between the post-fire period and the first pre-fire period (p = .01) (Figure 3a). Post hoc tests and the survival curves further showed that carcasses were detected similarly across open compared to closed canopy habitats in the first pre-fire period (Holm-Bonferroni log-rank test: p = .09), in the second pre-fire period (p = .39) and in the post-fire period (p = .55) (Figure 4).

For the avian scavengers, only one model of discovery time was competitive (ΔAICc < 2) (Appendix S3). This model included habitat and period (ΔAICc = 0.00) and showed that birds detected carcasses at a greater rate in open compared to closed canopy habitat (z = 3.30, p = .001) (Figure 3b; Appendix S3). Post hoc tests and the survival curves also showed that carcasses were detected faster in the post-fire period compared to the first pre-fire period (Holm-Bonferroni log-rank test: p = .005) and in the post-fire period compared to the second pre-fire period (p = .002), but there were no significant differences in detection time between the first pre-fire period compared to the second pre-fire period (p = .09) (Figure 3b).

For the reptile scavengers, there were three competitive models of discovery time (ΔAICc < 2) (Appendix S3). The first model included habitat (ΔAICc = 0.00), the second included the intercept only (ΔAICc = 1.20), and the third included both habitat and period (ΔAICc = 1.92) (Appendix S3). There were no significant differences in detection time for reptiles between open or closed canopy habitats (Model 1: z = −1.81, p = .07; Model 3: z = −1.70, p = .09) (Figure 3c; Appendix S3). Post hoc tests also showed that there were no significant differences in detection time between the post-fire period and the first pre-fire period (Holm-Bonferroni log-rank test: p = .42), the post-fire period and second pre-fire period (p = .42), or the first pre-fire compared to the second pre-fire period (p = .80) (Figure 3c).

3.3 Scavenging activity

Scavengers spent a mean 295.8 ± 40.4 SE minutes feeding on carcasses. For all scavenger species, two models of scavenging time were competitive (ΔQICc < 2). The first model included habitat and period (ΔQICc = 0.00) and the second model was the global model (ΔQICc = 1.78) (Appendix S4). We chose to only interpret the first model because it was the most parsimonious and the interaction was not found to be important. Scavenger species spent a significantly longer time feeding in open (397.2 ± 65.3 min) compared to closed canopy habitat (194.4 ± 49.7 min; z = 2.98, p = .003) (Appendix S4). Post hoc tests also showed that scavengers spent significantly longer feeding on carcasses in the post-fire period (467.0 ± 89.2 min) compared to the second pre-fire period (194.5 ± 46.0 min; Holm-Bonferroni test: z = 3.14, p = .005), but there were no significant differences between the post-fire period and the first pre-fire period (226 ± 52.5 min; z = 2.08, p = .07), and the first and second pre-fire periods (z = 1.06, p = .29).

For the mammalian, avian and reptilian scavengers, two models of scavenging time were competitive for each group (ΔQICc < 2). For mammals, the first model included habitat (ΔQICc = 0.00) and the second included the intercept only (ΔQICc = 0.62) (Appendix S4). For birds, the first model included habitat and period (ΔQICc = 0.00) and the second was the global model (ΔQICc = 0.96) (Appendix S4). For reptiles, the first model included the intercept only (ΔQICc = 0.00) and the second included habitat only (ΔQICc = 0.40) (Appendix S4). We did not detect differences in feed time between open and closed canopy habitat for mammals or for reptiles (mammals: open: 130.3 ± 24.7 min, and closed: 68.1 ± 16.5 min; z = 1.93, p = .054; and reptiles: open: 19.5 ± 6.7 min, and closed: 36.5 ± 9.6; z = −1.47, p = .14) (Appendix S4). For birds, we chose to only interpret the first model because it was the most parsimonious and the interaction was not found to be important. This model showed a significant difference in feeding times in open (280.4 ± 69.2 min) compared to closed (92.7 ± 28.3 min) canopy habitats (z = 3.02, p = .003) (Appendix S4). Post hoc tests also showed greater feeding between the post-fire period (394.7 ± 95.4 min) compared to the first (102.6 ± 32.6 min; Holm-Bonferroni test: z = 3.51, p = .001) and to the second
NEWSOME and SPENCER

(62.5 ± 24.0 min; z = 3.91, p < .001) pre-fire periods, although there were no significant differences found between the first and second pre-fire periods (z = 1.99, p = .09) for this scavenger group.

