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Good intentions with adverse outcomes when conservation and pest management guidelines are ignored: A case study in rabbit biocontrol

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Abstract

To mitigate the negative impacts of invasive rabbits in Australia, land managers are permitted to release the biocontrol virus, rabbit hemorrhagic disease virus (RHDV), to reduce rabbit numbers. However, it is strongly recommended that RHDV is not released when young rabbits are present in the population as infection in this cohort is sublethal and induces life-long virus immunity. The recruitment of these rabbits into the breeding population may make the population harder to control in future, potentially leading to increasing rather than decreased population size. To investigate whether the recommended release guidelines are followed, we obtained data on the supply and release of RHDV by land managers. We then used generalized additive models to investigate Australia-wide and state-specific annual and long-term temporal trends in the supply and release of RHDV. Half of all RHDV supply (47%) and three quarters of reported releases (74%) Australia-wide occurred during the anticipated major rabbit breeding seasons and when the risk of immunizing young rabbits is greatest. We found evidence of both RHDV supply and release during the anticipated major rabbit breeding seasons in almost all states for which data existed. RHDV supply increased with below average annual rainfall. This may indicate a tendency for land managers to notice, and want to control, rabbits

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and their impacts more following drier years when both rabbits and their impacts are potentially more damaging. Our study raises concerns regarding the inappropriate release of RHDV by land managers and whether its supply should be restricted to ensure ongoing and effective management of invasive rabbits. More broadly, our study serves as a warning to other conservation and pest management activities reliant on land managers or citizens following implementation guidelines. In some cases, good intentions may have adverse outcomes.

KEYWORDS

ecology, generalized additive model, land management, landholder, rabbit hemorrhagic disease, temporal, time series

1 | INTRODUCTION

Land managers play a major role in the implementation of conservation and pest management activities. For example, land managers within the Little Karoo region of South Africa contribute to tripling the number of conservation targets achieved and significantly increasing the types of habitats and species conserved within the region (Gallo et al., 2009). Similarly, tissue samples collected by land managers in Australia simultaneously contribute to both the conservation of dingoes (*Canis familiaris*) and their management as a pest species (Stephens et al., 2015). This involvement by land managers in conservation or pest management programs can be essential to their success and deliver high economic benefits (Gallo et al., 2009; Naidoo & Iwamura, 2007).

However, the success and economic value of conservation or pest management activities are often reliant on land managers closely following recommended guidelines for the activities in which they partake. This is because the success of some conservation or pest management activities are sensitive to where, when, or how they are conducted. An example of this is the management of the European rabbit (*Oryctolagus cuniculus*) in Australia.

Rabbits have the most significant environmental and economic impact of all pest animals in Australia. Rabbits adversely impact some 321 species of threatened plants and animals (Finlayson et al., 2021; Kearney et al., 2019). This is greater than twice the number of species impacted on by other high-profile pests. Rabbits also have immense impacts through land degradation and are economically important (Cooke et al., 2013).

Viral biocontrol agents have proved to be highly effective in suppressing rabbits and reducing their impacts in Australia. There are two viruses that have been used as biocontrol agents to reduce rabbit numbers: (1) myxoma virus, which causes myxomatosis; and (2) rabbit hemorrhagic disease virus (RHDV), which causes rabbit hemorrhagic disease (Cooke & Fenner, 2002; Fenner & Ratcliffe, 1965).

Following the introduction of myxomatosis into Australia in 1950, the resulting decline in pest rabbit numbers led to enormous benefits for agriculture; this has been estimated to be approximately $1 billion AUD in net benefits annually (Cooke et al., 2013). These benefits have been maintained through the additional release of RHDV, although there is a residual annual cost to agriculture of about $200 million AUD in terms of the damage caused by the remaining rabbits and the ongoing costs of controlling them (Cooke et al., 2013; Gong et al., 2009).

While myxoma virus is no longer released, two different RHDVs are available for intentional local release. One of these variants is RHDV GI.1c, from the former Czech Republic (designated "v351"), initially released in Australia in 1995. However, because infection with a nonpathogenic rabbit calicivirus, endemic in south-eastern Australia, offers cross-protection to infection with this original virus (v351), a novel variant of RHDV, GI.1a, from South Korea (designated "K5"), was released through a coordinated national release program in 2017 (Cox et al., 2019; Le Pendu et al., 2017; Strive et al., 2013). Despite RHDV GI.1c and RHDV GI.1a both being intentionally released across Australia, another virus, RHDV GI.2 (RHDV2), emerged in 2015 and has become the dominant RHDV in the environment (Mahar et al., 2018). How these different viruses interact in their competition for the same host in the Australian environment is unknown, however, it has been speculated that RHDV2 could reduce the effectiveness of current biocontrol strategies (Ramsey et al., 2020).

There is only one supplier of RHDV in Australia. When it is dispatched to land managers who have

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requested it, a recommendation is made that the virus should not be released into rabbit populations when young rabbits are present. This recommendation follows widely recorded observations that young rabbits, less than approximately 60 days of age, are resistant to acute RHDV and generally experience a sublethal infection (Matthaei et al., 2014; Mutze et al., 1998; Nowotny et al., 1993; Prieto et al., 2000; Robinson et al., 2002). Thus, if either v351 or K5 are released when young rabbits are present, then those infected are likely to recover and become immune for life.

To determine whether RHDV release timing is potentially a problem worthy of significant future consideration, we investigated Australia-wide and state-specific temporal trends, in the supply and release of RHDV. We accessed two datasets: (1) a government curated dataset containing information on when the virus was sent to land managers; and (2) a dataset containing information voluntarily submitted by land managers through web-based apps on when the virus was released. We predicted seasonal trends in the supply and release of RHDV as rabbits are generally known to show strong seasonal breeding and it is recommended to not release the virus when young rabbits are present (Gilbert et al., 1987). We investigated long-term, year-to-year, variation in RHDV supply and release to help inform us of long-term patterns in virus use and possibly identify factors contributing to the release of the virus through time. We predicted that the supply and release of virus would peak during periods of high interest in RHDV. For example, in 1995, when the virus was initially introduced; in 2011, when reporting virus releases through mobile phone and web-based apps was novel; and in 2017, leading up to the national release of the K5 variant. Lastly, we predicted that the supply of RHDV would be associated with increased rabbit numbers following periods of high rainfall.

