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RESEARCH ARTICLE

Sociality reduces the probability of eradication success of arthropod pests

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Abstract

Social insects are successful and globally significant invaders. Compared to ongoing suppression, eradication is seen as an ideal solution and cost effective in the long term. The success of eradication attempts is not guaranteed and identifying key factors that could influence the success of such management programs would be beneficial. In this study, 239 eradication attempts were compiled and analysed to identify why eradication attempts fail, with a focus on how eusociality of the target species impacts eradication success. All else remaining constant, the odds of successful eradication were 79% lower when targeting social species compared to non-social insects. Eradication success was shown to increase when comparing more recent attempts to earlier ones but was found to decrease as the duration of the attempt went on. Eradication attempts that occurred on islands, and those that targeted species with a broader host range, were also associated with increased success. A review of cited reasons for eradication failure highlighted the importance of employing effective control treatments, management, and monitoring systems, as well as garnering adequate social and political support. This study indicates how social insects are particularly challenging to eradicate; it also notes the importance of considering both logistical and biological aspects of any eradication, before initiating eradication attempts.

Keywords Pest management · Invasive species · Logistic regression · Management success

Introduction

Biological invasions are one of the most significant threats to global biodiversity (Bellard et al. 2016). The reshuffle of species worldwide has led to many organisms establishing across new ranges, often to the detriment of resident species. In response, conservation managers have attempted to reduce populations of these invasive species in their non-native ranges by reducing or controlling their populations, typically with the ideal outcome to eradicate entire populations of invasive species.

The causes of success or failure of eradication programs have been discussed and debated over the decades. Dahlsten (1986) suggested that eradication of pest species, while attractive, can be costly and can cause more economic and environmental damage than the pest might have otherwise caused. They went on to highlight the need for more careful evaluation over whether the cost of the actions taken outweighs the cost of the harm exerted by the target species, something echoed in later discussion surrounding eradication attempts (Bomford and O'Brien 1995; Phillips et al. 2019). The success of eradication attempts has increased with time as we make technological advancements (Brockerhoff et al. 2010; Tobin et al. 2014; Spatz et al. 2022); however, there are still many factors that contribute to an eradication outcome and success is never guaranteed. Prior studies have examined a range of factors than might contribute to the success of eradication efforts. Key factors such as spatial extent, relative detectability of the target species and rate of response have been observed to significantly influence eradication programme outcomes (Pluess et al. 2012a, 2012b; Tobin et al. 2014).

Social insects are an especially well-represented group in biological invasions, despite only 2% of insects being considered eusocial (Wilson and Hölldobler 2005). Eusociality appears to confer many behavioural, reproductive and genetic traits that give an advantage for invasion and

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establishment in new ranges (Manfredini et al. 2019; Eyer and Vargo 2021). A generalist diet, high reproductive output, and behavioural plasticity have allowed social insects to successfully invade new habitats all over the world (Beggs et al. 2011; Manfredini et al. 2019) and they are frequently cited as some of the world's worst invasive species (Lowe et al. 2000; Chapman and Bourke 2001). The ability or even preference of some social insects to inhabit human altered environments may also lead to their invasion success (Lester and Beggs 2019; McGruddy et al. 2021). Weak nest mate discrimination has been hypothesised to lead to the promotion of polygynous reproductive strategies, while supercolonies in newly invaded ranges allow social insects to experience high reproductive success which aids their establishment (Eyer and Vargo 2021). We hypothesised that these same advantages that have enabled the widespread success of social insects may also make them distinct from other species, regarding the ability of conservation mangers to successfully eradicate them.

Social insects including ants, bees, wasps, and termites have frequently been the target of eradication and control campaigns worldwide (Wenner et al. 2009; Hoffmann et al. 2016; Leza et al. 2021; Horwood and Lo 2022). Previous analyses of eradication programs have not incorporated eusociality as a predictive factor to explain eradication outcomes (Pluess et al. 2012a; Tobin et al. 2014). To investigate the effects of sociality on eradication success a compilation of 239 eradication attempts, which included 50 aimed at social insects, was analysed. We first asked if the success of eradication programmes targeting social insects differed from those aimed at non-social species. Then, we considered what other factors may lead to reduced eradication success and whether eusociality had any further influence on these factors. Logistic regression was used to identify different predictors of eradication success. In addition, common causes of eradication failure were assessed for each failed eradication, to highlight where eradication programs should aim to improve for future success.