In terms of individual species responses, ravens fed the longest in both open (214.0 ± 54.1 min) and closed (87.8 ± 28.0 min) canopy habitats. Similarly, in the first pre-fire and the post-fire period on average, ravens fed on carcasses for the longest times (first pre-fire period: 87.6 ± 28.9 min; post-fire period: 323.3 ± 75.1 min), although dingoes fed on carcasses for the longest times in the second pre-fire period (122.1 ± 35.9 min) (Appendix S1).

3.4 | Carcass persistence

Mean ± SE carcass persistence time was 5.6 ± 0.3 days (n = 60). There were two models of carcass persistence time that were competitive (ΔAICc < 2) (Appendix S5). The first model included period (ΔAICc = 0.00) and the second included both period and habitat (ΔAICc = 1.55) (Appendix S5). Persistence time did not differ across open or closed canopy habitats (z = 0.82, p = .41) and post hoc tests and the survival curves indicated no significant differences between the first pre-fire and the post-fire period (Holm-Bonferroni log-rank test; p = .470), but they did show that carcasses persisted longer in the post-fire period compared with the second pre-fire period (p < .001), and in the first pre-fire period compared to second pre-fire period (p < .001) (Appendix S5; Figure 5).

4 | DISCUSSION

We present the first study examining the effects of wildfire on vertebrate scavenging dynamics and carcass persistence times. Our results reveal substantial variation in how fire influences different scavenger groups and indicate that avian scavenging was most strongly affected by the fire event. Our findings also highlight the potential importance of other factors such as habitat in influencing scavenger dynamics. Against Prediction 1, we did not find an overall decrease in scavenger species richness following the fire. Similarly, against Prediction 2, overall scavenger detection times did not decline from pre- to the post-fire period. Instead, we found that avian scavengers detected carcasses at a faster rate following the fire event. In support of Prediction 2, we did, however, find that scavengers detected carcasses faster in open compared to closed canopy habitats, although it was only birds and not mammals or reptiles that showed faster carcass detection in the open habitats. Overall, scavengers increased their feeding times in the post-fire period, against Prediction 3. However, this trend was likely driven by avian scavengers, as mammals and reptiles did not change their feeding times across the three study periods. Finally, in partial support of Prediction 4, we found that carcasses persisted longer in the post-fire period, but only when compared to the second pre-fire period. We interpret these findings and explore potential implications of the study below.
the scavenging activity of mammal and reptile scavengers. It is possible that the fire did not reduce the overall numbers of scavenging animals at our study site. Our study site experienced a long, slow burn that took approximately 1.5 months to move completely across the area. This might have allowed animals to flee into safer territory or to move around the fire front into previously burnt areas. Most
of the scavengers we recorded were relatively mobile, with 8 of 9 scavengers comprising species of birds or larger mammals (e.g. red foxes and dingoes), which are all capable of rapid movement over long-distances (Geary et al., 2020; Nimmo et al., 2019). For scavengers that were not as mobile, such as lace goannas, finding refuge in their own or other animal burrows (e.g. wombat burrows see Old et al., 2018; Thornett et al., 2017) may have allowed them to survive burnovers.

It is also possible that some scavenging animals increased in number following the fires. Indeed, we found that fire had a positive effect on avian scavengers who detected carcasses faster and increased their scavenging activity during the post-fire period. Corvids and large predatory birds including eagles and raptors are known to travel to fire-affected areas to hunt fleeing prey and to take advantage of burnt landscapes that provide reduced cover for their prey (Nimmo et al., 2019). This could translate to localized increases in avian populations and higher scavenging activities post-fire. This may explain why avian scavengers, and particularly Australian ravens and wedge-tailed eagles (see Appendix S1), scavenged more in the post-fire period during our study. Some scavenging mammals, including red foxes and dingoes, may also respond positively to fire (Geary et al., 2020), but these species are probably slower to disperse when compared to large birds with the capacity of soaring flight. This might at least partially explain why bird but not mammal scavenging activities increased in our study following the fire.

