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Cats, foxes and fire: quantitative review reveals that invasive predator activity is most likely to increase shortly after fire

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Abstract

Background Predators and fire shape ecosystems across the globe and these two forces can interact to impact prey populations. This issue is particularly pertinent in Australia where there is considerable scientific and public interest in the post-fire impacts of two invasive predators—the feral cat and red fox. It remains unclear, though, whether increased cat and fox activity in response to fire is a general phenomenon, or whether the responses are highly context-specific and not generalisable.

Results We reviewed and analysed existing literature and found that a range of positive (e.g., increased activity in burnt areas), negative (decreased activity), and neutral responses have been recorded across different studies and locations. Mixed effects modelling revealed that positive responses to fire were more likely when areas were burnt more recently (shorter time since fire). The mean likelihood of increased activity by cats decreased from 41% at 0 months post-fire to 10% at 100 months post-fire, whereas the mean probability for foxes decreased from 53 to 10%. This suggests that there may be a critical time period immediately post-fire when prey are most vulnerable to elevated impacts of predators, and within which management interventions are likely to be most impactful.

Conclusions Many of our findings can be identified as potential cases of either mechanistic or apparent context dependency (variation in recorded patterns due to observational and ecological factors). This provides a pathway for the design of future studies that will enhance our understanding of predator responses to fire, both in Australia and globally. Conservation policy and management will benefit from additional research spanning a greater range of ecosystems and fire events, along with a more comprehensive and nuanced interpretation of existing evidence.

Keywords Feral cat, Fire ecology, Interaction, Invasive predator, Multiple threats, Predator, Prescribed burning, Red fox, Synergy, Wildfire

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Resumen

Antecedentes Los predadores y el fuego modelan los ecosistemas alrededor del globo y estas dos fuerzas pueden interactuar para impactar poblaciones-presa. Este tema es particularmente pertinente en Australia, donde hay un considerable interés científico y público sobre los impactos post-fuego de dos predadores invasores, el gato salvaje y el zorro colorado. Aparece como poco claro, entonces, si el incremento de la actividad de gatos salvajes y zorros en respuesta al fuego es un fenómeno general, o si esas respuestas son contexto-específicas y no generalizables.

Resultados Revisamos y analizamos la literatura existente y encontramos que un rango positivo (i.e. el incremento de la actividad en áreas quemadas), negativo (actividad decreciente), y de respuestas neutrales, han sido registrados a través de diferentes estudios y ubicaciones. Los modelos de efectos mixtos han revelado que las respuestas positivas al fuego fueron plausibles cuando el lugar fue recientemente quemado (muy poco tiempo luego del fuego). La media de la probabilidad de un incremento de la actividad por gatos salvajes decreció de un 41% en el mes cero luego de un incendio al 10% cien meses después del incendio, mientras que la probabilidad media para zorros decreció del 53% al 10%. Esto sugiere que puede haber un período crítico en el post-fuego inmediato para las presas, cuando son más vulnerables a impactos elevados por parte de los predadores, y dentro del cual las intervenciones de manejo tengan probablemente un mayor impacto.

Conclusiones Muchos de nuestros hallazgos pueden ser identificados como casos potenciales tanto mecanísticos como de aparente contexto de dependencia (la variación de los patrones registrados debido a factores ecológicos u observacionales), que proveen de un camino para diseñar futuros estudios que permitirán aumentar nuestro entendimiento de las respuestas de los predadores al fuego, tanto en Australia como a nivel global. Las políticas de conservación y manejo se beneficiarán de investigaciones adicionales que abarquen un mayor rango de ecosistemas y eventos de fuego, junto con una más comprensiva y matizada interpretación de la evidencia ya existente.

Background

Predators are a dominant force in the world's ecosystems (Ripple et al. 2014). They have suppressive effects on their prey and competitors through both lethal (i.e. predation) and non-lethal pathways (i.e. fear effects) (Pessarrodona et al. 2019; Gable et al. 2020). These effects cascade down through trophic levels to influence a range of organisms and processes, including plant communities, energy transfer, and nutrient dynamics, amongst others (Schmitz et al. 2000; Pringle et al. 2019). Fire is also a dominant force that has lethal and non-lethal effects in ecosystems (Bowman et al. 2009; Jolly et al. 2022). Fire can kill animals, destroy and create habitat, alter resource availability, and modify other ecosystem components, ultimately influencing animal behaviour, population dynamics, and community structure (Nimmo et al. 2019; Doherty et al. 2022; Gigliotti et al. 2022).

Because predators are ubiquitous and fire affects an average of 400 million hectares of land globally each year (Giglio et al. 2018), there is strong potential for these two forces to interact. Predators can show a range of responses to fire, with fire benefiting some predators by opening up vegetation and reducing shelter for prey, hence making it easier to hunt (Bonta et al. 2017; Abernathy et al. 2022). Conversely, fire can disadvantage predators by killing them, reducing food availability, impairing hunting ability, or otherwise reducing habitat suitability (Eby et al. 2013; Kramer et al. 2021; Blakey et al. 2022). Accordingly, some predators are more common in recently burned compared to unburned areas (e.g., McGregor et al. 2014), some show the opposite response (e.g., Thompson et al. 2013), and others are seemingly unaffected (e.g., Turschak et al. 2010).

In Australia, there is growing interest in how two widespread invasive predators—the feral cat *Felis catus* and red fox *Vulpes vulpes*—respond to fires and how this affects prey populations. Cats and foxes have contributed to the decline and extinction of many native animal species in Australia (Saunders et al. 2010; Woinarski et al. 2019). It has been hypothesised that fire may exacerbate the impacts of these predators by making it easier for them to hunt (Christensen 1980; Short and Turner 1994; Sutherland and Dickman 1999), but high-quality, mechanistic evidence supporting this idea was only collected relatively recently. The primary evidence comes from a series of studies documenting the exploitation of recently burnt areas by feral cats in tropical northern Australia (McGregor et al. 2014, 2015b, 2016a, b). Since then, the number of studies on cat and fox responses to fire has increased markedly (e.g., Bliege Bird et al. 2018; Parkins et al. 2019; McHugh et al. 2020; Stobo-Wilson et al. 2020; Lothian et al. 2022; Spencer et al. 2022; Nalliah et al. 2022; Senior et al. 2022; Hohnen et al. 2023). Hradsky (2020) provided a narrative review of this topic in the context of threatened mammal conservation, but the evidence base has not been subjected to structured, quantitative review. There is considerable scientific and public interest in this issue (e.g., Jones 2018; Gredley and O'Mallon 2020; VanHoose 2020), but it remains unclear whether increased cat and fox activity in response to fire is a general phenomenon, or whether the responses are highly context-specific and cannot be generalised.

