The lost lizards of Christmas Island: a retrospective assessment of factors driving the collapse of a native reptile community

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Abstract

Until recently, the reptile fauna of Christmas Island in the Indian Ocean comprised five endemic species (two skinks, two geckos and one snake) and one native, non-endemic skink. Four of these species were common and widespread until at least 1979, but by 2012 had disappeared from the wild. During the years of decline, little research was undertaken to examine why the species were disappearing. Here we use a retrospective expert elicitation to rank potential factors that contributed to the loss of Christmas Island's reptiles and to assess the likelihood of re-establishing populations of two species now listed as Extinct in the Wild. We additionally considered why one endemic lizard, the Christmas Island giant gecko (*Cyrtodactylus sadleiri),* and three introduced lizards remain common. Experts considered that the introduced common wolf snake (*Lycodon capucinus*) was the most likely cause of decline, as its temporal and spatial spread across the island closely matched patterns of lizard disappearances. An Asian co-occurrence in recent evolutionary timeframes of the common wolf snake with the Christmas Island giant gecko and three introduced reptiles was the most marked point of difference between the extant and lost lizard species. The demise in less than 20 years of 80% of Christmas Island's native lizard assemblage highlights the vulnerability of island fauna to invading species.

Keywords: Christmas Island, expert elicitation, extinction, island, invasive species, *Lycodon capucinus,* reptile

1 | INTRODUCTION

The current rate of world extinctions is estimated to be between eight and 100 times higher than the background extinction rate (Ceballos et al. 2015). Habitat loss is the single biggest threat to biodiversity, but invasive species, exploitation, disease and anthropogenic climate change also pose significant ongoing threats (Sax & Gaines 2008; Maxwell et al. 2016; Díaz et al. 2020). Diagnosing the causes of species' decline and extinction is often complex, as threats may operate independently, synergistically, successively, or at different locations. Compared to continental landmasses, species inhabiting oceanic islands are particularly vulnerable to threats resulting from human occupancy, and are susceptible to even small changes in their environment. As such, 85%, and 95% of recorded mammal and bird extinctions, respectively, have occurred on islands since 1500 (Blackburn et al. 2004; Szabo et al. 2012).

Christmas Island (10°30′S, 105°40′E) in the Indian Ocean supported a rich and distinctive biota (James et al. 2019), but has undergone substantial loss of native and endemic species since its colonisation in 1888. These losses amount to four of the five endemic species of mammals, four of the six native reptiles (one Extinct, two Extinct in the Wild and one extirpation) and likely numerous extinctions in the invertebrate fauna whose conservation status remains largely unknown (Andrew et al. 2018; James et al. 2019). Since the early 1990s, outbreaks of supercolonies of the introduced yellow crazy ant (*Anoplolepis gracilipes*) (YCA) have caused additional widescale ecological changes by killing millions of the endemic Christmas Island red crab (*Gecarcoidea natalis*) which are the key regulator of ecosystem function on the island (Green et al. 2011). Such a systematic and rapid removal of a keystone species has resulted in an 'ecosystem meltdown' on Christmas Island (O'Dowd et al. 2003).

Christmas Island's squamate fauna includes eleven species first recorded between 1886 and 1987, of which six (four endemic lizards, one widely-distributed lizard and one endemic blind snake) represent the native, pre-settlement complement of terrestrial reptiles. The island's native lizard species were widespread and abundant until 1979 (Cogger et al. 1983), with the blue-tailed skink (*Cryptoblepharus egeriae)* considered hyper-abundant within the island's settlement area until at least 1990 (Peter Green *pers. obs.*). However, four native lizard species (the blue-tailed skink, Lister's gecko *Lepidodactylus listeri*, Christmas Island forest skink *Emoia nativitatis* and coastal skink *Emoia atrocostata*) underwent a precipitous decline over the following three decades, and by 2012 had vanished from the wild (Smith et al. 2012; Andrew et al. 2018). Intermittent and limited monitoring made it difficult to delineate the timing and spread of decline, and the variable incidence, extent and impact of putative threat factors (Smith et al. 2012). Rumpff (1992) first documented the decline of the blue-tailed skink in the Settlement (in the Island's North-east) and suggested that the then recently introduced common wolf snake *(Lycodon capucinus*) was likely involved. In the next notable assessment, Cogger and Sadlier (1998) reported major declines in blue-tailed skinks and Lister's geckos (relative to their former abundance in 1979), although this assessment was not quantitative. Between 2004-2007, James (2007) undertook systematic reptile surveys and found that populations of three lizard species (blue-tailed skink, Christmas Island forest skink and coastal skink) were rapidly declining and becoming fragmented, with some spatial variability in the decline (losses were most severe in the north-east near the Settlement, and least evident in the south-west of the island). Fortunately, just preceding their extirpation from the wild, Parks Australia initiated a captive breeding program, which although was ultimately unsuccessful for the Christmas Island forest skink, has prevented extinction of blue-tailed skinks and Lister's geckos (Andrew et al. 2018).

Despite increased monitoring in the years before 2012, the primary mechanism for decline was not resolved, and hence there was little scope for targeted remedial management. Smith et al. (2012) described patterns of the collapse of the native lizard fauna, and concluded that predation from introduced species was the most likely cause of decline while acknowledging other factors may have also contributed. Notably, that assessment did not attribute causality to a single factor or set of factors, and hence the driver(s) for the collapse of the reptile community remains uncertain. As there are few records of the Christmas Island blind snake (*Ramphotyphlops exocoeti*) (Maple et al. 2012) we focus here on the decline of endemic lizards, and the factors that may have contributed to their declines.

Ideally, conclusions and inferences underpinning extinction and extinction risk should be assessed using high-quality empirical data (Brook & Alroy 2017). However, when species have undergone rapid population declines or extirpation before such data can be obtained, as was the case on Christmas Island, it is challenging to determine causality and hence to develop management responses. Expert elicitation is a well-established approach for dealing with uncertainties in biodiversity conservation when primary evidence is limited or inconsistent, as consolidated opinions of a range of individuals are generally more accurate than those of one or few experts (Burgman et al. 2011; Martin et al. 2012; McBride et al. 2012). For example, Geyle et al. (2020) used expert elicitation to evaluate the extinction risk of Australia's most imperilled squamate species, Dalibard et al. (2020)

and used expert judgement to assist with identifying the primary threats to the Pyrenean brook newt (*Calotriton asper*). Expert elicitation is becoming increasingly sophisticated as the biases in judgement are better understood (Hemming et al. 2018; Roy et al. 2020). In our approach, we sought to apply the knowledge and perspectives of relevant researchers and managers involved in the conservation of biodiversity on Christmas Island, to assess retrospectively the factors thought to be responsible for the decline of its reptile fauna. Such identification of causality will not now benefit the extinct Christmas Island forest skink, but may inform (and be necessary for) any reintroduction attempts for the two Extinct in the Wild species; and may help safeguard the conservation of endemic reptile faunas on islands elsewhere. We acknowledge that other approaches, such as assessments of food webs linked with fuzzy cognitive mapping (Gray et al. 2015) and path analysis (Lindenmayer et al. 2018) could also provide useful insights into this decline, but may be at least as constrained by major knowledge gaps, as is the case in the example we consider.