2 | METHODS

2.1 | RHDV supply and release

Both V351 and K5 are manufactured and sold by New South Wales Department of Primary Industries' Elizabeth Macarthur Agricultural Institute (EMAI). Since 1997, RHDV has been available to eligible land managers to assist with the management of rabbits, although legislation governing the supply and release of RHDV varies between Australian states and territories (Supporting Information S1). Eligible land managers must specify which virus, and the number of vials of RHDV they require. Either a single vial, or multiple vials, of RHDV may be supplied to land managers following a single request. Requests for RHDV are handled by email. This communication includes directions on how and when to use the virus, a website link to the standard operating procedures and the virus product label (Centre for Invasive Species Solutions, 2017; NSW Department of Primary Industries, 2016; Sharp, 2016). The optimal virus release conditions are also stated, including specific advice to avoid release when young rabbits are present. All the website links and the standard operating procedures reinforce the consistent message; avoid releasing RHDV when young rabbits are present (Supporting Information S1).

Land managers can then optionally report their rabbit management activities through RabbitScan, an online webpage and mobile phone application (Invasive Animals Ltd., 2020). Land managers become aware of RabbitScan through various newsletters, local government officers, social media, community workshops, field-days, and via word-of-mouth. To record actions taken to manage rabbits, land managers provide the coordinates of the locality and specify the control activity, such as the release of RHDV. No incentive is provided for land managers to report any rabbit management activities, but the data entered become a publicly accessible record to help coordinate rabbit control activities at larger scales.

2.2 | Rabbit breeding and identifying unseasonal RHDV release

Rabbits are sexually mature by 3–4 months of age and have a short gestation period, lasting 28–31 days (Tablado et al., 2009). Rabbits are also seasonally polyoestrous and can breed continuously with immediate post-partum mating. This enables them to begin a new pregnancy while lactating to raise a previous litter. Combined, these characteristics of a rabbit's breeding biology allow them to breed rapidly and readily take advantage of favorable environmental conditions.

Breeding can occur year-round but predominately follows the availability of green, protein-rich vegetation (Poole, 1960). Rainfall and temperature are the key drivers of vegetation growth and consequently of rabbit breeding (Tablado et al., 2009). Gilbert et al. (1987) summarized and analyzed reproductive data from 11 Australian rabbit populations across a range of environments from arid to sub-alpine. Even in arid Australia, rabbits usually bred between May and October. Failure to breed during these months was unusual and only occurred during the severest of droughts (Cooke, 2019). In high rainfall areas of North Queensland, rabbits breed year-round. However, because they use fat reserves for lactation to

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reduce heat-stress in a hot, humid climate, these reserves must be recovered before additional litters can be produced, and consequently breeding does not occur continuously (Cooke, Brennan, & Elsworth, 2018a). In southern Australia, rabbits also breed in hot weather after heavy summer rainfall, although such breeding is also not usually continuous (Myers & Gilbert, 1968; Wells et al., 2016).

Based on the studies summarized by Gilbert et al. (1987), it would be highly unusual if rabbits in southern Australia did not breed continuously between June and October (winter and spring) at a minimum. However, young rabbits would not be present in the population until 28–31 days after the start of breeding and they experience sublethal RHDV infections up to approximately 60 days of age. We therefore classified any RHDV supply/release that occurred between July and December (winter and early summer) as unseasonal and at high risk of immunizing young rabbits by infecting animals with existing innate immunity or maternal antibodies.

We acknowledge that in some states, including Western Australia, Queensland, and South Australia, some government webpages recommend the release of RHDV from October to December (spring or late spring) (Department of Primary Industries and Regional Development, 2021; Department of Primary Industries and Regions, 2021). However, such recommendations are not consistent with the available data on rabbit breeding and consequently the anticipated availability of young rabbits. Our judgment of an appropriate use of RHDV is therefore driven by the recommendation that is provided with the RHDV product, to avoid release when young rabbits are present, and published data on rabbit breeding times.

2.3 | Data and exclusion criteria

Data were available on the date of RHDV supply between January 1997 and April 2021. This exhaustive dataset included information on every instance within Australia where a land manager was ever supplied virus for release within our study period. However, the supply of RHDV for research purposes was excluded. Each RHDV supply record included information relating to the date RHDV was shipped/posted to land managers, the number of vials of virus supplied and the geographic region to which the virus was sent. Data on the release of RHDV were available for the period February 2011 to June 2021. This voluntarily submitted release data included information on the date and coordinates of virus release.

We excluded all data relating to the national K5 release as this was a government coordinated activity that encouraged land managers to release K5 in March 2017. For our RHDV supply data this meant excluding all records for February 20, 2017; for our RHDV release data this meant excluding virus releases that were reported between March 1, 2017 and May 31, 2017, inclusive (Cox et al., 2019).

2.4 | Data analysis

2.4.1 | Temporal and spatial trends in RHDV supply/release

All statistical analyses were performed in R version 4.0.2 (R Core Team, 2021). Plots were created in *ggplot2* (Wickham, 2016).

We modeled the monthly count of RHDV supply and release records using generalized additive models (GAMs) within the *mgcv* package (Wood, 2012, 2017). All models were constructed with a negative binomial family specification to account for overdispersion indicated in rootograms (Kleiber & Zeileis, 2016), with smoothing parameters estimated using restricted maximum likelihood. We included state/territory as a fixed effect to test for differences in RHDV supply/release across Australia.

We expected two different temporal patterns to be present in our data: (1) annual temporal patterns (repeating yearly seasonal oscillations) in the supply/release of RHDV due to the seasonal presence of young rabbits; and (2) long-term trends in the supply/release of RHDV due to the long-term nature of our dataset and efforts in recent years to promote the use of RHDV to manage rabbits. To test for the presence of these two different temporal patterns at both the Australia-wide and state level, we included separate cyclic cubic regression splines and thin plate regression splines for Australia-wide and for each state. This enabled us to simultaneously (within the same model) test for possible annual and long-term temporal patterns in our data, respectively, at both spatial scales.

To account for the number of RHDV vials supplied per request, we calculated a weighting variable by multiplying the number of RHDV requests from a particular region on a particular day by the number of vials requested by that region on that day. Regional level weights were then summed at the state level to create a weighting for each state each month. We then included this weighting variable as a fixed effect in our RHDV supply model.