Materials and methods

The Global Eradication and Response DAtabase (GERDA) contains a compilation of summaries of various eradication programmes (Kean et al. 2022). Each entry represents a single eradication project and contains a range of information about the eradication attempt and the target species (Table 1). In this analysis the GERDA database was used to find a selection of eradication projects that could help to identify reasons why eradication projects fail. When applying filters, we selected entries that looked at Arthropods and where the outcome was specified as "eradication confirmed" or "eradication failed". Only records after 1950 were considered in this analysis, since prior to that date the eradication actions were still relatively crude, or they were poorly reported. Supporting literature was used to back up the information provided in the GERDA database. Both peer reviewed and "grey" literature such as government reports were considered. To supplement this list, 20 additional eradication attempts that occurred, since the development of the GERDA database was found using web searches (Online Resource 1). In some cases, we were unable to find data for some fields, so some entries remain incomplete. It must be acknowledged that publication biases are likely present to some degree. These may include biases around reporting eradication failure, target species of high economic importance or of geographically widespread eradication attempts. It is assumed that the data used in these analyses are as representative as possible; however, these biases must be considered and acknowledged.

Logistic regression was used to investigate how different variables influenced eradication success. A wide range of predictor variables was initially compiled (Table 1). A logistic regression model with eradication success or failure as the response was fitted with these predictors, using the 'glm' function of the 'stats' package in R version 4.2.0 (R Core Team 2022). It should be noted that this function ignores cases that contain missing data for any variable used in the model. When building the model, the number of cases excluded was considered and minimised where possible. Explanatory variables Cost and Area were removed due to the high amount of missing data (≥ 117 cases missing). The variable End year was considered redundant due to the inclusion of Start year and Duration. Variables that showed no statistically significant relationship with the success of eradication attempts were removed from the logistic regression. Interaction terms were also included in the model initially, namely, interactions between Sociality and variables, such as Start year, Duration and Insularity. These variables were a priori chosen for investigation but were ultimately removed from the model due to statistically insignificant effects. From the final model, effect coefficients (β_i) for each variable are reported with associated standard errors. Relationships between the response and explanatory variables were assessed using type II analysis of Deviance tables produced using the 'Anova' function from the 'car' package (Fox and Weisberg 2019). The likelihood-ratio chi square statistic (G^2), degrees of freedom (df) and associated p values (p) are reported. Statistical significance was assumed at $p < 0.05$. All plots were produced in R studio using the package 'ggplot2' (Wickham 2016).

Alongside the statistical analysis, to further investigate common reasons for eradication failure, a qualitative review of the failed eradications within the compiled data set was performed. Failed eradication attempts retrieved from the GERDA database often listed reasons for failure and these

Table 1 List of potential predictor variables collected for each eradication attempt

Variable name	Explanation of variable
Success/failure	0 = failure of eradication attempt, 1 = success of eradication attempt
Order	Taxonomic classification
Family	Taxonomic classification
Genus	Taxonomic classification
Species	Taxonomic classification
Sociality	0 = non-social, 1 = eusocial
Host range	1 = monophagous (host is specific to one genus), 2 = oligophagous (hosts span multiple genera within one family), 3 = polyphagous (hosts span more than one family)
Feeding guild	1 = leaf/flower feeder, 2 = predator/parasite, 3 = root/stem/wood feeder, 4 = scavenger/generalist. Species that could be placed in multiple categories were include within the scavenger/generalist guild
Voltinism	The number of generations per year that a target species produces. 1 = univoltine (one or fewer generations per year), 2 = multivoltine (2 or more generations per year)
Continent	The continent on which the eradication took place; Africa, Asia, Europe, North America, Oceania, South America
Country	Country where eradication attempt took place
Location	More specific geographical information such as City or State. This variable was included to provide additional context to some entries (e.g., an eradication attempt in the Mariana Islands would be listed as taking place in Oceania, despite falling politically within the country of the USA, a nation more associated with the continent of North America)
Area	Stated extent of spread or treatment in hectares (ha)
Start year	Year in which eradication efforts began
End year	Year in which eradication efforts halted
Duration	Number of years that eradication efforts were sustained. Calculated as the difference between the 'Start year' and 'End year'. In cases where the eradication attempt was completed within the same year as initiation, the duration was rounded to 1 to remove instances of durations lasting 0 years
Method of control	Each cited treatment or type of control action. The treatments or control actions were comprised of 12 categories based on what was reported in the GERDA database (Kean et al. 2022) (Online Resource 1)
Cost	Cost of total eradication attempt (USD 2015)
Insularity	This variable relates to whether the eradication attempt occurred on an island or mainland/continental setting and was informed by the Global Island Database (Sayre et al. 2019): 0 = continental mainland, 1 = Island