Sound knowledge of how predators respond to fire is important for conservation science, policy, and practice, including threatened species conservation (McHugh et al. 2020; Nalliah et al. 2022), invasive species control (Hradsky 2020), fire management (Scheller et al. 2011), and land use planning (Jennings 2013; Tortato et al. 2021). This need is being heightened by changing fire regimes, caused by land-use change (Chergui et al. 2018), planned burning (Fernandes and Botelho 2003), fire suppression (Schmidt and Eloy 2020), displacement of Indigenous Peoples (Bird et al. 2020), and climate change (Mariani et al. 2018). Some areas are experiencing increases in fire size, frequency and severity, while in other areas fire is now less common or completely excluded (Bowman et al. 2020). The increasing occurrence of catastrophic fires in North and South America, Europe, Australia, and elsewhere underscores the importance of having clear and reliable knowledge of how, why, and when predators respond to fire.

For this study, we reviewed and analysed cat and fox responses to fire in Australia to answer the questions listed below. When referring to predator responses to fire, we use 'positive response' to mean that cat or fox activity was higher in the fire treatment relative to the control (e.g., burnt vs unburnt, or post- vs pre-fire). A 'negative response' means that cat or fox activity was lower in the fire treatment relative to the control. A 'neutral response' means that there was not a statistically detectable difference between treatment and control areas. In general, we refer to the response variable as cat or fox 'activity' because that is the terminology used in the majority of reviewed studies (sometimes interchangeably with relative abundance, occupancy or occurrence), although a minority refer to habitat use or selection (see Methods and Results). The questions we address are:

1. How common are positive (increased activity), negative (decreased activity), and neutral responses to fire by cats and foxes?
2. Does the type of response (positive, negative, neutral) depend on time since fire?
3. Does the type of response depend on climate type or fire type?

We tested the effects of climate type and fire type because individual species can show varying responses to fire depending on fire and ecosystem characteristics (Nimmo et al. 2014; González et al. 2022). The dataset includes responses spanning a range of times since fire, from less than two weeks post-fire to greater than 40 years post-fire. We did not expect that changes in predator activity across these varying fire ages would be consistent, and we model this explicitly using the minimum and maximum time since fire values for every comparison. Based on our findings, we make recommendations for how future studies can best be designed to advance our understanding of predator responses to fire and thus improve the policy and management of invasive predators in fire-prone landscapes.

Methods

Study species

The domestic cat (2.5–7.3 kg) was introduced to Australia by Europeans in the late eighteenth century and feral populations colonised almost the entire continent within 100 years (Abbott 2008). Red foxes (4–8.3 kg) were introduced by Europeans in the mid nineteenth century but did not become established and spread until the late nineteenth century and early twentieth century (Abbott et al. 2014). Cats and foxes inhabit almost all arid, temperate, tropical, Mediterranean, and alpine ecosystems in Australia, including urban and agricultural landscapes, with the key exception being that foxes are absent from most of tropical northern Australia (Van Dyck et al. 2013). Cats are obligate carnivores and prey on a wide range of vertebrate and invertebrate prey (Doherty et al. 2015b; Fleming et al. 2022). Foxes are omnivorous, consuming a range of vertebrate and invertebrate prey, plus plant material and carrion (Fleming et al. 2022). Both cats and foxes use mobile (e.g., searching, stalking) and sedentary (e.g., ambush, sit-and-wait) hunting techniques (e.g., Corbett 1979; Jarnemo 2004), with cats primarily relying on sound and sight when hunting (Bradshaw et al. 2013), whereas foxes primarily use sound and smell (Osterholm 1964; Bytheway et al. 2016).

Database creation

To find studies on cat and fox responses to fire in Australia, we searched Scopus in January 2022 using the following search string in the TITLE-ABS-KEY field: (cat OR cats OR "felis catus" OR fox* OR "vulpes vulpes" OR predator* OR carnivor*) AND (*fire* OR burn*) AND (australia*). After limiting the results to the subject areas of Agricultural and Biological Sciences, and Environmental Science, 275 results remained. We read the titles and abstracts to identify potentially suitable studies for full-text review ($n = 25$). We also checked the reference lists of those studies and found 10 additional studies that were not revealed in our Scopus search. Additionally, we updated the database in November 2022 using unstructured searches of Google Scholar, which added three additional studies. For a study to be included, it needed to contain data on cat or fox activity, abundance, occupancy, or habitat use in relation to fire. We only included studies where it was possible to record the time elapsed since fire in months. Study designs included sampling of burned and unburned areas, before and after fires, time since fire chronosequences, and GPS tracking studies. Ultimately, 24 sources provided suitable data (see Table 2 in the meta-data file at https://osf.io/sq3df/). A ROSES systematic review flow diagram (Haddaway et al. 2018) is provided in the Supporting Information (Fig. S1).

We extracted the following information from each of the included studies (see Table 1 for additional details): (i) study species (cat or fox); (ii) study design; (iii) survey method; (iv) survey metric; (v) fire type; (vi) climate type; (vii) minimum and maximum time since fire (TSF) in months for each relevant comparison; (viii) a brief description of the change in activity, abundance, occupancy, or habitat use; (ix) a classification of the response to fire as either positive, negative, or neutral; and (x) any notes about data extraction and interpretation. Classification of responses as positive (e.g., higher activity in burnt compared to unburnt areas), negative (e.g., lower activity post- compared to pre-fire), or neutral was based on the statistical analyses and inferences of each study. Any subjectivity in classifying responses is recorded in the notes column of the dataset. For studies that compared multiple fire age classes to one another using a space-for-time design (Hradsky et al. 2017c; Parkins et al. 2019; Nalliah et al. 2022), we used the oldest age class as the reference category, which we compared all younger classes to. For instance, for Nalliah et al. (2022), we compared each of the recent (0–3 years), early (4–9 years) and mid (10–33 years) age classes to the late age class (34–79 years). Where studies tested the relationship between cat or fox activity and the amount of a particular fire age class around sampling points (Payne et al. 2014; Doherty et al. 2015a; McDonald et al. 2016; Bliege Bird et al. 2018; Geary et al. 2018; Stobo-Wilson et al. 2020), we classified the response as positive if activity increased with the amount of that age class, and negative if activity decreased. For the Arthur et al. (2012) study, we only recorded data for the first year after each of the fires in 1972 and 1980 because it was difficult to confidently classify cat and fox responses to fire in subsequent years given no variance estimates or relevant statistical tests