To achieve the best and most parsimonious model we used the *select* = *TRUE* option within the *gam()* function in *mgcv* to penalize the range and null space of smoothing matrices during fitting (Marra & Wood, 2011). To assess model fit and assumptions we used model

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TABLE 1 Cumulative RHDV supply from government curated records and reported releases from RabbitScan by land managers for each month, season, and state

	Total number of RHDV supply/releases												
	Summer		Autumn			Winter			Spring			Summer	
State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
RHDV supply	59	81	127	104	80	74	52	66	97	89	105	62	996
Aust. Capital Territory	1	4	5	3	3	0	0	2	3	1	0	0	22
New South Wales	11	33	50	44	24	26	17	24	28	24	43	22	346
Northern Territory	0	1	0	3	1	1	0	2	4	3	0	0	15
Queensland	4	10	6	10	13	11	7	19	18	19	10	7	134
South Australia	7	2	6	8	5	8	3	4	11	6	4	3	67
Tasmania	4	5	7	1	5	2	0	1	0	0	1	2	28
Victoria	19	10	33	17	19	17	19	11	11	22	14	14	206
Western Australia	13	16	20	18	10	9	6	3	22	14	33	14	178
RHDV releases	14	25	12	87	2	21	16	15	20	111	173	113	609
New South Wales	1	6	3	0	1	6	1	0	3	62	2	0	85
Northern Territory	0		0	0	0	0	0	1	0	0	0	0	1
Queensland	0	3	1	0	0	0	0	0	1	2	0	0	7
South Australia	0	1	0	0	0	0	0	0	9	1	3	1	15
Tasmania	0	1	0	0	0	0	0	0	0	0	0	0	1
Victoria	0	8	8	1	1	0	1	0	0	0	0	1	20
Western Australia	13	6	0	86	0	15	14	14	7	46	168	111	480

Note: RHDV supply and releases data relate to the periods 1997–2021 and 2011–2021, respectively.
Abbreviation: RHDV, rabbit hemorrhagic disease virus.

diagnostics produced by *gam. check()* in *mgcv* and assessed rootograms (Kleiber & Zeileis, 2016; Wood, 2017).

We did not distinguish between the supply/release of v351 or K5 in any models as the recommendations regarding their use have remained consistent. Both v351 and K5 have acted as landscape-scale biocontrols, although in the majority of releases they likely only act as local biocides. Similarly, we did not account for the emergence of RHDV2 in models as its emergence and dominance within the Australian landscape does not change best practice RHDV release recommendations. Despite RHDV2 being capable of lethally infecting young rabbits, the high RHDV seroprevalence in the Australian rabbit population at the time that RHDV2 emerged would have conferred substantial partial protection against lethal RHDV2 infection in young rabbits due to the transfer of maternal RHDV antibodies (Cooke, Duncan, et al., 2018b; Ramsey et al., 2020; Strive et al., 2013). The opposite also occurs, where RHDV2 immunity confers partial protection against lethal RHDV infection. Therefore, both prior to, during and after the emergence and dominance of RHDV2, young rabbits would have always been present to some extent during the periods of rabbit breeding and potentially susceptible to immunization from unseasonal RHDV releases.

In the context of our fitted GAM models, the significance of a spline term is a test of deviation from a flat or null function that is constant at 0 over all observed values of the predictor variable (Wood, 2013). A flat function would occur when there is no pattern in the data and hence significant deviation from this indicates the presence of a pattern. The complexity of the spline is then indicated by its effective degrees of freedom (EDF), where an EDF of 1 represents a linear function, an EDF >1 represents a nonlinear function, and an EDF of ~0 indicates that the term has been penalized out of the model due to contributing little to explaining variation in the outcome variable (Marra & Wood, 2011).

2.4.2 | Exploring the relationship between RHDV supply and rainfall

We used the Bureau of Meteorology "Climate Data Online" and "Climate change—trends and extremes"

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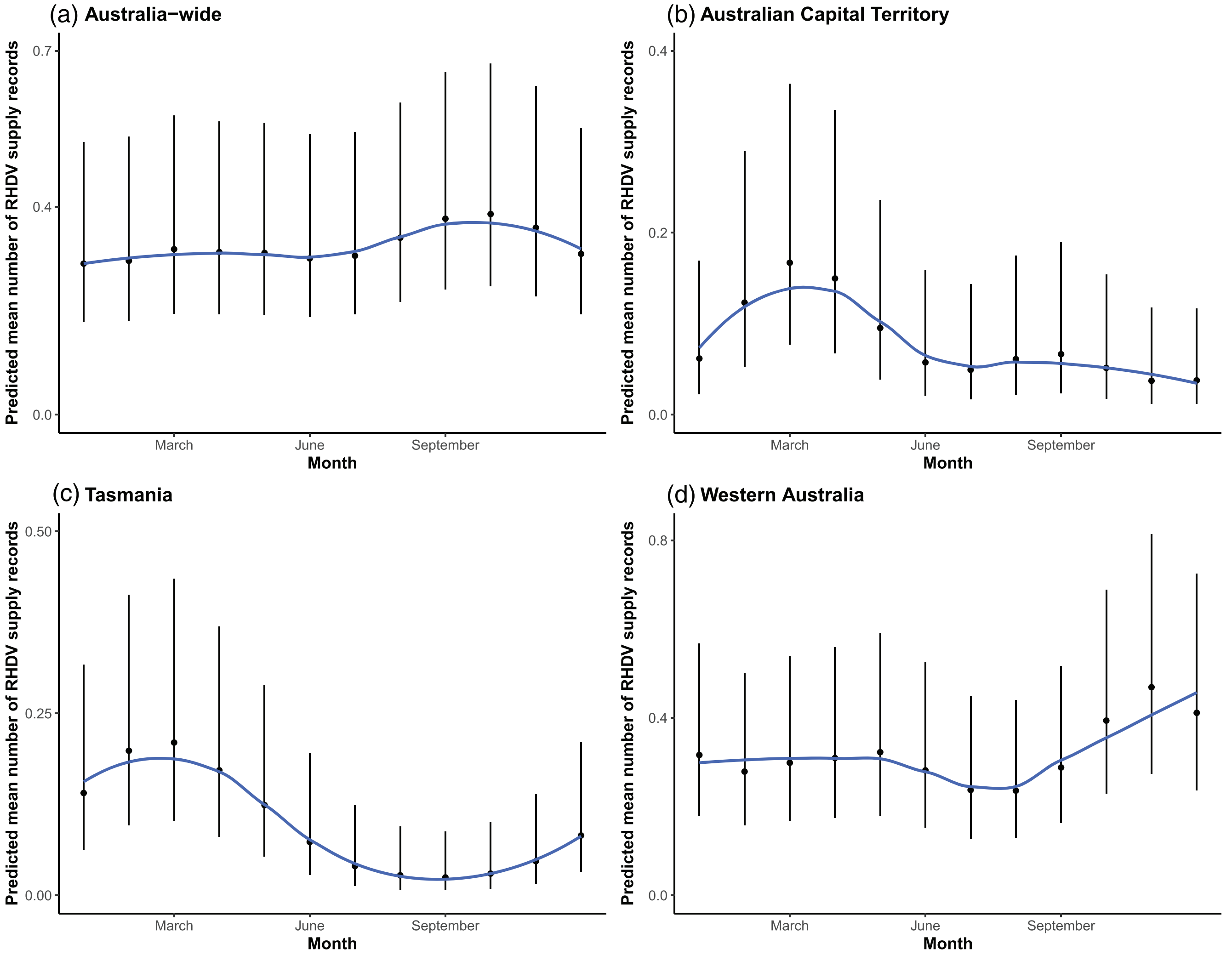