Data for some predictors were missing, resulting in a data set with cases of incomplete records

were recorded. In other entries, the source information was searched and any cited reasons for eradication failure were categorised and recorded. The results were compiled and tallied among both social and non-social target species. Common themes were compiled and discussed in the context of results discovered from the quantitative analysis carried out in this paper.

Results

Compilation and model building

We compiled 239 eradication programs for statistical analysis. Two hundred and nineteen of these eradication attempts came from the GERDA database with a further 20 added from web searches.

Variable selection was largely a priori with the main focus of this study being how sociality impacts eradication success. Feeding guild did not have a significant association with eradication success ($p = 0.526$). The variable Voltinism was removed for the same reason ($p = 0.092$). Interaction terms were initially included to investigate relationships between Sociality and Starting year, Duration, and Insularity. These were all statistically insignificant ($p \geq 0.113$) and so were removed from the model and the data re-analysed. Start date and Duration were weakly correlated ($r = -0.131$, $p < 0.05$). Ultimately, the explanatory variables selected for the logistic regression model were Sociality, Starting year, Duration, Insularity and Host range.

Of the 239 eradication attempts compiled, 12 were excluded from the statistical model due to missing data leaving 227 eradication attempts for quantitative analysis. Of these eradication attempts, 169 were successful, while 58 failed. Eighty-one target species across eight arthropod Orders are represented within this selection of eradication attempts. Social species were the target of 50 eradication attempts, with ants (Formicidae) making up the majority of these with 33 eradication attempts. Wasps and hornets (Vespidae), Bees (Apidae) and termites (Kalotermitidae and Rhinotermitidae) were also represented. Fruit flies belonging to the family Tephritidae were the most represented group

(58 eradication attempts) with the Mediterranean fruit fly (*Ceratitis capitata*) being the target of 29 of these eradication attempts, nearly twice the next most represented species (New-World screw-worm fly, *Cochliomyia hominivorax*, which was the target of 15 eradication attempts). To ensure that *C. capitata* was not influencing the results, analysis was repeated removing all eradication attempts targeting the species. This exclusion made no significant impact to the results so eradication attempts targeting *C. capitata* were kept in the analysis.

Logistic regression

Sociality appeared to negatively influence eradication success. Just under 24% of eradications targeting non-social species resulted in failure, compared to 33% of eradications targeting social species (Fig. 1). Logistic regression supported this relationship, showing sociality of the target species was negatively associated with eradication success ($\beta_{social} = -1.541 \pm 0.475$, $G^2 = 10.530$, df = 1, $p < 0.01$). The model output suggests that all else remaining constant, an eradication targeting a social species has 79% lower odds of success than an eradication attempt targeting a non-social species.

The starting year of the eradication programme was positively associated with eradication success, indicating that the likelihood of eradication success increases with more recent eradication attempts ($\beta_{start} = 0.046 \pm 0.011$, $G^2 = 18.313$, df = 1, $p < 0.001$) (Fig. 2A, B). The duration of the eradication attempt was negatively associated with eradication success ($\beta_{duration} = -0.117 \pm 0.040$, $G^2 = 9.363$, df = 1, $p < 0.01$). To ensure this result was not too heavily influenced by a small number of outliers, the analysis was repeated with a subset of the data that included only those eradication attempts that lasted 5 years or less. We found that eradication duration still had a significant negative association with eradication success ($\beta_{duration} = -0.451 \pm 0.150$, $G^2 = 9.262$, df = 1, $p < 0.01$) and so we chose to keep all data in the analysis. Our analysis indicated unsuccessful eradication attempts were typically sustained for over twice as long as successful attempts (Fig. 2C, D). The median duration of unsuccessful attempts was 5 and 3 years for non-social and social species, respectively (4 years over all), compared to successful attempts with a median duration of 2 and 1 years for non-social and social species, respectively (2 years over all).