Table 1 Definitions and summary statistics for predictor, response and study characteristic variables. The main values for study design, survey method, survey metric, fire type and climate type represent the number of studies in that group and the values in parentheses are the number of individual cases

Variable	Definition	Categories	Cats	Foxes
Study design	Classified as either BACI (before-after, control impact), Before-After (BA), Control-Impact (CI), or Impact only (I)	BACI: BA: CI: I:	3 (14) 2 (6) 2 (6) 9 (18)	2 (13) 3 (10) 6 (28) 4 (9)
Survey method	The survey method of the original study, classified as either camera traps, GPS tracking, or sign surveys (scats and tracks)	Cameras: GPS: Sign:	9 (27) 3 (8) 4 (9)	8 (30) 1 (18) 5 (12)
Survey metric	The survey metric (response variable) of the original study, classified as either species activity (often synonymised with relative abundance, occurrence or occupancy), or habitat selection (HS)	Activity: HS:	12 (35) 4 (9)	13 (42) 1 (18)
Fire type	Classified as either planned burn, wildfire, or mixed (study areas were burnt by a combination of planned burns and wildfire)	Planned burn: Wildfire: Mixed:	6 (17) 8 (23) 2 (4)	5 (14) 5 (21) 4 (25)
Climate type	Classified as either arid (including semi-arid), temperate (including one sub-alpine study), or tropical	Arid: Temperate: Tropical:	6 (11) 5 (20) 5 (13)	5 (10) 9 (50) 0 (0)
Min_TSF	The youngest fire age of the fire treatment for each comparison. E.g., the value is 12 months for 1–3 years post-fire	Median: Range:	9.5 mo 0–480 mo	12 mo 0–420 mo
Max_TSF[a]	The oldest fire age of the fire treatment for each comparison. E.g., the value is 36 months for 1–3 years post-fire	Median: Range:	18 mo 0.5–156 mo	30 mo 2–430 mo
Response	Changes in cat or fox activity in response to fire were classified as either positive (increased activity in the fire treatment), negative (decreased activity in the fire treatment), or neutral (no difference)	Positive: Negative: Neutral:	11 cases 8 cases 25 cases	14 cases 7 cases 39 cases

[a] Maximum time since fire could not be determined for six cases, thus the following values are not represented in the maximum ranges presented here: one cat study that surveyed areas > 40 years post-fire and three fox studies that surveyed areas > 6 and > 35 years post-fire

were provided and there was high inter-annual variability across the whole study period (1972–2008).

Data synthesis and analysis

We plotted the range of TSF for each comparison from each study and represented responses as either positive, negative, or neutral. In some cases, it was difficult to determine the precise TSF in months because the month/s of burning or sampling were unclear. For instance, if the vegetation age was described as '2–4 years post-fire', it was unclear if the TSF range should be recorded as 24–48 months, 24–59 months, or something else. This is because for an area classed as '4 years post-fire', the fire may have occurred in February 2010 and the sampling occurred in July 2014 (53 months). To represent this uncertainty when plotting the time ranges of each comparison, we added an extra six-month interval where necessary, which is distinguished from the main intervals on the plots. In other cases where the fire or sampling was described as occurring within a season, but an exact month was not provided, we added a three-month buffer to the intervals. We did not, however, use these extra buffers in the analyses.

We used categorical response mixed effects models to assess whether predator responses to fire depended on minimum and maximum TSF, climate type, and fire type. The response variable was the classification of fire responses as either positive, negative, or neutral. We fitted models separately for cats and foxes, and only included one predictor variable per model due to the modest sample sizes and because minimum and maximum TSF were positively correlated for both foxes ($r = 0.80$) and cats (0.75). We take these correlations into account when interpreting the results of the multiple models. We also fitted a null model for each species to calculate the mean likelihood of positive, negative and neutral responses. All models included a random effect of study ID because some studies provided multiple data points.

We fitted models using the *brms* package in R v4.2.2 (Bürkner 2017; R Core Team 2022). All modelling was conducted in a Bayesian framework, with each model run with four chains of 5,000 iterations each (with a burn-in of 1,000 iterations), resulting in 16,000 samples. We specified weakly informative normal priors (mean = 0, SD = 10) for the fixed effects and weakly informative student t priors for the random effect (df = 3, mean = 0, SD = 2.5) (Bürkner 2017). 'Arid' and 'mixed' were used as the predictor variable reference categories in the climate type and fire type models, respectively. We assessed convergence by inspecting trace plots and ensuring that the Gelman–Rubin statistic was < 1.1 (Gelman and Rubin 1992). We visually assessed plots of posterior predictive checks to ensure models were an appropriate fit for the data (Fig. S2; Gabry et al. 2019). We present posterior means and 95% credible intervals. For the fox model relating to minimum TSF, we excluded two rows of data that were outliers (420 months, *cf.* 0–120 months for the remaining data). Similarly, we excluded an outlier from the cat minimum TSF model (480 months *cf.* 0–108). There were only two cat studies for mixed fire type (McGregor et al. 2014, 2016b), so we excluded that data from the fire type model and used planned burn as the reference level.

We considered conducting a more formal meta-analysis using log response ratios based on treatment means (Hedges et al. 1999), but appropriate data could only be extracted for less than half of the comparisons and there were biases in data availability between positive, negative, and neutral responses. These biases meant that average effect sizes would be inflated for foxes and neutralised for cats, and thus the results would not be an accurate reflection of ecological reality.