FIGURE 1 Predicted annual temporal pattern in RHDV supply for: (a) Australia-wide, (b) Australian Capital Territory, (c) Tasmania, and (d) Western Australia. This figure shows mean point predictions (black dots) and 95% confidence intervals (black lines), and loess smooth (blue line). RHDV, rabbit hemorrhagic disease virus

portals to obtain region- and state-specific rainfall data for each RHDV supply record, respectively (Australian Government Bureau of Meteorology, 2021a, 2021b). Specifically, we obtained the total rainfall that fell in a region/state in approximately the 12 months prior to each RHDV supply record and the long-term average annual rainfall for that region/state.

At a regional level we were able to access data relating to the exact 12-month period of interest. Using the 12 months previous and average annual rainfall at the regional/state level, we calculated the percentage of average annual rainfall that fell during the 12 months prior to each RHDV supply record.

At the state level, data were only available across annual windows and we could not obtain rainfall data for the 12 months prior to the exact date of the RHDV supply record. In this case, if a supply record occurred between January and June, it was assigned the annual rainfall for the previous year and if the supply record occurred between July and December, it was assigned the annual rainfall for the year in which the record occurred.

Using Pearson's correlation, we then assessed the association between the percentage of average annual rainfall in the previous 12 months and each of the number of RHDV vials dispatched per supply record and the total number of RHDV supply records in the 12 months prior to each supply record.

3 | RESULTS

3.1 | Temporal and spatial trends in RHDV supply

Between January 1997 and April 2021, there were 1015 RHDV supply records; 19 were excluded from analysis as

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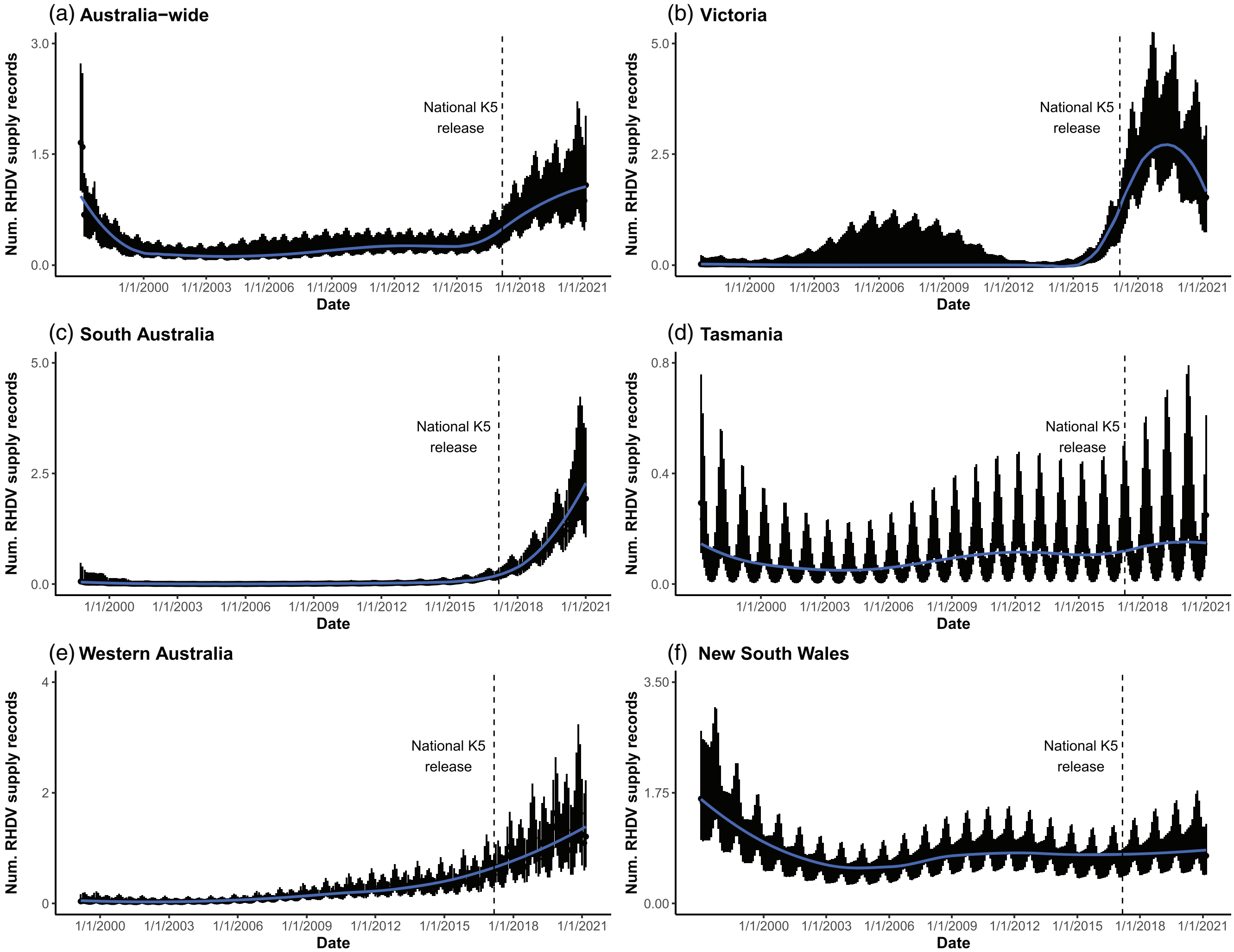

FIGURE 2 Predicted long-term temporal pattern in RHDV supply for: (a) Australia-wide, (b) Victoria, (c) South Australia, (d) Australian Capital Territory, (e) Western Australia, and (f) New South Wales. This figure shows mean point predictions (black dots) and 95% confidence intervals (solid black lines), and loess smooth (blue line). Dashed black line shows date of national K5 release. RHDV, rabbit hemorrhagic disease virus

they were associated with the national K5 release. This left 996 RHDV supply records from 428 different land managers for inclusion in the analysis (Table 1). RHDV supply was highly variable, with the median number of requests filled per month and year being 0 (range 0–21) and 22 (range 5–185) over the 1997–2021 period, respectively. We found evidence of RHDV being supplied during the major anticipated rabbit breeding seasons for all eight states and territories. Australia-wide 47% of RHDV supply occurred during the major anticipated rabbit breeding seasons and when the risk of immunizing young rabbits is greatest.