The primary aim of this study was to rank the factors thought responsible for the extinction and extirpations of four lizards from Christmas Island, and to concurrently evaluate conservation options for two Extinct in the Wild species (blue-tailed skink*s* and Lister's geckos) using information generated from expert knowledge. Secondly, over the period of these declines, four other reptile species (one endemic and three introduced) remained widespread (Table 2); hence a further aim was to identify any life history or ecological traits shared by these unaffected species that were distinctly different to those of the lost lizard fauna.

2 | MATERIALS AND METHODS

2.1 | Study area

Christmas Island is a remote Australian territory in the Indian Ocean (Figure 1). The average annual rainfall is approximately 2000 mm (Bureau of Meteorology 2020). Approximately 65% of the 135 km^2 island is covered in natural vegetation, with 63% of the island protected by National Park (Figure 1). The island is vegetated with tall tropical rainforest on the plateau and by semi-evergreen thicket on coastal terraces. Ecosystem dynamics on the island are highly influenced by abundant land crabs, which regulate seedling recruitment and litter breakdown, and hence vegetation structure and floristics (Green et al. 2011). This limestone island has been emergent for at least the last 4.5 to 5.7 million years and today houses a population of approximately 1500 people (Ali & Aitchison 2020).

2.2 | Putative causal factors

Globally, six key factors have been identified as the most threatening processes to reptiles (Gibbons et al. 2000): habitat loss and degradation; introduced invasive species; environmental pollution; disease and parasitism; unsustainable use; and global climate change. Using these factors as a guide, and further informed by the review from Smith et al. (2012), we compiled a list of 13 candidate factors that may have been influential in the decline of the Christmas Island native reptile community (Table 1).

2.3 | Expert elicitation

We used a semi-structured expert elicitation process for, (1) estimating the contribution of identified factors thought responsible for the extinction and extirpation of four Christmas Island lizards, and (2), estimating the likelihood of establishing populations of the two Extinct in the Wild lizards on either Christmas Island or elsewhere. We identified 27 experts using purpose sampling (individuals were chosen based on their expertise). Most respondents have had direct involvement in the Christmas Island herpetofauna, but other experts had knowledge on the threatening processes that are present on Christmas island. This group comprised almost all of those researchers who had worked on the species in the field, the researchers who had most experience with the island's ecology, a representative set of the island's environmental managers and of those who worked on the captive breeding. Twenty of the 27 people invited to participate responded, with 7 respondents either opting not to participate or did not respond. Eighteen of the respondents are co-authors, with two people opting not to be involved beyond the initial survey. Further details of selection of elicitors are given in Supplementary material 2.

Respondents were classified as either managers or researchers. Managers were individuals who have or had active involvement in resource operations on Christmas Island (e.g. pest, weed control, wildlife management, conservation breeding) or in the conservation breeding program at Taronga Zoo in Sydney, whereas researchers were not directly involved with day-to-day management, but had knowledge of the island’s reptile fauna. We undertook a survey to assess expert opinion on the relative magnitude of the 13 factors outlined above, and asked experts to assess the relative contributions of each factor to ensure that all factors together tallied to 100%. We additionally asked experts to estimate between 0-100% (1) their confidence that the highest contributing factor they chose was the primary driver of the declines, and (2) their confidence that the declines of all four native lizard species were due to the same cause or set of causes. Finally, as blue-tailed skinks and Lister’s geckos currently persist in captivity on Christmas Island and at Taronga Zoo (Andrew et al., 2018), we asked experts to assess the likelihood of re-establishing viable populations of these two species on Christmas Island (with the assumption that the same set of putative factors that contributed to the extinctions were still present, albeit subject to realistic control efforts) or translocated populations somewhere other than Christmas Island (with the assumption that a hypothetical destination site could be found without such threat factors), within ten years. We distributed the survey via email in November 2017, and experts were asked to respond individually within three weeks, without collusion, and to base their assessments on their personal knowledge and available reports and publications (see Supplementary material 1 for a copy of the elicitation pro-forma).

2.4 | Persistence of one endemic lizard and three introduced lizards

In the absence of empirical evidence to delineate the causes of decline, comparing traits of species that have persisted to traits of species that disappeared may provide insights (Foufopoulos & Ives 1999; Slavenko et al. 2016; Tingley et al. 2016; Allen et al. 2017). Over the period that the blue-tailed skink, coastal skink, Christmas Island forest skink and Lister's gecko disappeared from the Christmas Island landscape, the remaining endemic lizard, The Christmas Island giant gecko (*Crytodactylus sadleiri*), and three introduced lizards, the common house gecko (*Hemidactylus frenatus)*, the four-clawed gecko (*Gehyra mutilata)* and the Bowring's supple skink (*Subdolups bowringii;* formerly *Lygosoma bowringii)* remained common. Hence, we collated available information from the literature (both peer-reviewed and grey) on the life history, evolutionary and ecological traits of each species (Table 2), and used this information to formalise nine hypotheses concerning why four species have persisted (to date) on Christmas Island, whilst four other species did not (Table 3). A hypothesis was considered supported if there was low concordance in traits between that of the declined lizard species and lizard species that had not declined.

2.5 | Statistical analyses

We analysed the survey data submitted by experts using descriptive statistics and linear mixed effect models. As opinions on the relative contribution of each factor varied, we additionally ranked each expert's response according to the percentage contribution (e.g., predation by the common wolf snake 80% ranked at 1, habitat loss 15%; ranked at 2, and predation by feral cats (*Felis catus*) 5% ranked at 3). Where experts considered two factors to be equally important, we assigned both factors the same rank. We compared differences of opinions between the set of managers and the set of researchers for the highest contributing threat and whether length of field experience (> four weeks) prior to extinction to those with < four weeks or none using a Mann-Whitney U tests, in part to consider whether differences in perspectives among respondents represented a shifting baseline effect (Pauly 1995). To investigate the likelihood of successfully introducing each of the two Extinct in the Wild species either to Christmas Island, or elsewhere we undertook linear mixed-effects model with species (blue-tailed skink ⁄Lister's gecko), and location (Christmas Island/elsewhere) as fixed effects, and individual as a random effect (Geyle et al. 2018). Models were fitted using the 'nlme' package in the statistical program R (R Core Team 2013).