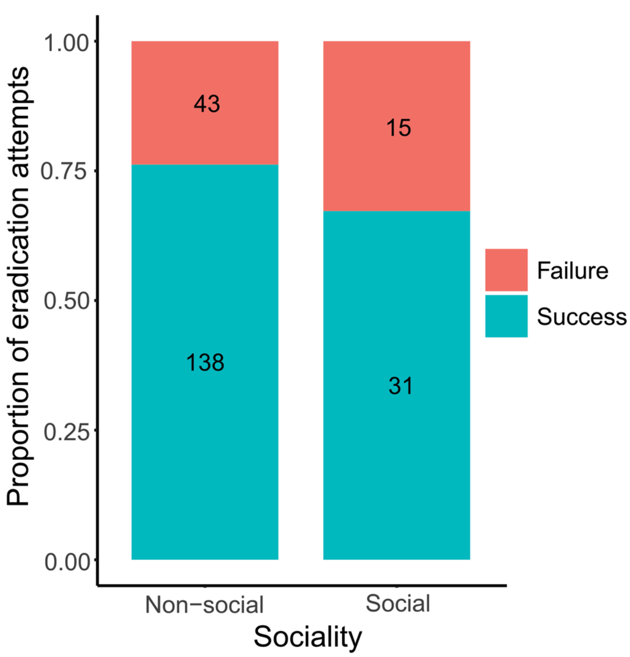

Fig. 1 Eradication success by sociality of the target pest arthropod species. Based on the results of our analysis, target species sociality was found to be negatively correlated with eradication success. Only 23.8% of eradication attempts targeting non-social species ended in failure compared to 32.6% of eradications targeting social species. This difference was statistically significant ($p < 0.01$)

Insularity was found to have a significant influence on eradication success, as success rates of eradication attempts that took place on islands were significantly higher than on continents ($\beta_{island} = 1.088 \pm 0.432$, $G^2 = 7.026$, df = 1, $p < 0.01$) (Fig. 3A). Our model estimates that, all else remaining constant, the odds of an eradication attempt succeeding are nearly 3 times higher when conducted on an island than on a continent. An example of this phenomenon is in the eradication attempts of fire ants (*Solenopsis* spp.). Four out of 7 eradications occurring on continents were unsuccessful. In comparison, eradication attempts of *Solenopsis* spp. on islands were much more successful with only 1 of 5 eradication attempts ending in failure.

Logistic regression suggested that eradication success was higher for those eradication attempts targeting species with broader host ranges ($\beta_{oligo} = 0.742 \pm 1.117$, $\beta_{poly} = 2.932 \pm 1.039$) (Fig. 3B). This association between host range breadth and eradication success was statistically significant ($G^2 = 17.832$, df = 2, $p < 0.001$). This association suggests target species with a more generalist feeding habit may be more susceptible to control methods such as toxic baits than a more specialist species.

Qualitative analysis of causes for eradication failure

Across the 239 compiled eradication attempts there were 66 failed attempts with cited reasons for failure. The reasons for failure were varied but the most common cause cited was that of ineffective treatment (Table 2). Thirty-seven of the 66 failed eradications (56%) were said to fail at least in part because the treatment failed to achieve adequate control of the target species. A decline in political or social will was also a highly cited reason for eradication failure, with