We observed a significant nonlinear Australia-wide pattern in the annual supply of RHDV (Figure 1a; Table S1) and significant and nonlinear state-specific patterns in the annual supply of RHDV (Figure 1b–d; Table S1). Australia-wide, RHDV supply was relatively consistent year-round, with a slight increase in spring (September–November; Figure 1a). There were significant patterns in the Australian Capital Territory and Tasmania, with RHDV supply peaking in autumn, with decreasing or minimal supply throughout winter and spring (June–November; Figure 1b,c; Table S1). In Western Australia, the pattern in annual RHDV supply approached significance and was consistent from late summer through to the end of winter (January–August), although increased through spring and into early summer (September–December; Figure 1d; Table S1). For each of the other states and territories, annual temporal trends in RHDV supply were either weak and nonsignificant or completely penalized out of our model. This suggested that no consistent annual temporal trends could be identified in these states and territories.

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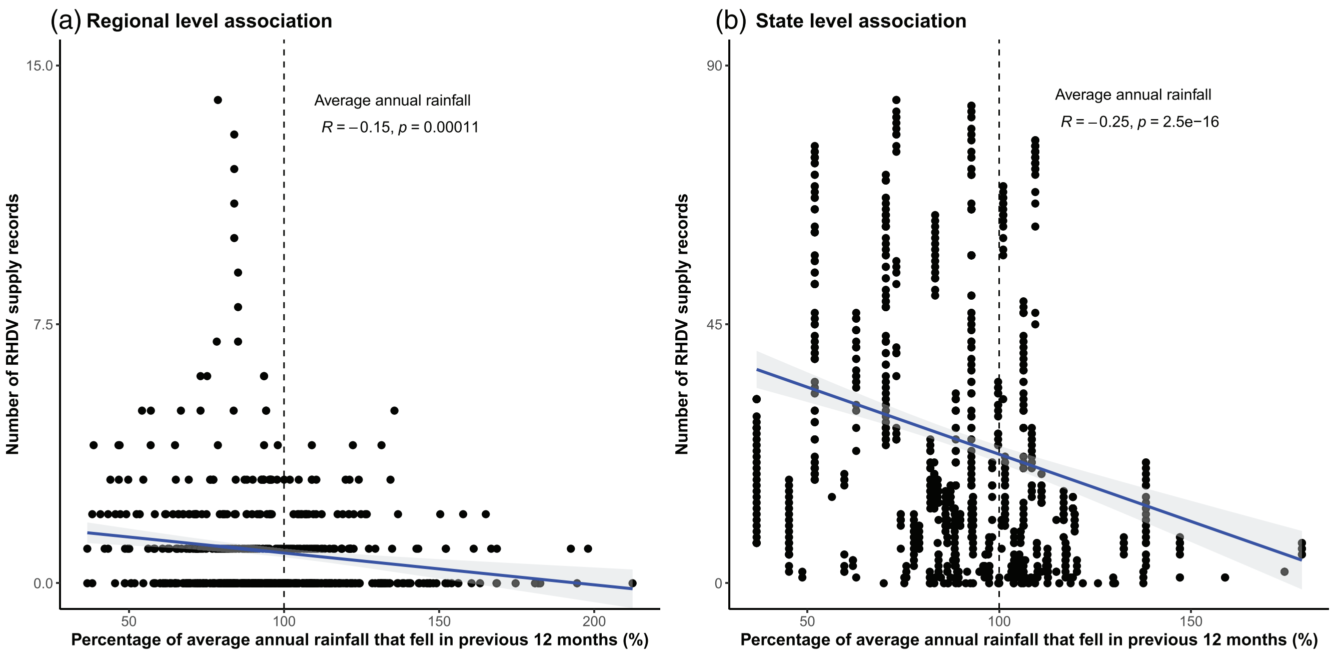

FIGURE 3 Association between RHDV supply and rainfall at the regional (a) and state level (b). *Y* axis represents the total number of RHDV supply records in the 12 months prior to each record. *R* and *p* show Pearson's correlation coefficient for the correlation and its associated *p*-value, respectively. Blue line with gray shading shows the line of best fit and associated 95% confidence interval. Vertical dotted line at $x = 1$ shows the average annual rainfall; left of this line represents below average rainfall and right of this line represents above average rainfall. RHDV, rabbit hemorrhagic disease virus

We found significant long-term temporal patterns in the supply of RHDV Australia-wide (Figure 2a; Table S1) and within specific individual states and territories (Figure 2b–f; Table S1). RHDV supply was initially high, between 1997 and 1998, but low between 1999 and 2008, before slowly increasing from 2009 onwards (Figure 2a). After 2017, the rate at which RHDV was supplied increased substantially Australia-wide (Figure 2a). Victoria, South Australia, Western Australia, and New South Wales each showed significant long-term patterns in RHDV supply (Figure 2b,c,e,f), and in Tasmania this trend approached significance (Figure 2d). In Victoria, South Australia, and Western Australia, RHDV supply was generally low until just prior to or after the national release of K5, in 2017, when supply began to increase (Figure 2b,c,e). In New South Wales, RHDV supply was initially high, between 1997 and 2000, after which it remained relatively consistent for the remainder of our study period (Figure 2f). In Tasmania, RHDV supply consistently fluctuated seasonally over the study period (Figure 2d). In contrast, for the Australian Capital Territory, Northern Territory, and Queensland, long-term trends in RHDV supply were either weak and nonsignificant or completely penalized out of our model. This suggested that no long-term temporal trends could be identified in these states and territories. The overall fit of our RHDV supply model was good, as indicated by the model's percentage deviance explained (Table S1) and in rootograms (not shown).

3.2 | RHDV supply and rainfall

The total number of RHDV requests increased in dry years at both a regional and state scale (Figure 3). However, the number of vials of RHDV ordered per request was not correlated with rainfall (regional level: $R = .05$, $p = .21$; state level: $R = .04$, $p = .24$).