Results

There were 16 studies with suitable data for feral cats ($n = 44$ comparisons) and 14 studies for foxes (60), with six studies providing data for both species (Fig. 1). Most studies for both species used cameras traps and activity as the survey method and survey metric (response variable), respectively, with smaller numbers using GPS tracking, sign surveys (tracks and scats), and habitat selection metrics (Table 1). Cat studies had the following study designs: three BACI, two before-after, two control-impact, and nine impact only (Table 1). For foxes, there were two BACI studies, three before-after, six control-impact, and four impact only (these numbers sum to 15 because one study had separate BA and CI components; Green and Sanecki 2006). For cats, the climate of study locations was arid for six studies, temperate for five, and tropical for five (Table 1). For foxes, there were five arid studies, nine temperate, and zero tropical, with the latter reflecting the absence of foxes from most of tropical Australia. Six cat studies related to planned burns, eight to wildfire, and two with mixed fire type (Table 1). There were five fox studies for each of planned burning and wildfire, and four with mixed fire type (Table 1). Fox studies tended to survey later post-fire periods than cat studies, with the median time spans being 12–30 months post-fire for foxes and 9.5–18 months for cats (Table 1; Figs. 2 and 3).

For cats, eight responses were classified as negative, 25 as neutral, and 11 as positive (Figs. 2 and 3). Seven fox responses were negative, 39 neutral, and 14 positive (Figs. 2 and 3). The mean likelihoods of each response as predicted by the null model were

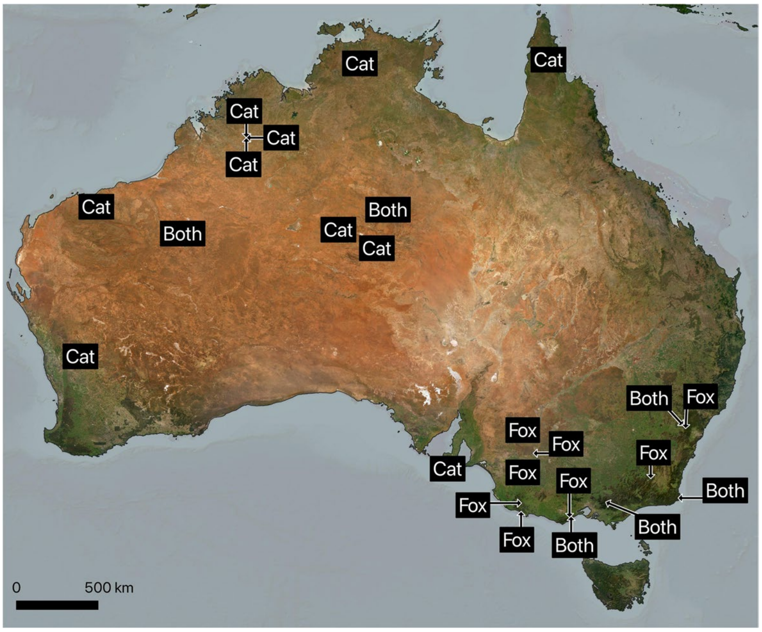

Fig. 1 Map of study locations. 'Both' represents studies that included both feral cats and red foxes. Some labels are offset from study locations with arrows to aid visual interpretation

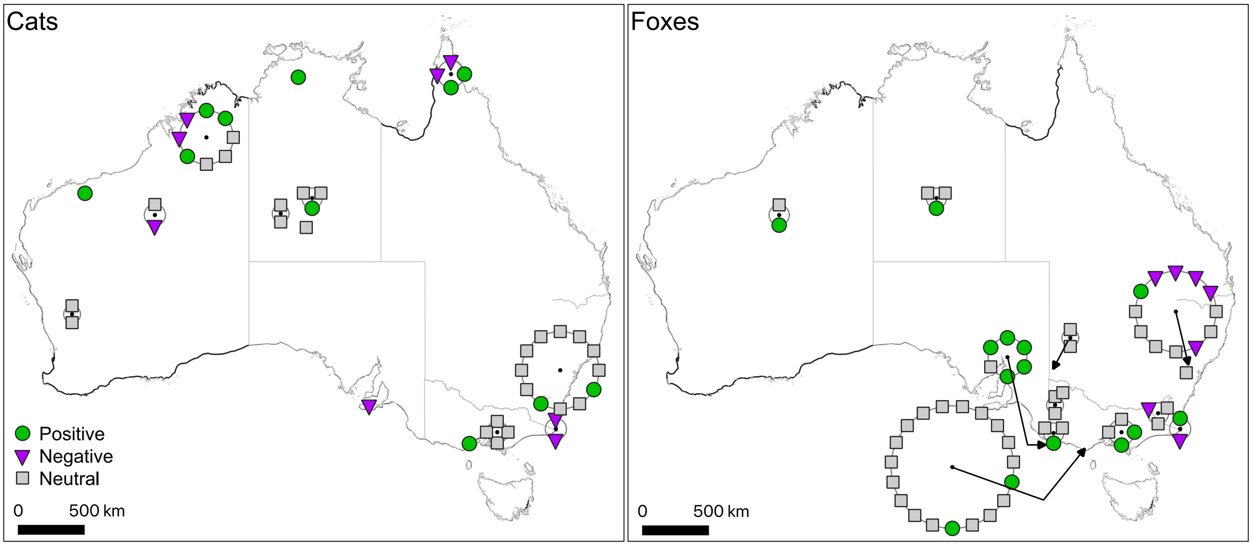

Fig. 2 Distribution of positive, negative, and neutral responses of feral cats (left) and red foxes (right) to fire in Australia. A ring of symbols represents multiple effects from a single location, sometimes pooled across multiple studies. Some of the symbols on the fox map are offset from the exact study location (denoted by the arrows) to improve visual interpretation

13% negative for cats and 7% for foxes, 31% positive for cats and 26% for foxes, and 55% neutral for cats and 67% for foxes. Mixed effects models revealed that positive responses to fire by both cats and foxes were more likely if the area had been burnt more recently, whereas neutral responses were more likely in older fire ages (Table 2, Fig. 4). The effects for foxes were stronger and had higher certainty than those for cats. More specifically, for foxes, the probability of a positive response decreased from 53% at 0 months post-fire to 10% at 100 months, whereas the probability of a neutral response increased from 40% (0 months) to 95% (100 months). The corresponding values for cats are a decrease from 41 to 6% for positive responses,