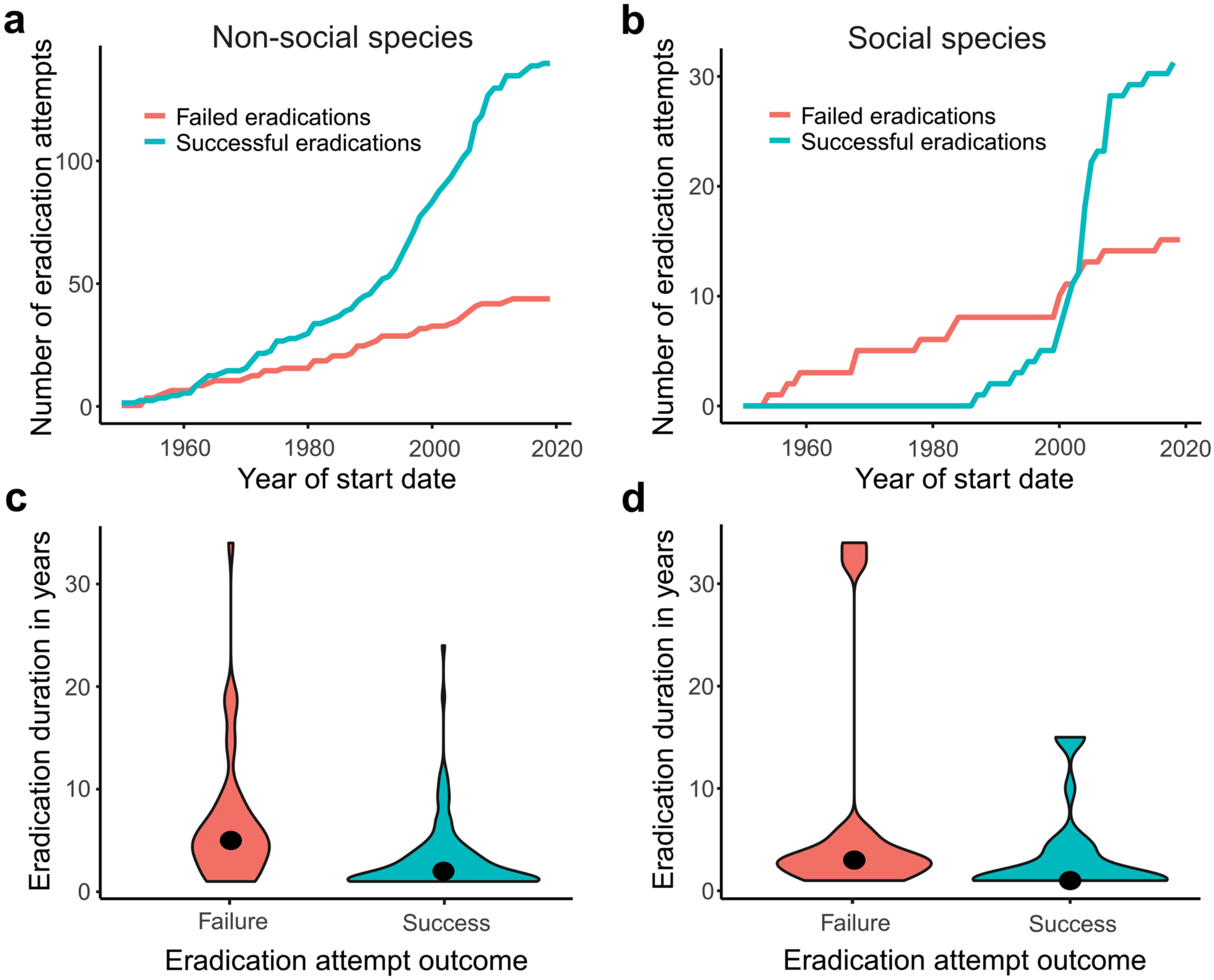

Fig. 2 **a** Number of successful and failed eradication attempts targeting non-social species since 1950. **b** Number of successful and failed eradication attempts targeting social species since 1950. Our analysis shows that eradication start year was positively associated with eradication success, suggesting more recent eradications were more likely to be successful. **c** Duration of successful and failed eradication attempts targeting non-social species. **d** Duration of successful and failed eradication attempts targeting social species. The dots in both violin plots represent the median duration of the eradication attempts, with medians for failed eradications of 5 and 3 years for non-social and social species, respectively. Successful eradications typically lasted under half this time, with 2- and 1-year medians for non-social and social species, respectively