3 | RESULTS

3.1 | Expert elicitation

Of the twenty experts who responded to the survey, nine were managers and eleven researchers. Of these respondents, 45% had more than four weeks field experience on Christmas Island over the period of decline (prior to 2012), whereas 70% had more than four weeks field experience after the declines. Collectively, 35% of respondents had at least four weeks fieldwork experience both before and after 2012, and four respondents (20%) had no field experience on Christmas Island. Half of the experts are involved in the conservation breeding program, either on Christmas Island or at Taronga Zoo. Some elicitors had worked on the island, at least intermittently, over at least a 20-year span.

Experts considered that predation by the common wolf snake was the most influential factor in the decline of Christmas Island reptiles (mean contribution 43%, SE: 36-49%), but there was substantial variation around perceptions of the contribution of this factor (Figure 2A). The set of managers and the set of researchers did not differ in their assessment of the contribution of the common wolf snake to reptile declines and extinctions ($w = 56.5$, $p = 0.605$). Similarly, experts with more than four weeks fieldwork experience on Christmas Island prior to 2012 did not have different views to those with less or no experience prior to 2012 ($w = 46.5$, $p = 0.93$). The factor considered next most important was predation by introduced giant centipedes (*Scolependra subspinipes)* (mean contribution 19.5%, SE: 17-22%), followed by habitat loss (mean contribution 9%, SE: 7-10%). All other factors were considered to have a negligible role in the decline of Christmas Island reptiles (Figure 2A). Thirteen experts (65%) ranked the common wolf snake as the top contributor to reptile declines, and four ranked the giant centipede as the top contributor. The other top-ranked threats (by one respondent each) comprised competition, habitat loss and degradation, and disturbance by yellow crazy ants (Figure 2B).

Despite considerable uncertainty around attributing the cause of decline, experts were confident that the top factor they chose was the primary cause of decline (mean= 71%: SE: 67-75%). There was strong agreement among experts that whatever factor was responsible, it likely led to all four reptile species disappearing from the wild (mean= 79.5%: SE: 76-82%). Experts were more optimistic that populations of blue-tailed skinks and Lister's geckos could be established in a location other than Christmas Island (i.e., a benign introduction), compared to reintroducing these species on Christmas Island (Table 3).

3.2 | Persistence of one endemic and three introduced lizards

The hypothesis with the most support to explain the persistence of the extant reptile fauna was 'shared evolutionary history with introduced predators'. The three introduced lizards are native to South East Asia and molecular evidence shows that the closest relative of Christmas Island giant gecko is also from South East Asia (Table 2 and Table 3) where the common wolf snake and giant centipede originated. An inconsistency with this hypothesis is that the extirpated native coastal skink is also widespread in South East Asia. There was some support for differences in ecological traits; notably, three of the four extant lizards (excluding Bowring's supple skink) are arboreal and nocturnal; whereas two of the four extirpated lizards are diurnal and terrestrial, with additional species being semi-arboreal. There was little support for the remaining hypotheses (i.e. 'surviving species use different microhabitats', 'surviving species occurred in greater numbers', 'surviving species are less palatable to introduced predators' and 'surviving species had higher reproductive output') as both extirpated and surviving species either used similar microhabitats, extirpated species had greater prior abundances, all lizards had comparable clutch size and all reptile species are known to be consumed by introduced predators (see Tables 2, 4 for further information).

4 | DISCUSSION

There have been far fewer recorded extinctions of reptiles globally in comparison to those of mammals and birds since 1500, however the number of threatened reptiles is rapidly increasing (IUCN 2020). Island species have borne a disproportionate share of reptile extinctions (Slavenko et al. 2016), so the case described here is an example of a more general phenomenon. Without more effective and targeted conservation response, the rate of reptile extinctions is likely to increase. For example, a recent assessment of Australian squamates identified up to 11 species that could be lost in the next 20 years (Geyle et al. 2020), a substantially higher tally than those of Australian mammals and birds (Geyle et al. 2018) and freshwater fish (Lintermans et al. 2020). Identifying factors involved in species declines is crucial to mitigate further loss and to devise management actions to enhance a species' conservation status (Woinarski et al. 2017). In this review, guided by expert elicitation, we (1) identified the likely candidates for the extinction and extirpation of four of the five native lizards from Christmas Island, (2) assessed the likelihood of translocations for the two Extinct in the Wild lizards and (3) identified potential differences in traits between extirpated and persisting lizard species.

Overall, experts considered the common wolf snake as the most likely contributor to the extirpation of Christmas Island lizards, followed by the introduced giant centipede. There was however substantial variation in responses from experts to both factors, and indeed most factors identified. Such variation from experts likely represents the scarce availability of empirical evidence to attribute causality to decline. In medicine, Koch's postulates of causality are often used systematically to attribute disease causality to infection. These postulates typically include consistency of the relationship, a temporal relationship (the factor preceding the emergence of the condition), a gradient in the relationship, experimental proof of the relationship and a plausible biological mechanism (Sutterland et al. 2019). In the case of the declining Christmas Island reptiles, some of these links could not be clearly established, but the strongest evidentiary argument related to the temporal relationship between the arrival of the common wolf snake and the subsequent decline and extinction of four native lizard species. Below we discuss these two primary agents of decline in detail, discuss other factors collectively, and explore potential reasons why four reptile species remain present in the wild.

The first confirmed sighting of the common wolf snake on Christmas Island was in 1987 at the Settlement (Smith 1988), however, they are thought to have arrived in the mid-1980s as shipping stowaways (Rumpff 1992). Upon arriving on Christmas Island with no predators, no competitors and a hyper-abundance of naive skinks at the point of arrival; the common wolf snake population rapidly increased, and by 1992 reached extraordinary densities of between 45 and 500 individuals per hectare in the Settlement (Rumpff 1992). By 1997, blue-tailed skinks had disappeared from the settlement region, but introduced lizards remained common (Cogger et al. 1997). At this time (1997), common wolf snake records were restricted to the Settlement region, but periodic monitoring over the next 12 years revealed an expansion in a southwest direction that largely mirrored that of the lizard decline (Smith et al. 2012). Whilst correlation does not imply causation, the arrival of a lizard specialist predator just prior to the rapid decline of 80% of the island's native lizards strongly suggests its involvement.