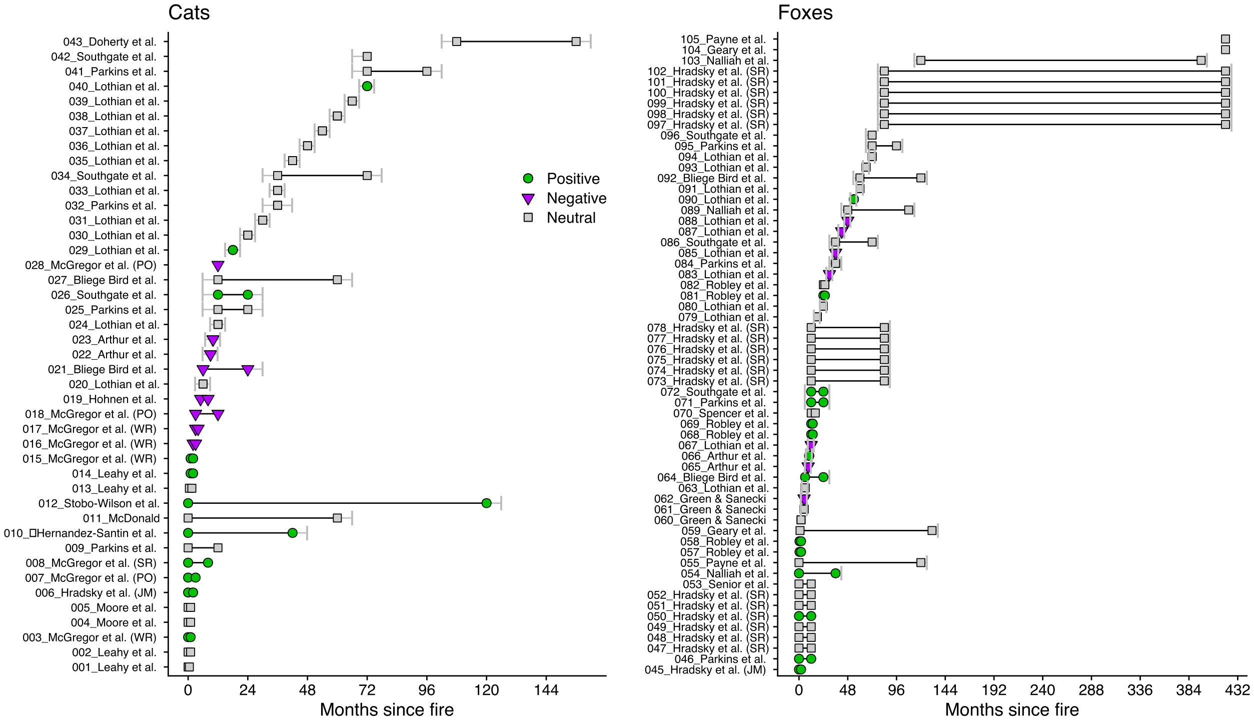

Fig. 3 Classification and time span of documented responses of feral cats (left) and red foxes (right) to fire in Australia. Minimum and maximum time since fire is shown for each comparison and grey bars either side of symbols represent uncertainty about precise values for time since fire (see Methods). Labels on the y-axes correspond with the Case_ID variable in the dataset. Note that different scales are used on the two x-axes. To aid interpretation, one data point for cats from Doherty et al. (2015a) is not shown here (neutral at 480 months)

Table 2 Mixed modelling results for the effects of minimum and maximum time since fire (TSF), climate, and fire type on feral cat and red fox responses to fire in Australia. Values represent posterior means, and 95% credible intervals (CI) are provided in parentheses. Bold text indicates terms where the CIs do not include zero. Neutral responses were used as the reference category for the response variable and 'arid' and 'mixed' were used as the reference category for the climate and fire type predictor variables, thus there are no values to display here

Species	Predictor	Level	Positive	Negative
Cat	Min TSF	–	**-0.05 (-0.11, -0.00)**	-0.06 (-0.20, 0.04)
	Max TSF	–	-0.02 (-0.06, 0.02)	**-0.09 (-0.23, -0.00)**
	Climate	*Temperate (vs. Arid)*	0.49 (-4.20, 5.97)	3.91 (-3.56, 12.84)
		Tropical (vs. Arid)	**4.54 (0.22, 11.44)**	4.17 (-4.00, 12.51)
	Fire type	*Wildfire (vs. Planned)*	0.25 (-3.56, 4.78)	0.49 (-6.16, 7.60)
Fox	Min TSF	–	**-0.07 (-0.14, -0.02)**	-0.03 (-0.08, 0.02)
	Max TSF	–	**-0.05 (-0.09, -0.02)**	**-0.03 (-0.07, -0.00)**
	Climate	*Temperate (vs. Arid)*	1.44 (-1.50, 5.07)	6.82 (-0.56, 18.78)
	Fire type	*Planned (vs. Mixed)*	**3.22 (0.94, 5.85)**	-1.64 (-15.17, 8.63)
		Wildfire (vs. Mixed)	1.20 (-1.35, 3.94)	**6.55 (1.35, 15.68)**

and an increase from 38 to 87% for neutral responses, but with high uncertainty (Fig. 4). The probability of a negative response by both cats and foxes decreased as maximum time since fire increased (older fire ages), but the effect was very weak for foxes (Table 2, Fig. 4). For cats, the probability of a positive response was higher for tropical studies relative to arid studies, but with high uncertainty (Fig. 4c). For foxes, positive responses were more likely for planned burns, whereas negative responses were more likely for wildfires, and neutral responses were more likely for mixed fire type (Fig. 4f). Fire type was not influential