a third of all failed eradication attempts citing this reason as a contributing factor. Flawed management of eradication attempts encompassed issues such as the inability to monitor target species populations, falsely announcing eradication, or an inability to apply control treatment uniformly or effectively. Flawed management was cited as a contributing cause of failure in just over 31% of all failed eradications, though was more prevalent in eradication attempts targeting non-social species. Conversely, an inability to access or treat pest populations was cited in just over 13% of all failures, disproportionately more in attempts targeting social species. Reinfestation, rapid spread of target species, and an inability to detect or delimit target species populations were also heavily cited. Interestingly, eradications that cited budget depletion as a reason for failure were relatively rare in this data set, as were those that cited failures due to extreme climatic or disturbance events (Table 2).

Discussion

Based on a logistic regression analysis of 227 eradication attempts, we found that the sociality of insects had a significant impact on eradication success. Social insects have adaptations that allow them to better deal with changes in their environment (Menzel and Feldmeyer 2021). It has been suggested that eusociality confers a higher basic reproductive output and reduced risk of extinction when compared to

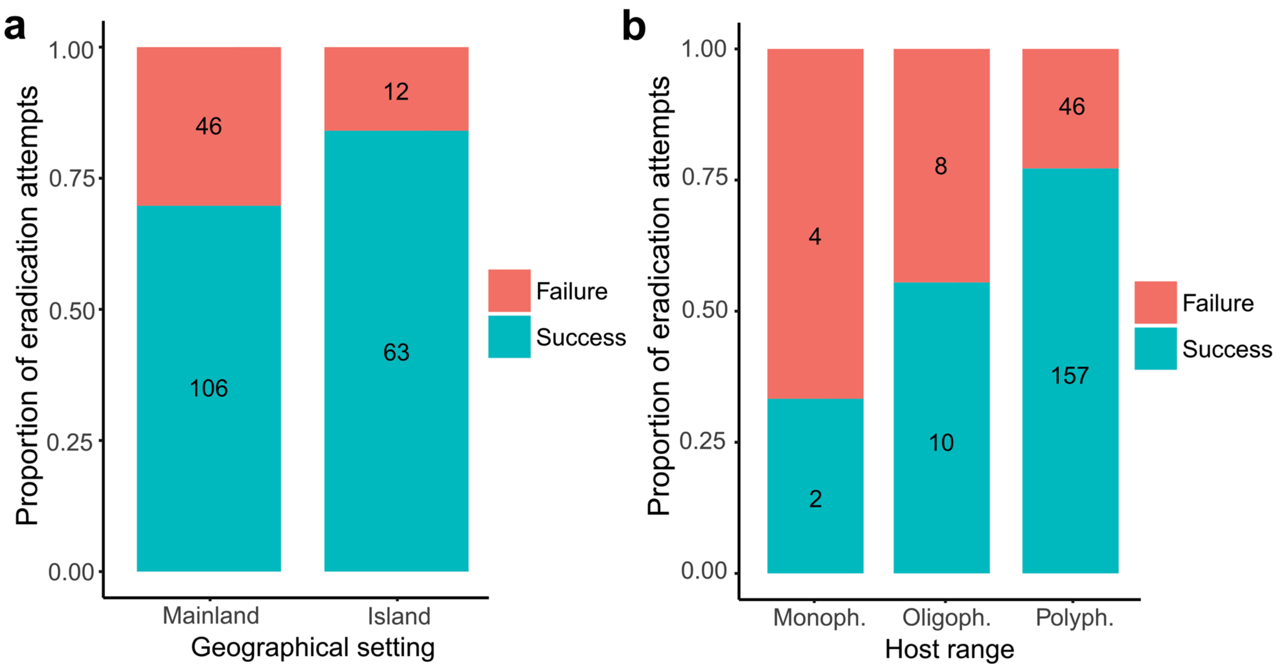

Fig. 3 **a** Eradication success based on insularity. Insularity was significantly associated with eradication success, suggesting eradications that take place on islands are more likely to succeed ($p<0.01$). **b** Eradication success by target species host range, with monophagous, oligophagous and polyphagous species represented. Logistic regression confirmed host range significantly influenced eradication success ($p<0.001$)

Table 2 List of cited reasons for failure with associated number and percentage of eradication attempts