Animal scavenging in post-fire periods may have also been influenced by decreased opportunities for preferred food sources, such as live prey. In Australia, there are no obligate scavengers, and most carnivores that feed on carcasses function also as predators (DeVault et al., 2003). Thus, Australian scavengers could show dietary preferences for live prey and only scavenge carcasses opportunistically or when their preferred food is limited. Fewer live prey resulting from a widespread fire event could thus trigger animals to switch from predation to scavenging. This switch may be further

---

**FIGURE 4** Kaplan–Meir estimate of the survival function for carcass discovery time for mammalian scavengers across open (yellow) and closed (green) canopy habitats in the (a) first pre-fire period during January 2018 (b) second pre-fire period during January 2019 and (c) post-fire period during March 2020 in the Wolgan Valley. Light shading shows 95% confidence intervals.
facilitated if scavenging opportunities in the post-fire environment increase. Indeed, carcasses may be produced frequently due to fire related deaths, starvation and predation in post-fire environments (van Eeden et al., 2020). If carcasses were present in high numbers during the post-fire period, this may have also influenced our findings. For example, if scavengers were heavily using carcass resources other than those supplied by our survey effort, the results may have underestimated scavenging rates post-fire. We did not, however, observe elevated carcass densities in the post-fire environment (based on conducting several 1 km transect searches for other carcasses) and therefore feel it is unlikely that this influenced our results.

Fires might also influence scavenging dynamics by burning and reducing vegetation cover, which could increase the conspicuousness of carcasses and, in turn, how easily they are detected by scavengers. Indeed, habitat is often considered an important factor in shaping scavenging dynamics, with open habitats typically showing higher rates of scavenging compared with closed canopy habitats (e.g. Carrasco-Garcia et al., 2018). While we did not identify any clear trends suggesting that fire influenced changes in the detectability of carcasses by all scavengers combined, or by the three scavenger groups, we did observe changes in vegetation coverage between pre- and post-fire periods in the closed canopy habitat, where canopy cover was reduced in the post-fire period. Further, we also found differences in the detection times of specific scavenger species across habitats in the pre- and post-fire periods. For example, in both pre-fire periods Australian ravens took substantially longer to detect carcasses in closed compared to open habitats (first pre-fire period, open: 66.54 ± 28.12, closed 212.24 ± 65.81; second pre-fire period, open: 15.70 ± 6.13, closed 296.95 ± 95.95), while detection times across habitats in the post-fire period were more comparable (open: 19.14 ± 5.43, closed 52.73 ± 21.60). The importance of habitat influencing carcass conspicuousness is also evidenced by our findings that show increased carcass detection and scavenging activity by birds in open compared to closed canopy habitat. While it is possible that the differences observed across habitats occurred as a result of variation in scavenger density between the two habitat types, it is most likely that carcasses were scavenged at a greater rate in open canopy habitat because they were more conspicuous than those in closed canopy habitat. For example, while ravens at our study site nest and forage in the closed canopy (forest) habitat, on average they detected carcasses at a much faster rate in the open canopy (grassland) habitat (mean ± SE; open: 35.8 ± 11.4 min; closed: 157.6 ± 41.7 hr). That open canopy habitat had a positive effect on birds but not mammals may provide further explanation for why birds were more strongly influenced by the fire event compared to mammals.