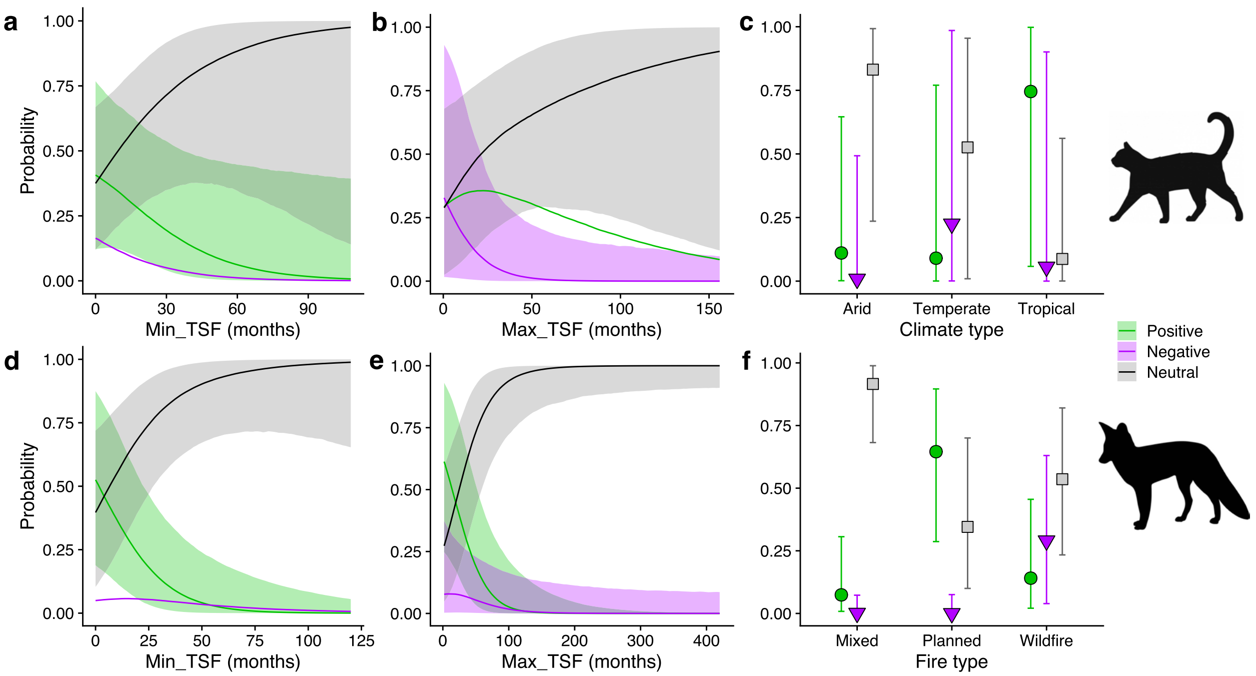

Fig. 4 Model predicted effects of minimum time since fire (Min_TSF), maximum time since fire (Max_TSF), climate type, and fire type on feral cat (top row) and red fox (bottom row) responses to fire in Australia. Fire type is not shown for cats and climate type is not shown for foxes because those predictors were not influential (see Table 2). Solid lines in **a**, **b**, **d** and **e** represent mean effects and bands represent 95% credible intervals (CI). To aid interpretation, CI bands in the TSF panels are only provided where the CIs did not overlap zero (see Table 2)

for cats and climate type was not influential for foxes (Table 2).

Discussion

We have provided the first quantitative review of how introduced cats and foxes respond to fire in Australia. Our review reveals that there is no general response to fire—rather, responses appear to be highly context-specific, likely depending on a combination of factors such as time since fire, study design, and ecosystem type. When viewed through the contextual lens of fire ecology, this result is unsurprising—many species, including mammalian predators, exhibit variable responses to fires across different locations (Nimmo et al. 2014; Geary et al. 2020). The context dependency framework recently developed by Catford et al. (2022) can help in understanding these varying results. Mechanistic context dependency may occur if the response of cats or foxes to fire depends on ecological conditions such as vegetation type or productivity (Stobo-Wilson et al. 2020; Catford et al. 2022). For instance, the response of other species to time since fire can be mediated by climatic factors (Connell et al. 2022), landscape context (Verdon et al. 2019), and vegetation type (Zylinski et al. 2022), and these contextual factors may also influence fox and cat responses to fire. In contrast, apparent context dependency may occur due to either (i) confounding factors that are inconsistently measured or accounted for across studies, (ii) problems with statistical inference (e.g., differing statistical power or accuracy), or (iii) methodological differences across studies (e.g., differing times since fire) (Catford et al. 2022). As discussed below, each of these scenarios could be present among the studies we reviewed.

We found that as minimum time since fire increased (i.e. older fire ages), the probability of a positive response to fire decreased for both cats (-35% in absolute terms) and foxes (-43%). Similar responses were found for maximum time since fire, which is unsurprising because minimum and maximum time since fire were highly correlated. Hradsky (2020) suggested that most fox responses to fire are short-lived, and we have now demonstrated this quantitatively for both cats and foxes. We also found that negative responses by cats were more common if maximum time since fire was lower. These findings support—and are partially driven by—work from northern Australia showing that cat responses to fire in northern Australia depended on the recency of burning (McGregor et al. 2014, 2016a, b). Predation theory also predicts that the amount of time elapsed post-fire should influence how predators respond to fire (Doherty et al. 2022). Based on the assumption that cats and foxes are attracted to recently burnt areas due to improved foraging opportunities (McGregor et al. 2016b; Hradsky et al. 2017a), we expect that this attraction should last only as long as the foraging benefits do. If prey resources are depleted after some time (e.g., due to emigration, death, or predation), or if vegetation recovery lessens hunting efficiency (by reducing visibility and providing shelter for prey), predators should decrease their activity in those burnt areas and potentially avoid them (Doherty et al. 2022). Such behaviour would help explain the increased probability of negative responses by cats when maximum time since fire was lower. Increased predator activity post-fire may be more protracted in ecosystems or situations where vegetation recovery is slower (e.g., woodlands and shrublands, dependent on fire severity or post-fire rainfall), but the current literature is not suitable for testing an interaction between ecosystem type and time since fire.

Fewer studies detected negative responses to fire by foxes (12.5%) compared to cats (23%), and the predicted likelihood of a negative response by foxes (7%) was around half that for cats (13%). Notwithstanding methodological differences between the available studies, this suggests that foxes may be better able to persist in or exploit burnt areas than cats. Of the six studies that included data for both cats and foxes, four studies fully or partially support this notion, with foxes more frequently responding positively to fire than cats (Arthur et al. 2012; Bliege Bird et al. 2018; Parkins et al. 2019), or showing a stronger positive response (Hradsky et al. 2017a). One study found the opposite response, with fox responses being mostly neutral or negative over six years post-fire, whereas cat responses were primarily neutral (Lothian et al. 2022). While both predators are carnivorous and highly mobile, foxes typically have a more omnivorous diet and are more likely to scavenge food than cats (Doherty et al. 2015b; Fleming et al. 2021). Changes in cat diet post-fire have not been studied, but foxes are known to alter their diet, including greater dietary occurrence of mammals post-fire (Green and Sanecki 2006), and decreased occurrence of large macropods and increased occurrence of medium-size mammals post-fire (Robley et al. 2016; Hradsky et al. 2017a). It is not known to what degree scavenging of carrion post-fire drove those results.