Reasons for eradication failure	Eradication attempts of non-social insects	Eradication attempts of social insects
Treatments failed to achieve adequate control	26 (54.2%)	11 (61.1%)
Decline in political or social will	15 (31.3%)	7 (38.9%)
Program management systems were flawed	18 (37.5%)	3 (16.7%)
Unable to access or treat all infestations	4 (8.3%)	5 (27.8%)
Re-infestation from elsewhere	13 (27.1%)	4 (22.2%)
Disruption by climate or disturbance event(s)	2 (4.2%)	0 (0%)
Unable to detect or delimit infestations adequately	11 (22.9%)	6 (33.3%)
Local infestations spread more rapidly than anticipated	6 (12.5%)	4 (22.2%)
Allocated budget ran out	3 (6.3%)	1 (5.6%)

Across the total 239 compiled eradication attempts, 66 failed and noted one or more reasons for failure. Of these failed attempts, 48 targeted non-social species, while 18 targeted social species. Percentages do not add to 100 as eradication attempts could cite multiple reasons for failure. Percentages were calculated as how many attempts cited the reason out of the total number of failed attempts for non-social and social species, respectively. These values are rounded to 1 decimal place

solitary nesting strategies (Field and Toyoizumi 2020). This hypothesis would imply that eusocial species could experience higher rates of individual colony member mortality, while a colony as a whole might experience a reduced risk of failure. The structure of social insect colonies can allow for high worker mortality, without necessarily reducing the reproductive output of the colony (Lemanski et al. 2020). This resilience to individual mortality can confer advantages to these invasive social species in the face of control actions against them. For example, Toft and Harris (2004) conducted a study simulating mass trapping of invasive Asian paper wasps (*Polistes chinensis*). They were able to show that despite paper wasp nests experiencing mortality rates of up to 75% they exhibited almost no changes in nest growth rate or survival when compared to control nests. This outcome highlights how control methods for social species must target not just workers but, more importantly, the reproductive castes and be effective at the colony level.

Our analysis also shows eradication attempts appear to be getting more successful over time. This trend is likely a reflection of pest management getting more sophisticated as control techniques and monitoring technologies get more advanced. Advances in toxicant development and application have been shown to improve mammal eradication success on islands (Towns and Broome 2003).

Successful eradication attempts were on average shorter in duration than unsuccessful attempts. This association may be the logical result of ending an eradication attempt once the target species has been successfully removed, while unsuccessful eradications are continued until support for the program is lost or resources are exhausted. Insularity exhibited a positive association with eradication success. Islands are generally smaller in scale and more isolated from propagules than mainland or continental settings. Smaller project scale and reduced risk of reinvasion have been linked to eradication success (Phillips et al. 2019) and may explain this association.

Finally, host range was shown to have a significant positive association with eradication success. A species with a more generalist feeding habit may be more susceptible to control methods such as toxic baits than a specialist. It should be noted that the vast majority of invasive species included in this study are polyphagous. A broad host range is a common trait in invasive species, however, as generalist feeding behaviours have been noted as a trait that promotes invasive success (Crowder and Snyder 2010).

Reasons for eradication failure identified in this study were varied. The most cited reason for failure was due to ineffective control method treatment. For an eradication attempt to be successful, the control method must effectively reduce the population of the target species populations, regardless of density (Bomford and O'Brien 1995; Phillips et al. 2019). The incorporation of multiple methods of population control has been suggested to ensure that target species are vulnerable to control at all stages of development (Phillips et al. 2019). In some cases, sufficiently effective treatments have not been developed yet and it is only with technological advancement that eradication could become possible in the future. In the case of spongy moth (*Lymantria spp.*) eradications in the USA, most attempts to control or eradicate the species prior to the 1980s used blanket spraying of pesticides, such as carbaryl and DDT, largely unsuccessfully (Dreistadt and Weber 1989). The development of more advanced treatments such as *Bacillus thuringiensis kurstaki* (*Btk*) and delivery techniques during the following decades have increased eradication success (Dreistadt and Weber 1989; Hajek and Tobin 2009). The development of more specific and sophisticated treatments may explain the association of increasing probability of eradication success over time; a trend also identified by Tobin et al. (2014). In the case of social species, invasive wasps (Vespidae) have historically been controlled by destroying nests that are found. While a single nest can easily be destroyed this method of control is largely ineffective when attempting eradication (Crosland 1991; Davies et al. 2020). Improvement has come with the advent of poison baits which provide control at a larger scale (Edwards et al. 2017); however, large scale eradication may have to wait for future technological advancements (Davies et al. 2020).