3.3 | Temporal and spatial trends in RHDV release

Between February 2011 and June 2021, 710 RHDV releases were reported; 101 of these were excluded from analysis due to likely being associated with the national K5 release. This left 609 releases from 76 different land managers for inclusion in analysis (Table 1). RHDV releases were highly variable, with the median number of releases per month and year being 0 (range 0–110) and 16 (range 0–315) over the 2011–2021 period, respectively. Nonetheless, RHDV was released during the major anticipated rabbit breeding seasons in six of the seven states and territories included in our data. Australia-wide 74%

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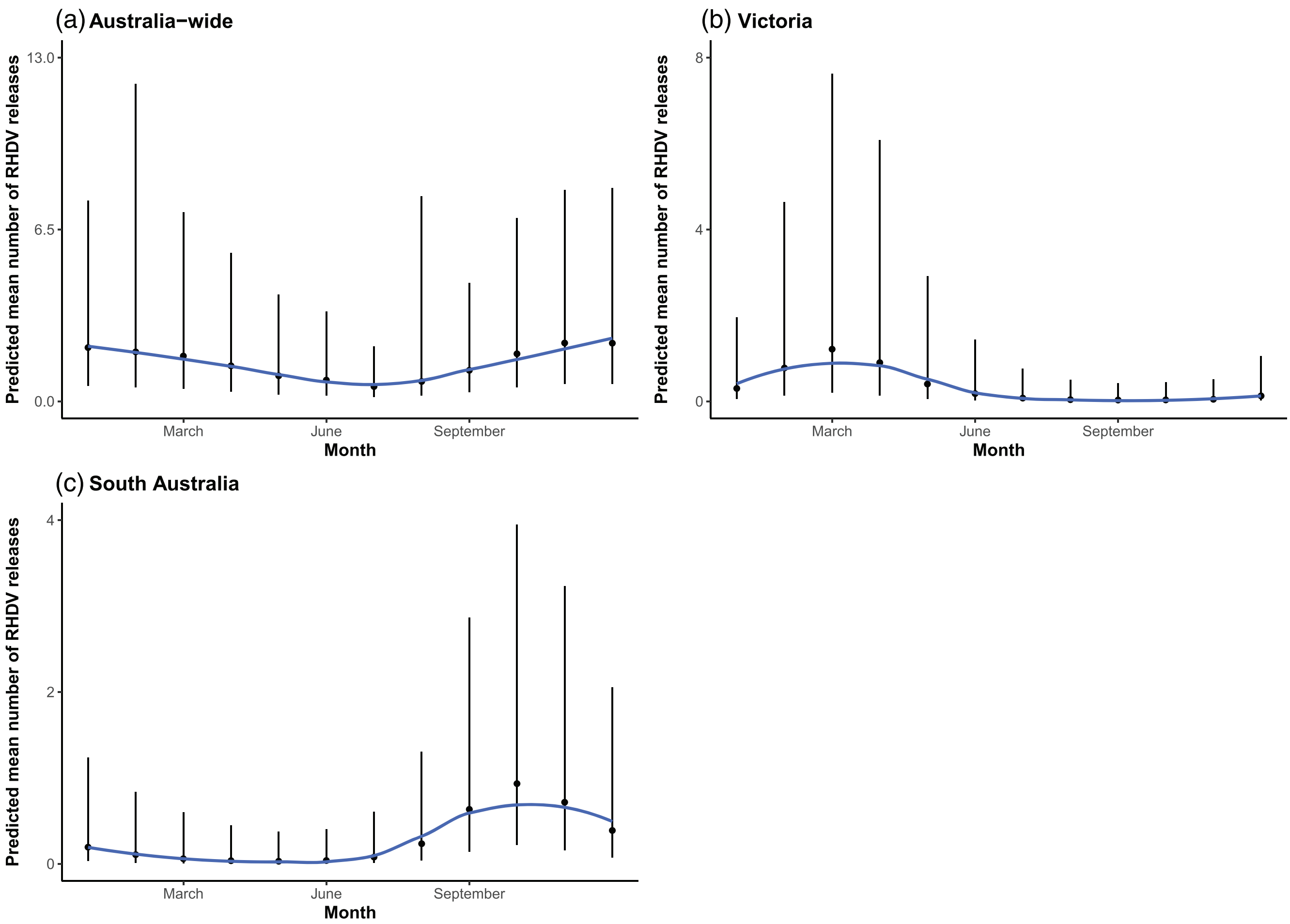

FIGURE 4 Predicted annual temporal pattern in the release of RHDV for: (a) Australia-wide, (b) Victoria, and (c) South Australia. This figure shows mean point predictions (black dots) and standard errors (black lines), and loess smooth (blue line). RHDV, rabbit hemorrhagic disease virus

(95% CI: 70–77) of RHDV releases occurred during the major anticipated rabbit breeding seasons and when the risk of immunizing young rabbits is greatest.

We found a significant nonlinear Australia-wide pattern in annual RHDV releases (Figure 4a; Table S2) and significant and nonlinear state-specific patterns in annual RHDV releases (Figures 4b,c; Table S2). The Australia-wide annual temporal trend in RHDV releases increased either side of winter (June/July) and was highest in summer and spring (Figure 4a). There was a significant annual temporal trend in RHDV releases in Victoria and this trend approached significance in South Australia (Figure 4b,c; Table S2). RHDV releases appeared to conform to release guidelines in Victoria, with releases peaking in late summer/early autumn (February–April; Figure 4b). The opposite occurred in South Australia, with RHDV releases peaking in spring (September–November), outside the recommended period of release (Figure 4c). We did not identify annual temporal trends in the release of RHDV in any other state or territory.

Significant long-term temporal patterns in RHDV releases were apparent only in New South Wales and Western Australia, with the long-term temporal pattern in RHDV releases also approaching significance in Queensland (Figure 5; Table S2). In New South Wales, RHDV releases increased and declined in association with the national release of K5 but were otherwise relatively low (Figure 5a). In Western Australia and Queensland, RHDV releases did not appear to be associated with the national release of K5 (Figure 5b,c). In Western Australia, RHDV releases increased, but fluctuated, from 2018 onwards (Figure 5b). In Queensland, RHDV releases were initially high in 2011, when the RabbitScan reporting app first became available for use, followed by a prolonged period of very few reported releases between 2012 and 2018, after which they showed some evidence of increasing from 2019 onwards (Figure 5c). For each of the other states and territories, and Australia-wide, long-term temporal trends in RHDV releases were not identified. The overall fit of our RHDV release model was