In addition to dietary differences, it is also possible that in areas where the two predators are sympatric, the presence of foxes may suppress any positive response by cats to fire, given that other studies have shown foxes can influence cat behaviour and habitat use (Molsher et al. 2017; Roshier and Carter 2021). If foxes moderate the response of cats to fire, this would be an example of mechanistic context dependency, whereby a third variable (in this case a larger predator) moderates the response of cats to fire. Geary et al. (2018) found evidence of such an interaction for dingoes *Canis dingo* and foxes in Australia, and Gigliotti et al. (2022) suggested that the strong positive response of lions *Panthera leo* to burning in South Africa may have hindered the ability of hyenas *Crocuta crocuta*, leopards *Panthera pardus*, and cheetahs *Acinonyx jubatus* to exploit burnt areas. Further studies are needed to clarify whether interactions between predator species in burnt areas lead to mechanistic context dependency.

All instances of decreased fox activity in response to fire were from studies of wildfires and this pattern was borne out in the statistical analysis, with the highest probability of a negative response occurring if fire type was wildfire. In contrast, increases in fox activity were most likely to be detected if fire type was planned burn. This may suggest that severe wildfires are more likely to elicit a negative response by foxes. However, the result may be biased by differing sampling timeframes between studies, because wildfire studies tended to sample later post-fire compared to planned burn studies. Consequently, wildfire studies may be missing temporary increases in fox activity post-fire. Indeed, recent data from a national park in New South Wales shows that fox activity after the severe 2019/20 fires was initially higher at burnt compared to unburnt areas (3–5 months post-fire) before decreasing (V. Miritis, *unpublished data*). The distinction between wildfires and planned burns is imperfect because the severity of planned burns can be similar to wildfires in some cases, resulting in comparable changes in vegetation structure and resource availability. More detailed aspects of fire, such as fire size, severity and patchiness, are likely to be more ecologically relevant than fire type, but the limited data available from the reviewed studies precluded incorporating these factors into our analyses. One recent study found that spatial characteristics of fire such as patchiness and distance to unburnt vegetation were not influential for foxes, but nor was a simple burnt/unburnt contrast (Senior et al. 2022). Further studies that explicitly test these relationships will help shed light on how foxes and cats respond to fires of varying size, severity and patchiness.

We do note, though, that there were some studies that did not meet our inclusion criteria regarding time since fire, but which nonetheless contained relevant information. Cat activity and abundance increased with fire frequency on Melville Island (Davies et al. 2020), whereas fire frequency did not affect cat occupancy when sampling at large geographical scales (100 s of kms) in New South Wales and the Wet Tropics (Bruce et al. 2022; McHugh et al. 2022). Fox occupancy also did not vary with fire frequency in New South Wales (McHugh et al. 2022). Fox activity did not vary with growth stage (spanning 0 to > 36 years post-fire) in the Mount Lofty Ranges (Zylinski et al. 2022). In East Gippsland, cat occupancy was higher at low severity compared to high severity sites ~ 6 months post-fire, whereas there was no difference for foxes (Robley et al. 2022). In the Otway Ranges, fox occurrence did not vary with a unitless index of time since fire, whereas cat occurrence showed a weak positive relationship (Hradsky et al. 2017b). These studies further demonstrate the varying responses of predators to fire across different ecosystems and fire types, and thus reinforce the need to draw on a breadth of information when contextualising the results of individual studies.

There are some biases in how different predictor variables are represented. For instance, tropical studies focussed on younger fire ages than arid and temperate studies, which reflects the lower fire return intervals in savanna grasslands and woodlands. As such, the higher likelihood of detecting positive responses of cats to fire in tropical studies may be because time since fire was lower in those studies. As mentioned previously, planned burning studies typically studied younger fire ages than wildfire studies, which similarly may have contributed to the higher likelihood of detecting positive responses by foxes to planned burns. Nonetheless, we are confident that our results regarding time since fire are robust. We expect that more detailed analytical approaches will become feasible once further studies spanning a range of ecosystems and fire events become available.

We did not find widespread evidence of cats responding positively to fire in temperate Australia, despite considerable concern about this phenomenon, particularly in the wake of the 2019/20 megafires (DELWP 2020; NSW DPIE 2020; VanHoose 2020). One study from the Blue Mountains recorded higher cat activity in burnt compared to unburnt areas at 1.5 and 6 years post-fire, with neutral responses in between (Lothian et al. 2022). Cat activity increased after fire in the Otway Ranges, but there was some uncertainty about classification of this positive response because the estimates of cat occurrence had wide and overlapping confidence intervals between treatments and no statistical test for cats by themselves was provided (Hradsky et al. 2017a). Of the remaining three temperate studies, two recorded negative responses by cats 5–10 months after severe wildfires (Arthur et al. 2012; Hohnen et al. 2021). Direct mortality of cats in those fires may have driven those responses, but there may also have been positive responses by cats immediately post-fire (i.e., 0–5 months post-fire) that were missed by the sampling. As such, it remains unclear how common positive responses by cats to fire are in temperate Australia.

Although we focussed on cats and foxes in Australia, these two species are among the world's most widely distributed mammalian carnivores, thus our findings are likely to extend to other parts of the world. Our results for cats in particular have broad conservation relevance because feral cats are a major threat to native wildlife globally, particularly on islands (Medina et al. 2011; Doherty et al. 2016). Island ecosystems where cats and fire might interact to affect threatened species include New Caledonia, Hawaii and Madagascar, amongst others. We expect that the recency of burning will be an important factor driving changes in cat and fox activity in other fire-prone regions, and possibly also for other carnivores of similar body size and ecological strategies. There is some evidence supporting this from Macedonia where cats were recorded in moderately and intensely burned areas in the second but not third year post-fire, but showed the opposite the response for unburned areas (Birtsas et al. 2012). Foxes showed a different response, decreasing in unburned and intensely burned areas from the second to third year, while increasing in the moderately burned area (Birtsas et al. 2012). There are few other studies of the responses of feral cats and red foxes to fire outside Australia (Geary et al. 2020), but gray fox *Urocyon cinereoargenteus* and coyote *Canis latrans* activity in Arizona, USA similarly showed a decline in burnt areas over time (Cunningham et al. 2006). A fruitful area for further research will be the synthesis of data from other well sampled species, and one way this could be achieved is by integrating disparate camera trapping datasets spanning a range of fire events.