World-wide, island endemic species have suffered a disproportionate share of the world's extinctions, mostly due to invasive species (Blackburn et al. 2004), but there are relatively few examples of introduced snakes as the main causal factor. The most well documented example is for Guam, where the expansion of invasive brown tree snakes (*Boiga irregularis*) from their point of arrival coincided with the loss of many vertebrate species (Fritts & Rodda 1998; Wiles et al. 2003; Rodda & Savidge 2007). In the Mascarene islands, the introduced Indian wolf snake (*Lycodon aulicus;* a closely related species to the common wolf snake), is believed to have been instrumental in the extirpation of island populations of Bojer's skink (*Gongylomorphus bojerii*) (O'Shea et al. 2018). Finally, while not an island example, the introduction of Burmese pythons (*Python molurus bivittatus*) to the Everglades National Park in Southern Florida led to a trophic cascade in only 15 years due to significant mammal declines (Willson 2017), with a marked spatial decline in mammal abundance from areas where Burmese pythons became established. These examples highlight that invasive snakes are capable of being the primary cause of fauna declines, and that declines often spread from a predator's point of introduction or establishment. Hence, it is possible that common wolf snakes were the primary cause of the reptile decline on Christmas Island. We note that this consequence was predicted: within six years of their detection, three authors warned that should the common wolf snake become established on Christmas Island it could pose a significant threat to the island's fauna (Smith 1988; Rumpff 1992; Fritts 1993). Regrettably, those predictions appear to have been borne out. It is likely that the impact of the introduced common wolf snake on Christmas Island fauna was not restricted to the island's native reptile fauna, as a comparable retrospective assessment for the extinction of the island's only endemic insectivorous bat over the same time period as the loss of lizards also concluded that the wolf snake was the most likely causal agent (Woinarski 2018).

Introduced giant centipedes were the only other threat considered by some experts to have been an important contributor to decline. Centipedes from the family Scolopendridae are large (to 25 cm) voracious predators capable of killing and consuming vertebrates as large as microbats and snakes (Molinari et al. 2005; Smart et al. 2010; Arsovski et al. 2014; Lindley et al. 2017). Estimated to have arrived on Christmas Island around 1900 as shipping stowaways, they quickly established and were considered common in the Settlement by 1909 (Andrews 1909), and occurred island-wide by 1940 (Gibson-Hill 1949). There is some anecdotal evidence that giant centipedes increased in abundance from the 1990s, likely due to the formation of YCA supercolonies reducing red crab abundance and creating more suitable habitat (Peter Green *pers. obs.*). However, within the Settlement, giant centipedes and blue-tailed skinks coexisted without an apparent population-level impact of the former on the latter for some 60 years. It is likely that giant centipedes killed and preyed upon native reptile species, but such predation levels were unlikely to have been substantial enough to cause declines (Emery et al. ; Donellan et al. 2011). As such, there is no compelling evidence that giant centipedes acting alone caused the population decline.

The remaining candidate factors were not considered major contributors to the population declines, despite some being key drivers of reptile declines and implicated in reptile extinctions elsewhere. For instance, Medina et al. (2011) considered feral cats to be the primary cause of extinction of at least two island reptiles in the West Indies (Navassa Island) and on San Stephano in Italy. In the Caribbean archipelago and Cape Verde, black rats (*Rattus rattus*) and Indian mongooses (*Herpestes auropunctatus*) were implicated in widespread declines in reptile populations and several extinctions of small lizard species (Corke 1992; Powell & Henderson 2005; Vasconcelos et al. 2013). On Christmas Island, feral cats were known to be predators of all native skinks and the Christmas Island giant gecko (Tidemann et al. 1994). Additionally, competition with introduced lizards has long been considered a strong force in shaping island reptile communities (Case & Bolger 1991). Invasive reptiles likely interacted with the native lizards on Christmas Island, however, native lizard populations disappeared from locations where introduced competitors were absent (James 2007; Smith et al. 2012). It is likely that common house geckos actively excluded and preyed upon the smaller Lister's geckos and juvenile blue-tailed skinks in areas where they co-occurred, as they do with mourning geckos (*Lepidodactylus lugubris*) on islands in the Pacific (Case & Bolger 1991). However, feral cats, black rats and introduced competitors were all common and widespread long before the decline of Christmas Island's reptiles, suggesting that any additional predation pressure or competition they exerted could be tolerated by the native reptile community.

The rapid pace and direction of decline of the island's lizards suggest a single threat arising and spreading across the island. However, focussing on single threats acting independently, without considering potential synergetic effects between threats, may oversimplify the mechanisms behind the declines. The most striking of these interactive impacts involved the formation of YCA supercolonies that led to ecosystem-wide changes during the period of reptile declines. YCA supercolonies were first detected in 1989, became progressively more widespread by the mid-1990s, and by 2001 covered more than 25% of forested areas. The expansion of YCA supercolonies caused the loss of millions of red crabs – the key consumer and regulator of seedling recruitment and organic matter on the island – resulting in an ecosystem 'meltdown' (O'Dowd et al. 2003; Green et al. 2011). Green et al.

(2011) found that supercolonies facilitated the secondary invasion of the introduced giant African land snail (*Achatina (Lissachatina) fulica*) through the removal of predation pressure by red crabs. By extension, YCA supercolonies may have facilitated the rate of spread and abundance of other invasive species, including common wolf snakes and giant centipedes, and indeed, giant centipedes have increased in abundance from the 1980s (Peter Green, *pers. obs.*).

It is unlikely that common wolf snakes and giant centipedes persisted in areas with YCA supercolonies. In 'ghosted areas' (areas where YCA supercolonies have never formed but where red crabs were lost as a consequence of their attempted migration through supercolonies), forested habitat would have become increasingly suitable for these invasive predators as a result of increased ground organic matter and more complex understorey. However, while there is a temporal overlap between the formation of YCA supercolonies, the lingering effects of ghosted areas, and lizard declines, any spatial concordance is low to absent. Most notably, lizard declines were marked in the settlement in the mid-1990s where no YCA supercolonies were detected, and lizards were subsequently lost from many other areas that never had YCA supercolonies. Hence, any synergistic effects from YCA were likely secondary to the primary threat (i.e. predation by common wolf snakes), but YCA supercolonies may have enhanced the rate of declines in parts of the island where the greatest proportion of the forest was affected by YCA formation.