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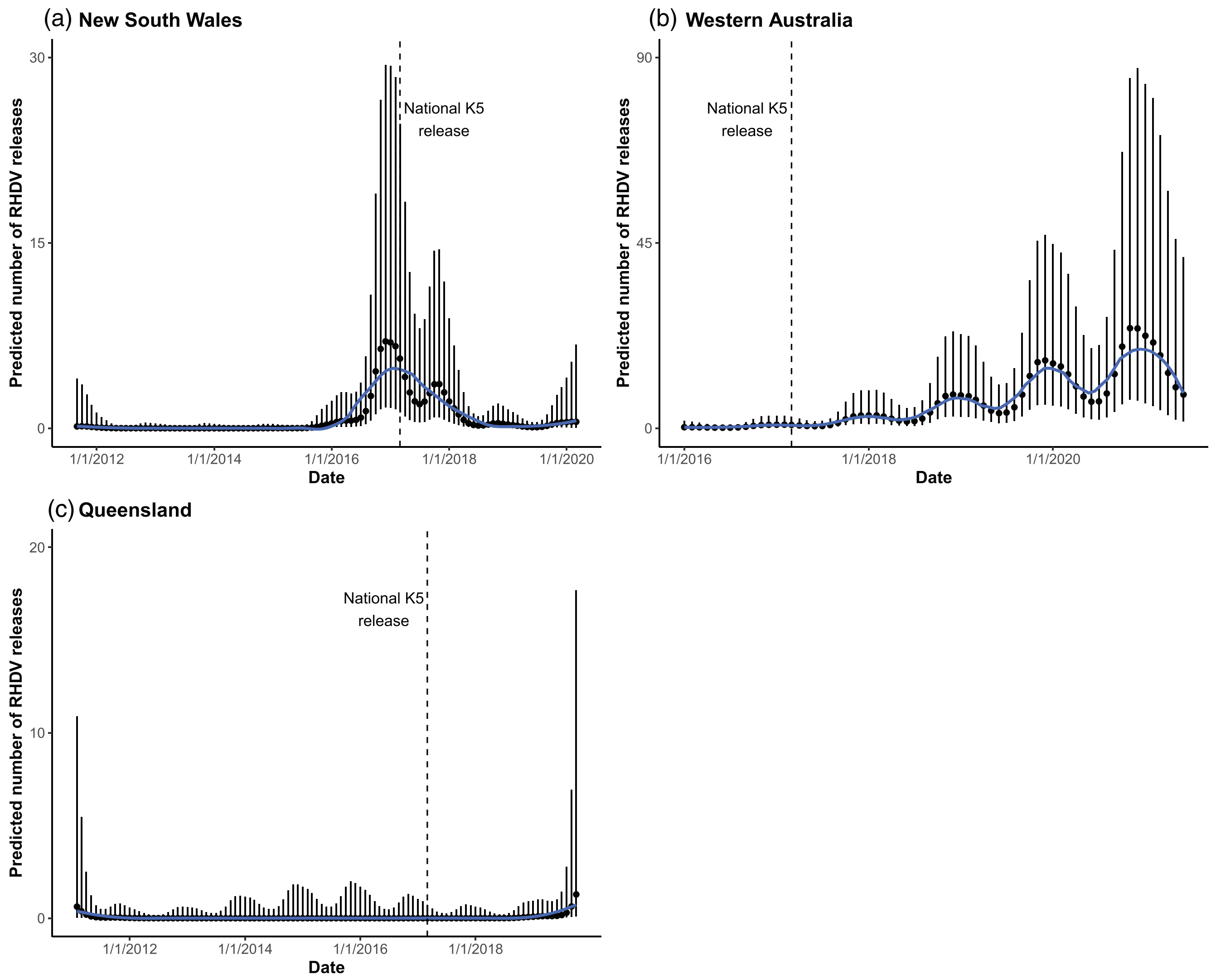

FIGURE 5 Predicted long-term temporal pattern in the release of RHDV for: (a) New South Wales, (b) Western Australia, and (c) Queensland. This figure shows mean point predictions (black dots) and standard errors (solid black lines), and loess smooth (blue line). Dashed black line shows date of national K5 release. RHDV, rabbit hemorrhagic disease virus

reasonable, as indicated by the model's percentage deviance explained (Table S2) and in rootograms (not shown).

4 | DISCUSSION

Land managers assist with the successful implementation of conservation and pest management programs worldwide (Naidoo & Iwamura, 2007). However, where programs require people to follow guidelines, regarding how, when or where these activities take place, outcomes may not meet expectations, and despite good intentions, may even have adverse outcomes.

The release of RHDV for rabbit management is an example of this. If released among susceptible adult rabbits, RHDV would be expected to effectively reduce rabbit numbers and successfully contribute to conservation and pest management objectives (Finlayson et al., 2021; Mutze et al., 1998). However, if released among young rabbits, less than approximately 60 days old, RHDV would be expected to cause few deaths and facilitate the entry of immune young into the breeding population (Mutze et al., 1998; Nowotny et al., 1993; Prieto et al., 2000; Robinson et al., 2002). This would be expected to lead to population increases and make future rabbit control harder.

Our data show that approximately half the supply (47%) and three quarters of releases (74%) of RHDV occur during the major anticipated periods of rabbit breeding in Australia, and therefore, when the risk of immunizing young rabbits is greatest (Poole, 1960; Wood, 1980).

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While annual temporal trends in the supply and release of RHDV conformed better to guidelines in some states and territories than others, our data nonetheless demonstrate that, many people who release RHDV do not follow recommended guidelines and potentially risk adverse outcomes.

The reality of inappropriate RHDV release may be better or worse than our data suggest. The total number of reported RHDV releases was fewer than the known supply volume, with 609 releases and 996 supply records. Moreover, often multiple vials of RHDV were supplied at the same time. This suggests that many RHDV releases are not reported through RabbitScan. However, irrespective of this, our data suggest that a large proportion of RHDV releases occur when the risk of immunizing young rabbits is greatest.

The inappropriate release of RHDV may be, in part, driven by state government organizations. Several government organization webpages suggest that the release of RHDV in spring or late spring is appropriate (Department of Primary Industries and Regional Development, 2021; Department of Primary Industries and Regions, 2021). Such webpages may act as major hubs of information on best practice pest management for land managers. However, as a general rule, recommendations to release RHDV between July and December (winter-early summer) are in contrast to the documented rabbit breeding behavior in southern Australia (Gilbert et al., 1987). In several states, RHDV is also predominately, or solely, released by government officials. Therefore, in addition to some state government webpages possibly misleading private land managers on the appropriate use of RHDV, a proportion of unseasonal RHDV releases are also likely actively conducted by government officials themselves. This suggests that the release of RHDV and guidelines around its use are not given the critical appraisal that they require, even by those stipulating guidelines for others. Our results show that we need to better understand and communicate the possible implications of releasing RHDV in the presence of young rabbits to all land managers, irrespective of their position (private, government, other), if the release of RHDV is to continue to contribute to rabbit management effectively.