A decline in public or political support for eradication was a common reason for failed eradication attempts. Duration of eradication attempts likely factor into this issue, especially when incorporating control methods perceived as harsh or restrictive. The prolonged use of chemical pesticides has long been challenged due to concerns for human or environmental health and risk of pesticide resistance. The extended use of pesticides has led to the development of resistance in invasive mosquitos (*Aedes aegypti* in the USA (Slosek 1986); *Aedes albopictus* in Italy (Kasai et al. 2019)) and likely contributed to failed eradication attempts in those respective regions. As non-target effects of some of these control methods became better understood, both political and social support for the use of these pesticides have declined. During the attempted eradication of fire ants (*Solenopsis* spp.) in the Southern USA, political and social pressures forced changes in the pesticides used. Chemicals used in these attempts were causing high rates of non-target species by-kill with limited success in reducing the ant population (Davidson and Stone 1989). Similarly, social pressure halted the large scale aerial spraying in the attempted eradication of the cereal leaf beetle (*Oulema melanpous*) when chemical residues damaged the paint on private vehicles (Haynes and Gage 1981). Without social and political backing, eradication and wider invasive species management are much less likely to succeed (Crowley et al. 2017; Phillips et al. 2019), so taking social considerations into account and a high level of public engagement will be key to continued success.

For an eradication program to be successful, the engagement and subsequent management of the program must be well-reasoned and organised to ensure successful outcomes. The decision to attempt eradication must be well-considered and once the effort is initiated, progress must be monitored effectively. Some eradication attempts are much more likely to fail due to issues of reinvasion, inability to detect target species and monitor progress, and failures in the broader organisation of such actions. The success of eradication attempts, especially in a continental setting, may benefit from increased international cooperation. The eradication of the cattle screw worm (*Cochliomyia hominivorax*) in Texas, USA from 1962 to 1972, failed due to populations reinvading from Mexico (Graham and Hourrigan 1977).

Similarly, the eradication attempt of the Carambola fruit fly (*Bactrocera carambola*) from Brazil, Suriname and Guyana failed after French Guiana ceased their efforts, creating a source of reinvasion (van Sauers-Muller 2008; Godoy et al. 2019). Leza et al. (2021) describe a successful eradication program targeting the yellow-legged hornet (*Vespa velutina nigrithrorax*) on the island of Majorca, Spain but notes that there was no coordination between the other countries in Europe, where this species has invaded. These examples highlight the importance of considering international actions when developing eradication plans, especially in a continental context. This issue is perhaps less important in island eradications and may explain the positive relationship we found between eradication success and insularity. Insularity often confers a reduced chance of reinvasion due to isolation (Carter et al. 2020; Schmack et al. 2020) and islands are generally smaller geographically. Smaller scale eradication efforts have been highlighted as criteria for eradication success (Phillips et al. 2019).

From this study we may conclude that when attempting an eradication, it should be based on solid research, progress be well-monitored and managed and, critically, it must be well-resourced and supported. Effective methods of reducing the target species population must either be employed or developed. Aspects of the target species behaviour and biology must be taken into consideration. Eusociality appears to confer certain advantages that make it harder for conservation managers to eradicate these invasive species. When conducting eradication attempts the geographical context of the invasion must be considered. Insular eradication attempts are likely subject to less reinvasion events than when conducting an eradication attempt on a continental setting. As time goes on and advances in control technologies improve, the chances of eradication success will likely improve. This analysis highlights the importance of political and social support for eradication attempts and how this influences the success of these conservation measures. To substantially increase the success of future eradication attempts both technical and societal aspects of those attempts must be considered jointly.

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Data availability The authors confirm that the data supporting the findings of this study are available within the supplementary materials. These data were derived from the Global Eradication and Response Database, resources available in the public domain: https://b3.net.nz/gerda/.

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