Surprisingly, we found few ecological or other differences between species that were extirpated and those that have survived (Table 2, Table 3). The most marked contrast was that three introduced lizards and Christmas island giant gecko have recent ecological/evolutionary exposure to south-east Asian lizard predators, providing them with the opportunity to evolve effective avoidance behaviours. The common wolf snake is a native predator of the common house gecko and four-clawed gecko in south-eastern Asia (O'Shea et al. 2018), and likely also preys upon small lizards including the Bowring's supple skink and geckos from the *Cyrtodactylus* species complex. An apparent inconsistency with this explanation is that the coastal skink is common throughout southern south-east Asia where it co-occurs with the common wolf snake. However, isolated populations are known to lose predator vigilance in the absence of predators. For example, in only 13 generations, introduced populations of northern quolls (*Dasyurus hallucatus*) lost their ability to recognise key mammalian predators (Jolly et al. 2018). Hence, the Christmas Island population of coastal skink arrived on the island when it was free of specialist lizard predators, with this population subsequently relaxing selection on anti-predator traits.

There was some evidence that a nocturnal and arboreal life history provided species with greater resilience to predation, as two of the four extirpated species were diurnal and terrestrial and one diurnal and semi-arboreal. The Bowring's supple skink is semi-fossorial and diurnal but may have retained anti-predator behaviours due to its co-evolution with the common wolf snake. However, this association is weak, probably because the common wolf snake hunts effectively on the ground and in trees.

We found no suggestion that life-history traits (e.g. reproductive output, body size), habitat specialisation or prior abundance played a role in the extirpation of Christmas Island lizards. Such factors are thought to be important contributors to extinction risk across many taxonomic groups including birds (Bennett & Owens 1997), reptiles (Foufopoulos & Ives 1999; Allen et al. 2017), desert fish (Olden et al. 2008) and declining species in general (Purvis et al. 2000). However, the extirpated native lizards possessed similar traits to the remaining lizards, providing some support that threatened and invasive reptiles do not necessarily lie at opposite ends of a biological spectrum (Tingley et al. 2016). Regardless, close attention needs to be paid to ongoing monitoring of the Christmas Island giant gecko, as the decline and extirpation of all other native Christmas Island lizards in only 20 years highlights the vulnerability of island species to novel threats.

Some clear lessons can be learnt from the events on Christmas Island for the conservation of reptile communities on islands elsewhere. Species loss can be rapid, and species can slip from presumed security to extinction before a management response can be devised. Stricter biosecurity, including tighter quarantine and effective surveillance to allow for early detection of newly arrived species, is an obvious priority management response (Paolucci et al. 2013). Christmas Island is heavily reliant on shipping freight (e.g. exporting phosphate to south-east Asia and receiving supplies from Perth and south-east Asia for the resident human population) so there is a constant risk of accidental introductions of invasive species. Introductions also include novel pathogens. On Christmas Island, despite a health assessment being undertaken over the period of the lizard decline, where no pathogens of concern were identified (Hall et al. 2011), captive populations of blue-tailed skinks and Lister's geckos have since experienced substantial mortality as a result of a novel bacterial pathogen, *Enterococcus lacertideformus* (Rose et al. 2017), and two new papillomaviruses have also been discovered (Agius et al. 2019). Hence regular population and health monitoring of the remaining endemic and invasive reptiles on Christmas Island will be important to allow for timely management responses to novel threats.

Our assessment of causality relied on the pooled knowledge and opinions of 20 people with the most expertise in the island's ecology and management, contributed independently through structured elicitation, and with experts selected to incorporate a diversity of experience and knowledge. We acknowledge that there may be some subjectivity in these assessments. In conservation, expert knowledge is especially valuable when empirical evidence is scarce (as is the case here), however assessments can be influenced by perceptions of risk, personal judgements and systematic biases (Regan et al. 2004). One bias that was difficult to control, and subsequently tease out, was the extent to which experts were anchoring on the small set of available knowledge. This may have manifested itself in two ways; because experts are experts because of their involvement on the island and due to the limited available literature. This may in part explain the consensus in the high level of concordance amongst experts that the common wolf snake was the primary target. Such biases are difficult to tease out, however it could have potentially been reduced by undertaking a second round of the elicitation process (e.g., Geyle et al. 2018), however, we consider that there was merit in reporting the independent perspectives of experts, rather than constraining responses to seek more consensus.

4.1 | Conclusions and future management

This study highlights the constraints of conducting a retrospective assessment of extinction. It is always more effective to identify and hence manage the key threat/s during the decline, but in this case, the pace of species loss and the range of possible threats made this impractical. On the available evidence and as judged by experts, predation by the common wolf snake, a niche lizard predator, fits most closely with the temporal and spatial decline of the Christmas Island native lizard fauna, and is the most plausible mechanism. As the experts consulted could not rule out other factors being involved in the declines, further investigation is required to determine if these threats operated independently or synergistically with the predation pressure exerted by the common wolf snake.

Our conclusion that the common wolf snake was the major contributor to the loss of most of the native reptile fauna on Christmas Island has important implications for future management of the two Extinct in the Wild species, and for the conservation of endemic island reptile assemblages elsewhere. The success of conservation breeding programs for the two Extinct in the Wild species is enabling managers and researchers to undertake controlled trials to assess survivorship and behavioural responses of the native reptiles to giant centipedes (Emery et al., 2020). On Christmas Island it is unlikely that the common wolf snake (and to a lesser extent giant centipedes) can be controlled at the landscape scale, at least using currently available mechanisms. Indeed, this recognition of an insuperable management challenge, at least in the short term, is probably the reason that elicitors rated very low the likelihood of reintroduction of blue-tailed skinks and Lister's gecko to the wild on Christmas Island. However, recently, Christmas Island National Park managers have constructed a 2600 m^2 habitat to exclude the common wolf snake and, to a lesser extent, giant centipedes, and reintroduction trials for blue-tailed skinks and Lister's geckos are in progress at this site with some short-term success observed (e.g. population stability and reproduction). Furthermore, consistent with the opinion of our elicitors of the more likely success of an assisted colonisation, conservation introductions of blue-tailed skinks to two small islets (each < 3 ha) in the Cocos (Keeling) island group, situated 1000 km^2 to the south-west of Christmas Island are now being trialled. These trials follow careful risk assessments, consistent with established national and international protocols. In the case of these translocation trials considerable pre-release monitoring was undertaken prior to the blue-tailed skink introduction and continues to be undertaken afterwards. Overall, the combination of reintroductions (in small areas at which threats can be excluded) and assisted colonisations will hopefully lead to the long-term recovery of two of Christmas Island's endemic reptiles outside of captivity.