It is difficult to estimate whether releasing RHDV during the rabbit breeding season creates only local or more widespread problems via the introduction of virus immunity into the rabbit population. If the released virus consistently spreads to other rabbit populations, beyond the local target population, widespread changes in rabbit serological profiles and immunity may result. In contrast, the spread of RHDV releases may be minimal, but if the volume and distribution of releases is great, widespread problems may also occur. We are unsure of the exact number of releases as often multiple vials of RHDV may be supplied per request, which may be distributed among several land managers for numerous individual releases, or all used at once for a larger release.

However, some rabbit biocontrol experts currently consider that most RHDV releases only act at a local scale. This is expected to occur due to the virus being released into a partially immune population (Mahar et al., 2018; Taggart et al., 2021). If the spread of an RHDV release is minimal beyond the target population, then its release during the rabbit breeding season may produce only localized changes in rabbit serological profiles and immunity.

Rabbits have high natural turnover in their populations but also breed rapidly. This complicates the interpretation of possible scenarios following unseasonal RHDV releases. If the release of RHDV during the rabbit breeding season spreads from the release site, it may produce minimal long-term impacts because of the high natural turnover in wild rabbit populations. Approximately 6% of rabbit kittens, or fewer, survive long enough to successfully reproduce (Robson, 1993; von Holst et al., 1999, 2002). Therefore, only a small proportion of rabbit kittens that are infected and gain immunity from an RHDV release may survive long enough to breed and have the potential to impact on the subsequent rabbit population. However, once rabbits reach adulthood, they breed rapidly, and their rate of mortality reduces substantially to approximately 50% per annum. Therefore, if a pair of adult, RHDV-immune, rabbits produces 25 young annually and one of the breeding adults dies, only one young needs to survive to maintain the breeding population. If two young survive, due to the immunizing effect of an RHDV release, the population of breeding adult rabbits is increased by 50% in the following year. This could result in significant detrimental impacts of unseasonal RHDV releases and rapid increases in population sizes. However, detailed data and modeling exploring the outcome of releasing RHDV at different times of the year are currently lacking.

Rainfall was also associated with people's behavior to access RHDV. The annual rainfall in the 12 months prior to each RHDV supply record was negatively correlated with the number of RHDV supply records over the same period. This was contrary to our expectations based on rabbits breeding following rain and hence their populations increasing during wetter periods. Instead this pattern may indicate a tendency for people to notice, and want to control, rabbits and their impacts more following drier years when both rabbits and their impacts are potentially more damaging. Anecdotally, this is a common problem in rabbit and pest control generally,

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whereby land managers implement management when they notice problems as opposed to implementing management earlier to prevent problems. However, we acknowledge that our analysis cannot determine cause and effect and consequently it is also possible that the effect of rainfall on people's behavior to access RHDV may be confounded by increased media or awareness of rabbit control during dry periods.

In some states, we found evidence that the supply or release of RHDV peaked when the supply service or RabbitScan reporting systems were novel. For the supply of RHDV, this related to the period 1997–1998, shortly after the virus was first introduced to Australia and when the virus could first be accessed by land managers to assist with rabbit management. For data on the release of RHDV, this period of novelty relates to 2011, when the RabbitScan reporting system first became available. Reported RHDV releases in New South Wales also appeared to increase in conjunction with the national K5 release in 2017, and we found evidence that both the supply and release of RHDV increased following the national K5 release in several states. This may reflect differences between state pest control agencies in the degree to which they encouraged land managers to release RHDV and report their rabbit management activities for the national release of K5.

Recent experimental studies on enclosed wild rabbit populations show that the release of RHDV2 during the rabbit beeding season induced infection in young rabbits and substantially reduced their mortality rate due to maternal antibody protection (Calvete et al., 2021). This is of direct relevance to the results of our study and the predicted implications of unseasonal RHDV releases. Combined, this brings forth several important questions and concerns including asking whether the release of RHDV contributes effectively to ongoing rabbit management. For example, what are the true consequences of releasing the RHDV virus during the rabbit breeding season? Does this have significant consequences for the subsequent rabbit population and its subsequent management? And; if so, are tighter regulations required on when RHDV can be accessed for release? If RHDV circulates effectively irrespective of releases and many land managers get release timing wrong, should additional releases of RHDV be permitted at all? Perhaps land managers should be restricted to using rabbit management techniques for which the risk of adverse impacts is low, or for which adverse impacts are unlikely to impact upon neighboring land managers. All of these questions and the recent literature highlight the importance of integrated pest management, whereby pest species are managed using a combination of methods, and no single management approach is expected to be sufficient. There is no "silver bullet."

More broadly, our study offers a warning for the success of other conservation and pest management activities that may rely heavily on land managers or citizens following implementation guidelines. Many pest animals and plants are managed worldwide for both environmental and economic reasons and land managers are often encouraged to contribute, but also asked to follow implementation guidelines. In Australia, examples include the management of cane toads (*Rhinella marina*), kangaroos (*Macropus sp.*), serrated tussock (*Nassella trichotoma*), and prickly pear (*Opuntia sp.*). We encourage others to assess to what extent the guidelines surrounding the implementation of conservation and pest management activities are adhered to by land managers. Even if well intentioned, land managers may not always contribute positively to conservation and pest management activities.

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CONFLICT OF INTEREST

Tiffany W. O'Connor, Peter D. Kirkland, and Andrew J. Read work for the New South Wales Department of Primary Industries' Elizabeth Macarthur Agricultural Institute where RHDV is manufactured and sold.

AUTHOR CONTRIBUTIONS

Patrick L. Taggart conceived the ideas and designed methodology; Tiffany W. O'Connor, Andrew J. Read, Peter D. Kirkland, Peter West, and Emma Sawyers collected the data; Patrick L. Taggart and Kandarp Patel analyzed the data; Patrick L. Taggart, Tiffany W. O'Connor, Brian Cooke, and Kandarp Patel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study brings together researchers and pest managers across multiple Australian states and Territories to which our data relate. Where possible, relevant literature published by scientists from the regions of interest was cited.

DATA AVAILABILITY STATEMENT

Data and R code are available from authors upon request.

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ETHICS STATEMENT

No animal or human ethics were required for this study.

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