4.2 Species interactions and carcass persistence

Scavenger dynamics are influenced by a range of abiotic and biotic factors (Newsome et al., 2021). Indeed, at a global scale, patterns in vertebrate scavenging have been shown to differ according to season, latitude, rainfall, habitat, presence of apex scavengers/predators and human impact (Sebastián-González et al., 2019; Turner et al., 2017). It is likely that some of the variation we observed across study periods was caused by factors other than fire. For example, red fox occurrence on carcasses was highest in the first pre-fire period (95%), lowest in the second pre-fire period (40%), and still low in the post-fire period where red foxes only visited 50% of carcasses. Scavenging activity by red foxes was also variable, and in the second pre-fire period red foxes did not feed on any carcasses, while in the post-fire period they scavenged for an average of only ~8 min compared to their average feed time of ~42 min during the first pre-fire period. While it is possible that red foxes were suppressed by the fire, a recent global review of predator responses to fires indicated...
that this predator species mostly responded positively to fire (Geary et al., 2020) and fire suppression does not provide an adequate explanation for their low scavenging activity in the second pre-fire period. Instead, red fox scavenging in our study site may have been influenced by competition with larger co-occurring scavenging species, specifically the dingo. Dingoes were detected (100%) and fed (90%) on most carcasses during the second pre-fire period, when red fox scavenging was at its lowest. Dingoes were also relatively active in the post-fire period (detected and fed on 85% of carcasses), when red fox scavenging was again low, and showed the lowest scavenging activity in the first pre-fire period (dingoes detected 85% of carcasses but only fed on 65%), when red foxes were most active. The ability of larger scavengers to outcompete and exclude smaller scavengers from carcasses has been shown in multiple studies (Prugh & Silvy, 2020) and is incorporated into theory (O’Bryan et al., 2019), and our results are consistent with the idea that red foxes avoid dingoes at carcasses (Forsyth et al., 2014).

The high occurrence of dingoes visiting and feeding on carcasses in the second pre-fire period potentially also explains why there were higher persistence times for carcasses in the first pre-fire period and to a lesser extent in the post-fire period. The ability of larger scavengers to rapidly consume carcasses is well recognized, but most research has focused on the scavenging efficiency of obligate scavengers such as vultures (Hill et al., 2018). Concurrent research in the study area and other parts of Australia has identified that dingoes can act as efficient scavengers and decrease carcass persistence times under some circumstances (Spencer & Newsome, 2021). Low scavenging activity by dingoes in the first pre-fire period may have been due to active poison baiting and shooting programmes that took place before the study began. Our carcass persistence results might therefore reflect both the cascading effects of removing dingoes, but also that the fire itself had little impact on dingo scavenging. However, more detailed analyses would help to determine the exact relationship between dingoes, red foxes and carcass persistence in our study area.

A key factor that we did not examine was the responses to fire by insect scavengers. Insects can accelerate decomposition, and flies, beetles and ants can double the rate of biomass loss from small vertebrate carcasses in only a few days (Barton & Evans, 2017). Future studies assessing the effects of fire on scavenging and carcass persistence should therefore assess patterns in insect scavenging. Our study was also only conducted in the warmer seasons when insect activity would have been at its height and therefore did not consider the effects of fire on scavenging activity or carcass persistence times during cool periods. This is important to note because in cool periods burnt landscapes may influence carcass removal differently, because vertebrates typically play a greater role in carcass removal during these times due to reduced competition with insects and microbes (DeVault et al., 2003). In addition, our study did not assess whether carcass state (i.e. as burnt or unburnt) influences scavenger dynamics or carcass persistence. Previous studies have shown that insect scavenging activity and decomposition rates are increased on burnt carcasses (McIntosh et al., 2017). Determining how burnt carcasses are scavenged post-fire would contribute to understanding on whether animals killed and burnt in the fires decompose differently to animals that die without any significant burn damage.

We also acknowledge that our study was opportunistic in the sense that we happened to be undertaking scavenging studies in an area that was severely affected by the 2019/2020 bushfires. Greater insights could be gained from using a more standard before-after-control-impact experimental design, but that would also likely require a study that is designed around controlled management burning. Our study site was also on the edge of a much larger fire that burnt 510,000 hectares of forest (Boer et al., 2020) and eventually joined four other fires to burn over 1 million hectares of land. The fire that impacted our study site was slow moving and was low intensity in some places, and our study site also was relatively close to unburnt habitat (<10 km). Major shifts in bird, mammal and reptile scavenging rates may therefore be expected in areas where the fire intensity was greater, or towards the core or middle of fire affected area where animals may have little refuge to escape into. An additional factor that we were not able to assess was the immediate impacts of the fire. Our post-fire survey occurred >2 months after the fire went through because the study site was not accessible straight after the fires. The local activity of predators such as dingoes and feral cats can increase within weeks rather than months post-fire (Leahy et al., 2015). Future scavenging studies should therefore aim to monitor carcasses straight after the fires, if feasible. Such studies would coincide with the period when the carcasses of animals directly killed by the fires might be present, albeit potentially burned. Later studies (months post-fire) would coincide with the period when animals might be dying from starvation depending on the extent of disturbance created by the fire. In our study, however, there were no signs of excess carcasses in the landscape or kangaroos in poor condition due to the follow-up rains that resulted in rapid grass growth in open areas.