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AUTHOR CONTRIBUTIONS

John Woinarski and Jon-Paul Emery conceived and coordinated the expert elicitation exercise, participated in the elicitation process, undertook data analysis, and wrote and reviewed the manuscript. Nicola Mitchell participated in the elicitation exercise process, designed figures, and co-wrote and reviewed the manuscript. All other authors participated in the elicitation process and provided editorial comments, except for Leonie Valentine, who provided editorial comments. Paul Andrew was involved in the elicitation process but passed away early in 2020 before he was able to contribute further.

ETHICS STATEMENT

All participants in the expert elicitation process were invited to be co-authors of this study and therefore no ethics was sought.

DATA AVAILABILITY

The raw data from participant answers are available upon request.

CONFLICTS OF INTEREST

The authors declare no conflict of interest

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661 **TABLE 1.** A summary of the 13 potential factors involved in the decline and extinction of four Christmas Island reptiles.

Factor	Date threat first identified	Mechanism for driving decline	Evidence for (on Christmas Island)	Evidence for (global or other case studies)	Evidence against
1. Habitat loss and fragmentation	~1888	Loss of habitat	25% of the island has been cleared for phosphate mining and civic purposes since 1888.	Land clearing and habitat loss have been major contributors to four modern reptile extinctions and a major contributor to worldwide reptile population declines.[2,3]	Most clearing on the island took place in the 1960s and 1970s before declines were observed. There has been little clearance since the 1980s. All species except for the coastal skink used rehabilitated mining areas. Additionally, coastal skink habitat (littoral areas) was not cleared or modified. The blue-tailed skink was most abundant in the settlement where the most disturbance has occurred.[1]
2. A decline in habitat quality facilitated by Yellow crazy Ant (YCA) supercolonies	YCA detected as early as the 1930s, however, the first supercolony was detected in 1989, and patchy but widespread by mid-1990s.[4,5]	Decline in habitat suitability	YCA's increased substantially in the 1990s in spatial extent, approximately coinciding with the first reptile declines.[5] Some evidence that YCA supercolonies excluded the blue-tailed skink and Christmas island forest skink from areas where they co-occurred.[6]	YCA's were linked to the disappearance of an endemic skink in the Seychelles.[7]	There is no spatial correspondence of the decline of reptiles matching patterns of outbreaks of YCA supercolonies. The largest supercolonies were located in the western portion of the island where these reptiles remained until 2010-12. Much of the island remained without YCA supercolonies.
3. Predation by giant centipedes (*Scolopendra subspinipes*)	Early 1900s[8]	Predation	Circumstantial evidence suggests giant centipedes became more abundant in the 1980s (in some areas) and into the 2000s, possibly via YCA suppressing red crabs. This resulted in better habitat for giant centipedes.	*Scolopendra* species prey upon vertebrates larger than themselves including microbats, snakes, amphibians and lizards.[9,10,11,12]	The giant centipede was widespread by 1940.

			Centipedes are voracious predators and been observed eating the Christmas Island giant gecko, Common wolf snake, blue-tailed skink and Lister's gecko on Christmas Island		
4. Predation by wolf snake (*Lycodon capucinus*)	First detected in 1987, but likely early to mid 1980s[13]	Predation	Temporal expansion of the common wolf snake fits well with the decline of all four reptile species. Early wolf snake specimens collected in the settlement had blue-tailed skinks, common house geckos and four-clawed geckos in their stomachs. Snakes reached densities in the settlement area between 45-500 snakes per hectare.[14] In the mid-2000s and 2017 over 200 common wolf snakes have been dissected, and many had reptiles in their stomachs.[6,15]	In the Mascarenes, the Indian wolf snake (*Lycodon aulicus)* is believed to have been instrumental in the decline and extinction of an island population of Bojers skink (*Gongylomorphus bojerii).*[16] Brown tree snakes (*Boiga irregularis*) in Guam are responsible for large scale declines, extirpations and extinctions of birds, mammals and reptiles. Decline in species on Guam resembles those on Christmas Island with respects to a spatial spread of decline from a point of origin.[17,18]	Other reptiles (Christmas Island giant gecko, Common house gecko, four-clawed gecko, Bowring's supple skink) persist on Christmas Island. There is limited evidence on the spatial spread of the common wolf snake; likely due to it being cryptic, semi-arboreal and limited targeted monitoring.
5. Predation by black rats (*R. rattus*)	September 1900[19]	Predation		Black rats have been involved in extinctions of other island reptiles in the Caribbean and Pacific.[3] A review in 2015 found that black rats have caused notable impacts on tropical island herpetofauna through predation.[20]	Little temporal and spatial evidence. Black rats were most abundant in the settlement where blue-tailed skinks were most common.
6. Predation by feral cats (*F. catus*)	~1900[8]	Predation	Stomach analyses in the late 1980s revealed cats consumed blue-tailed skinks, Christmas Island forest skink and the coastal skink.[21]	Cats have been the major contributor to at least two modern reptile extinctions.[22]	Little temporal and spatial evidence. Feral cats were likely more abundant in the settlement. Cats also consume the Christmas Island giant gecko, common house gecko and Bowring's

					supple skink, but these did not decline.[21]
7. Competition with invasive lizards	Common house gecko~ 1930s Four-clawed gecko~ 1950s Bowring's supple skink~ first detected in 1979, but likely earlier.[1]	Competition for resources (refuge and food) and predation	Recent stomach analysis of ~400 common house geckos on Christmas Island found that nearly 15% of individuals contained reptiles in their stomachs.[23]	Common house geckos have been implicated in declines of other geckos where it has been introduced (e.g. Mourning geckos, *Lepidodactylus lugubris*).[24]	All three invasive lizards were common in the settlement well before the decline.
8. Yellow crazy ant disturbance	~1989 but more widespread by mid 1990s[5]	Predation and behavioural change.	Supercolonies consume a significant amount of invertebrate biomass. YCA increased substantially in the 1990s in spatial extent, approximately coinciding with the first reptile declines. Some evidence that YCA supercolonies excluded blue-tailed skinks and the Christmas island forest skink from areas where they co-occurred.[5,6]		No spatial correspondence of the decline of reptiles matching patterns of outbreaks of YCA supercolonies. Much of the island remained without YCA supercolonies. The largest supercolonies were located in the western portion of the island where these reptiles remained until 2010-12.[6]
9. Fipronil use	~2001 widespread Fipronil use occurred until about 2009[5]	Bioaccumulation, food reduction and direct ingestion	From 2001 large scale Fipronil poisoning occurred across the island (to control YCA supercolonies).	Variable evidence on the effects of fipronil poisoning on reptiles. Under lab conditions, lizards exposed to food contaminated with fipronil had a mortality rate of 62.5%. However, unknown under field conditions.[25]	Reptile declines preceded the use of fipronil. Large scale fipronil application was undertaken in the western portion of the island in 2001 where lizards persisted until 2010-2012. A study found a minimal impact of fipronil on blue-tailed skinks and Christmas island forest skink populations, but sample sizes were low. Some evidence that blue-tailed skinks recovered after YCAs were controlled with fipronil.[6] Post baiting assessments in 2012 found no evidence of bioaccumulation of fipronil.[26]