Study design considerations and future research

There was a high likelihood of neutral responses being recorded for both cats (55%) and foxes (67%), and 29% of studies only recorded neutral responses. This calls for careful consideration of exactly how, why, and when positive and negative responses to fire are detected. This includes distinguishing true negatives from false negatives (when sampling fails to detect a true response), as well as cases of mechanistic and apparent context dependency. Reasons why cats and foxes may not show a clear response to fire include the fire not being large enough or severe enough to elicit a response (true negative), or study design and statistical power being insufficient to detect changes in predator activity or occurrence (false negative). Additionally, increases or decreases in predator activity may not be detected if sampling occurs too late post-fire. Predator responses to fire can be relatively short-lived (McGregor et al. 2016b; Doherty et al. 2022), thus sampling that begins after this time may miss the response, or may record the opposite response (e.g., if the activity of a predator switches from being higher in burnt areas at, say, 0–2 months post-fire to lower at 3–6 months post-fire; McGregor et al. 2016a, b). The effects of time since fire that we uncovered may be a case of apparent context dependency driven by methodological differences between studies (Catford et al. 2022).

We suggest that an ideal study design would use a BACI approach and include sampling for multiple time points post-fire (e.g., 0, 3, 6 and 12 months). The unburnt control area should be sufficiently distant from the burnt treatment to ensure spatial independence, thereby reducing the chance that the fire also triggers a response by predators in the unburnt control areas. Such a design would enable both immediate and protracted responses to be detected, while also accounting for any changes occurring in unburnt areas independent of fire. Notably, no studies in our database met these criteria. The closest was Lothian et al. (2022), which had multiple surveys pre- and post-fire, but the burnt and unburnt areas were not spatially independent. The next closest were Hradsky et al. (2017a) which used a BACI design with one round of sampling pre- and post-fire, and Robley et al. (2016) that used a before-after design with sampling once pre-fire and three times post-fire. The lack of studies that met these design criteria is indicative of the challenges in conducting large scale before-after fire experiments for wide-ranging species. A BACI field experiment that involves wildfire invariably needs to be opportunistic in nature, as researchers do not know in advance precisely where and when a wildfire will occur. Opportunities can arise where an unplanned fire burns through an area with recent or ongoing sampling (Arthur et al. 2012; Hohnen et al. 2021; Lothian et al. 2022). Planned burns provide better opportunities to conduct BACI experiments because sampling can be targeted in areas that are due to be burned, however study design should consider that the size of a planned burn is often smaller than an individual predator's home range. Although challenging to implement successfully, we also recommend GPS tracking predators before, during, and after fire. High-resolution movement data can help answer questions about where predators come from when they use burnt areas and how quickly they respond post-fire (Robley et al. 2016; McGregor et al. 2016b).

We also recommend that researchers employ power analysis during the study design phase to ensure that sampling intensity is sufficient for detecting ecologically relevant responses of cats and foxes to fire (Southwell et al. 2021, 2022). Robust study design can help avoid cases of apparent context dependency driven by issues related to statistical inference (Catford et al. 2022). Additionally, some studies detected indirect or mediated responses of cats and foxes to fire (McDonald et al. 2016; Geary et al. 2018; Stobo-Wilson et al. 2020), which emphasises the importance of considering and accounting for other variables that may be either interaction effects or confounding factors leading to context dependency (Catford et al. 2022). Further research across arid, tropical, and temperate ecosystems globally will help to shed more light on this complex topic and should facilitate further synthesis and meta-analysis in the future.

Conclusions

As fire regimes around the globe shift away from historic baselines, sound knowledge of how predators—particularly invasive predators—respond to fire is crucial for effective conservation management. We found a high level of variability in how cats and foxes respond to fire in Australia. However, many of our results can be identified as potential cases of either mechanistic or apparent context dependency, which provides a pathway for the design of future studies that will enhance our understanding of predator responses to fire both in Australia and globally. While we have revealed that positive responses to fire by cats and foxes are related to the recency of burning, our mechanistic understanding of this phenomenon is fairly immature. For instance, it is unclear if cats and foxes in temperate and arid Australia move long distances towards recent fire scars, as has been recorded for cats in northern Australia (McGregor et al. 2016a, b), but was not seen for foxes in southern Australia (Robley et al. 2016). Further studies will help grow the knowledge base, particularly those that: (i) begin sampling shortly after fire (i.e., < 1 month; although we acknowledge the logistical issues with gaining access to recently burnt areas), and (ii) develop mechanistic evidence regarding specific behavioural changes by both cats and foxes (McGregor et al. 2015a, 2016b).

The relationships we uncovered between increased cat or fox activity and the recency of burning suggest that there may be a critical time period immediately post-fire when prey are most vulnerable to elevated impacts of predators, and within which management interventions are likely to be most impactful. Millions of dollars are spent on controlling predators after fires (DELWP 2020; NSW DPIE 2020). It is critical that population studies of prey species are conducted to determine whether management interventions such as predator control and artificial refuges (Bleicher et al. 2020; Watchorn et al. 2022) improve prey survival and abundance in burnt areas. Tailored site-based actions conducted under an experimental framework can facilitate learning about cat and fox responses to fire and management interventions, and ultimately help improve and refine management approaches. We encourage further research to inform the policy and management of predators and fire, as well as more comprehensive and nuanced interpretation of existing literature.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00183-6.

Additional file 1. Figure S1. ROSES systematic review flow diagram illustrating the steps of the review process. **Figure S2.** Plots of posterior-predictive checks for Bayesian mixed effects models testing the effects ofminimum time since fire (Min_TSF), maximum time since fire (Max_TSF), climatetype (arid, temperate, tropical), and fire type (planned burn, wildfire) on theprobability of feral cats *Felis catus* and red foxes *Vulpes vulpes* inAustralia showing a positive, negative or neutral response to fire. Histogramsin the first and second columns show the observed mean (y; dark bar) anddistribution of values from 1000 simulated data sets from the posteriorpredictive distribution (y_{rep}; light lines). The mean iscalculated by converting the data to integers as follows: neutral = 1, negative= 2, positive = 3 (Gabry et al. 2019). Line plots in the thirdand fourth columns are kernel density estimates of the observed data (y;dark line) and 1000 simulated data sets from the posterior predictivedistribution (y_{rep}; light lines).

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Authors' contributions

TSD designed the study, collated and analysed the data, and drafted the manuscript. DJW, VM, AJLP and WLG contributed to writing the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The data are available in an Open Science Framework repository: https://osf.io/sq3df/

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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