5 | CONCLUSIONS

Our study identified that carcass use by avian scavengers increased post-fire, but that a slow-moving fire may not have a major influence on overall vertebrate scavenger species richness or carcass persistence times. Although the results are likely to be different in areas more severely affected by fires, we suggest that other factors such as the presence or absence of apex scavengers may have contributed to some of the trends we uncovered. Nonetheless, our study demonstrates that carcass monitoring can be used to assess species responses to disturbance events such as fires. Given the importance of scavenging in shaping ecosystems (Wilson & Wolkovich, 2011), combined with our limited understanding of the impacts of fires on scavenging dynamics, there is a need to better understand how fires influence ecosystem processes linked to decomposition in order to inform how post-fire landscapes should be managed.
ACKNOWLEDGEMENTS
We are indebted to the Emirates One & Only Wolgan Valley Resort for providing access, accommodation and other resources during field studies in the Wolgan Valley, Blue Mountains. The assistance provided by local landholders and landholders in the Mudgee region, central New South Wales, who helped provide materials for this project was very much appreciated. We are also very thankful to the many co-workers and volunteers who provided support and assistance in the field. Funding was provided by the Holsworth Wildlife Research Endowment and The Australia & Pacific Science Foundation.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publo ns.com/publon/10.1111/ddi.13390.

DATA AVAILABILITY STATEMENT
Data analysed for this paper have been uploaded to Dryad (https://doi.org/10.5061/dryad.1g1jwstwq).

ORCID
Thomas M. Newsome https://orcid.org/0000-0003-3457-3256

REFERENCES
Barnard, P. (1987). Foraging site selection by three raptors in relation to grassland burning in a montane habitat. African Journal of Ecology, 25, 35–45. https://doi.org/10.1111/j.1365-2028.1987.tb01088.x
Bartoń, K. (2020). Package `MuMln`. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf
Barton, P. S., & Bump, J. K. (2019). Carrion decomposition. In P. P. Olea, P. Mateo-Tomás, & J. A. Sánchez Zapata (Eds.), Carrion ecology and management (pp. 101–124). Springer International Publishing.
Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., & Manning, A. D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia, 171, 761–772. https://doi.org/10.1007/s00442-012-2460-3
Barton, P. S., & Evans, M. J. (2017). Insect biodiversity meets ecosystem function: Differential effects of habitat and insects on carrion decomposition. Ecological Entomology, 42, 364–374. https://doi.org/10.1111/een.12395
Barton, P. S., Evans, M. J., Foster, C. N., Pechal, J. L., Bump, J. K., Quaggiotto, M.-M., & Benbow, M. E. (2019). Towards quantifying carrion biomass in ecosystems. Trends in Ecology & Evolution, 34, 950–961. https://doi.org/10.1016/j.tree.2019.06.001
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1–48. https://doi.org/10.18637/jss.v067.i01
Benbow, M. E., Barton, P. S., Ulyshen, M. D., Beasley, J. C., DeVault, T. L., Strickland, M. S., Tomberlin, J. K., Jordan, H. R., & Pechal, J. L. (2019). Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs, 89, e01331. https://doi.org/10.1002/ecm.1331
Boer, M. M., Resco de Dios, V., & Bradstock, R. A. (2020). Unprecedented burn area of Australian mega forest fires. Nature Climate Change, 10, 171–172. https://doi.org/10.1038/s41558-020-0710-7
Bradshaw, C. J. A., Ehrlich, P. R., Beattie, A., Ceballos, G., Crist, E., Diamond, J., Dirzo, R., Ehrlich, A. H., Harte, J., Harte, M., Pyke, G., Raven, P. H., Ripple, W. J., Saltz, F., Turnbull, C., Wackernagel, M., & Blumstein, D. T. (2021). Underestimating the challenges of avoiding a ghastly future. Frontiers in Conservation Science, 1, 10. https://doi.org/10.3389/fcosc.2020.615419
Bureau of Meteorology (2021). Bureau of meteorology. Lithgow Weather Station [WWW document]. http://www.bom.gov.au/places/nsw/lithgow/