10. Disease	~N/A	Increased mortality	In 2014 (post extirpation) a novel enterococcus bacterium (*Enterococcus lacertideformus*) was discovered on Christmas Island affecting Lister's geckos, blue-tailed skinks, common house geckos, four-clawed geckos with a 100% mortality rate.[27]	Disease is well-known to drive rapid species declines. Two endemic rodents on Christmas Island were driven to extinction by disease[19] and the incremental spatial spread of declines loosely resembles how a disease outbreak would occur.	Disease and pathogen tests were undertaken in 2010 and found no evidence of significant disease occurrence in the reptile fauna.[28]
11. Climate change	Decline in habitat suitability; changes in prey availability; physiological stress	~N/A	Some very dry years at the beginning of the decline in the late 1980s and early 1990s.	Climate change is a primary threat to reptiles globally.[2]	Drier years did not continue throughout the period of reptile decline.
12. Loss of prey	Reduced food availability	Mid-1990s	Fipronil and the outbreak of YCA's.	There is evidence of reduced invertebrate (ant) abundance on and near YCA supercolonies.[29]	No declines in other reptile species that consume similar prey items.

1. Cogger et al. 1983, 2. Gibbons et al. 2000, 3. IUCN 2020, 4. Donisthorpe 1935, 5. O'Dowd et al. 2003, 6. James 2007, 7. Fear 1999, 8. Andrews 1909. 9. Molinari et al. 2005, 10. Smart et al. 2010, 11. Arsovski et al. 2014, 12. Lindley et al. 2017, 13. Smith 1988, 14. Rumpff 1992, 15 Sleeth 2017, 16. O'Shea et al. 2018, 17. Fritts & Rodda 1998, 18. Wiles et al. 2003, 19. Green 2014, 20. Harper & Bunbury 2015, 21. Tidemann et al. 1994, 22. Medina et al. 2011, 23. J. Agius, unpublished data 2017, 24. Case & Bolger 1991, 25. Peveling & Demba 2003, 26. Weeks & McColl 2011, 27. Rose et al. 2017, 28. Hall et al. 2011, 29. Abbott 2006.

Table 2: Summary of ecological, life history and other characteristics for five native and three introduced lizard species that co-occurred on Christmas Island (CI).

	Lister's gecko (*Lepidodactylus listeri*)	Blue-tailed skink (*Cryptoblepharus egeriae*)	Christmas Island forest skink (*Emoia nativitatis*)	Coastal skink (*Emoia atrocostata*)	Christmas Island giant gecko (*Crytodactylus sadleiri*)	Common house gecko (*Hemidactylus frenatus*)	Four-Clawed gecko (*Geyhra mutilata*)	Bowring's supple skink (*Subdolops. bowringii)*
Natural distribution	Endemic to Christmas Island (CI) (origins >25 mya) [1,2]	Endemic to CI (origins >5 mya)[1,2]	Endemic to CI (origins >10 mya) [1,2]	Native to CI. Occurs also from Taiwan, through South East Asia, New Guinea and to Vanuatu) [2]	Endemic to CI (origins >1 mya)[1,2]	Introduced to CI (~ca. 1930s); native range South East Asia[1,2]	Introduced to CI (~ca. 1950s) native range South East Asia[1,2]	Introduced to CI (~ca. 1970s); native range South East Asia[1,2]
Conservation status	Extinct in the Wild (last wild observation in 2012) [3]	Extinct in the Wild (last wild observation in 2010) [3]	Extinct (last wild observation in 2010) [3]	Extirpated (last wild observation in 2010) [3]	Critically Endangered [3]	Least Concern[3]	Least Concern[3]	Least Concern[3]
Former abundance and occurrence	Common and reasonably widespread, particularly on the plateau[2,4,5]	Abundant and hyper-abundant in the settlement[2,4,5]	The most abundant skink on Christmas Island in 1979, occupying all habitats[2,4,5]	Formerly patchy distribution; not abundant[2,4,5]	Extremely abundant and widespread in 1979; remains common in most areas[2,4,5]	Abundant, especially in disturbed areas[2,4,5]	Abundant, but less so than *H. frenatus*. Mostly restricted to disturbed areas[2,4,5]	Widespread, but not abundant[2,4,5]
Size (SVL*; mass)	46 (38-51.5) mm; ~2g[2]	43 (30-52) mm; 2.2-2.5g[2]	63 (40-78) mm; 9 g[2]	67 (48-88) mm; 14 g[2]	70 (44-88) mm; 14 g[2]	51 (47-59) mm; 4.5 g[2]	49 (38-55.5) mm; ~4 g[2]	36 (25-47) mm; 2 g[2]
Microhabitat[2]	Arboreal[2]	Arboreal and terrestrial[2]	Terrestrial[2]	Terrestrial[2]	Arboreal[2]	Arboreal[2]	Arboreal[2]	Fossorial[2]
Activity pattern	Nocturnal[2]	Diurnal[2]	Diurnal[2]	Diurnal[2]	Nocturnal[2]	Nocturnal[2]	Nocturnal[2]	Diurnal[2]

Habitat/s	Rainforest including secondary forest (mining/rehabilitation sites) [2,4]	Rainforest and disturbed areas[2,4]	Rainforest including secondary forest (mining/rehabilitation sites) [2,4]	Coastal habitats; rocky intertidal shoreline[2,4]	Rainforest including secondary forest (mining/rehabilitation sites) [2,4]	Rainforest and disturbed areas. Hyper abundant around human dwellings[2,4]	Disturbed areas[2,4]	Mostly disturbed areas (grassy areas, rehabilitated mining fields) [2,4]
Reproduction	Seasonal breeding; two eggs laid behind bark, on the ground or under rocks, logs. Peak breeding in the dry season[2].	Seasonal breeding (September-February), but likely breed year-round. Clutch of two. Eggs buried on the ground under rocks, logs[2].	Clutch size of two, little else known[2]	Clutch size of two. Unknown breeding season, but elsewhere the species complex breeds year-round[2].	Clutch size two; likely breeds year-round with a peak in the dry season[2].	Clutch size two; likely breeds year-round with a peak in the dry season[2].	Clutch size two; likely breeds year-round with a peak in the dry season[2].	Clutch size of two; little else known[2].
Foraging behaviour	Slow-moving; ambush predator of small invertebrates[2]	Fast-moving; uses ambush positions to hunt prey (small invertebrates) [2]	Fast-moving; predator of small ground dwelling invertebrates[2]	Fast-moving; consumes invertebrates in intertidal rocky zone[2].	Slow-moving; ambush predator[2]	Fast-moving; consumes invertebrates including flying insects[2]	Fast-moving; consumes invertebrates including flying insects[2]	Unknown, but likely uses leaf litter to avoid predators and catch prey[2]
Predated by wolf snakes	Yes[4,6]	Yes[4,6]	Yes[4,6]	Yes[4,6]	Yes[4,6]	Yes[4,6]	Yes[4,6]	Yes[4,6]
Predated by other invasive species? (e.g. centipedes, feral cat)	Yes[7]	Yes	Yes[7]	Yes[7]	Yes[7]	Yes[7]	Yes[7]	Yes[7]
Disease occurrence documented (Enterococcus sp.)	Yes[8,9]	Yes[8,9]	Unknown[8,9]	Unknown[8,9]	No - unaffected in areas with diseased common house geckos and four-clawed geckos[8,9]	Yes[8,9]	Yes[8,9]	Unknown[8,9]

 * snout-to-vent length

1. Oliver et al. 2018, 2. Cogger et al. 1983, 3. IUCN 2020, 4. James 2007, 5. Smith et al. 2012, 6. Rumpff 1992, 7. Tidemann 1994, 8. Hall et al. 2011, 9. Rose et al. 2017

TABLE 3. The likelihood of establishing ex-situ populations of blue-tailed skinks and Lister's gecko, depending on the location, and including 95% confidence intervals (CI)

Location	Species	Estimate	Lower CI	Upper CI
Christmas Island	Lister's gecko	0.09	0.04	0.20
Christmas Island	Blue-tailed skink	0.10	0.04	0.21
Elsewhere	Lister's gecko	0.44	0.26	0.62
Elsewhere	Blue-tailed skink	0.73	0.55	0.85

TABLE 4. Eight candidate explanations for why four lizard species persist and four lizard species were lost on Christmas Island.

Hypothesis	Evidence for	Evidence against	Conclusion
1. Surviving species had long evolutionary exposure to introduced predators (notably the common wolf snake)	Genetic analysis suggests the closest living relatives of the Christmas Island giant gecko occur in South East Asia (< 1 million years).[1] The common wolf snake and its species complex are native to South East Asia. Other introduced predators such as giant centipede also from South East Asia.[2] Common house and four-clawed geckos and the Bowring's supple skink are all native to South East Asia, and likely retained anti-predator skills associated with such predators. The remaining endemic reptiles evolved >5 Mya, and are likely to be evolutionary naive to novel predators. Blue-tailed skinks and the Christmas Island forest skink both have their closest relatives outside South East Asia.[1]	The coastal skink is not considered endemic and is widespread through South East Asia, where the common wolf snake and other introduced predators occur.[3] Despite its closest relatives being from South East Asia, the Christmas Island giant gecko has 1 million years of evolutionary divergence. However, it is unknown when the species arrived on Christmas Island, and it may be a relatively recent arrival, with its close relatives either unsampled or extinct.	**Most support** The introduced lizard species are all native to South East Asia and co-occur with the common wolf snake
2. Surviving species have different ecological traits.	Common house, four-clawed and the Christmas island giant geckos are all nocturnal and arboreal, whereas the extirpated blue-tailed skink, Christmas island forest skink and coastal skink are diurnal and terrestrial.[4] Most introduced predators on Christmas Island are predominantly nocturnal and terrestrial, however, all are capable climbers (eg. Common wolf snake, giant centipede and black rat) (Table 2).	The bowring's supple skink is diurnal and fossorial. However, as it is a recent arrival from South East Asia, it perhaps recognises potential predators. Lister's geckos are nocturnal and arboreal and was extirpated.	**Some support** There is some alignment of ecological traits that support them being a factor in reptile declines.
3. Surviving species are more resistant to yellow crazy ants (and the	Some evidence of the Christmas Island giant gecko, and the Common house and four-clawed geckos	Losses of the now EX** reptile species occurred in areas without YCA.	No support

habitat modification they cause).	occurring in areas with and near YCA* super-colonies.[5]		
4. Surviving species use different microhabitats.	None.	*L. bowringii* and *E. nativitatis* had overlapping habitats, yet only *S. bowringii* persists. *G. mutilata*, *H. frenatus* and *L. listeri* had overlapping habitat use, but only *L. listeri* disappeared. [4,5]	No support
5. Surviving species are more resistant to disease.	None	*H. frenatus* and *G. mutilata* have been found with multiple diseases including a novel *Enterococcus* bacterium and papillomaviruses.[6,7,8] At the time of decline, a disease examination found no signs of disease and no differences in the disease/pathogen load between species.[13]	No support
6. Surviving species are less affected by pesticides used to control crazy ants.	None	Losses of the now EX native reptile species occurred across the entire island (even in areas without fipronil application).[5]	No support
7. Surviving species may have occurred in greater numbers, so may have persisted longer before extirpation.	None	*C. egeriae* and *E. nativitatis* were the most abundant skinks on Christmas Island and were more abundant than invasive species.[4]	No support
8. Surviving species are less palatable to introduced predators.	None	All reptile species are preyed upon by introduced predators, notably by *L. capucinus*.	No support
9. Surviving species had greater reproductive capacity, so could better	Many extinct species had relatively low reproductive output	Clutch size is similar for surviving and lost lizard species	No support

withstand novel predation pressure

1. Oliver et al. 2018, 2. Gibson-Hill 1949, 3. Huang et al. 2011, 4. Cogger et al. 1983, 5. James 2007, 6. Rose et al. 2017, 7. Agius et al. 2019, 8. Hall et al. 2011

*YCA (Yellow Crazy Ants)

**EX (Extinct)