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Survival of an Extinct in the Wild skink from Christmas Island is reduced by an invasive centipede: implications for future reintroductions

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ABSTRACT

The blue-tailed skink (*Crytoblepharus egeriae*) is endemic to Christmas Island but underwent rapid population declines in the 1990's and 2000's and was listed as Extinct in the Wild in 2017. As invasive giant centipedes (*Scolependra subspinipes*) were implicated as a cause of a failed reintroduction of captive bred skinks into a fenced enclosure, we undertook a mesocosm experiment to investigate if skink survival and body condition was negatively affected by the presence and density of *S. subspinipes*. In addition, we used DNA barcoding to determine if wild centipedes consume other reptile species on Christmas Island. In the mesocosm experiments, survival of skinks was reduced by 30% and 44% at low and high centipede densities respectively over 12 weeks, and skink body condition also declined significantly over this period. DNA barcoding confirmed that skinks that were lost during the mesocosm experiment had been consumed by centipedes. Further, we detected DNA of two invasive reptiles (the Oriental wolf snake *Lycodon capucinus* and the House gecko *Hemidactylus frenatus*) in the stomachs of wild-caught centipedes, suggesting that centipedes are a generalist predator of reptiles in this island ecosystem. Based on these results, we recommend that attempts to reintroduce *C. egeriae* to Christmas Island should include the control of centipedes to increase the likelihood of success.

Keywords: Christmas Island, blue-tailed skink, *Scolependra subspinipes*, survival, invasive species, mesocosm

INTRODUCTION

Invasion of exotic species into naive ecosystems is one of the most important drivers of biodiversity loss (Vitousek et al. 1997; Courchamp et al. 2003; Sax and Gaines 2008; Carthey and Banks 2014). Damaging impacts of invasive species include both direct and indirect effects such as predation and competition for food and refuge selection (MacDougall, Turkington 2005), and affect taxa such as plants (Vilà et al. 2011), invertebrates (Green and O'Dowd 2009), reptiles (Case and Bolger 1991), mammals (Woinarski et al. 2015) and birds (Szabo et al. 2012). Island species are particularly vulnerable to the pressures exerted by invasive species (Reaser et al. 2007; Medina et al. 2011; Simberloff et al. 2013; Doherty et al. 2016). By-products of evolutionary isolation on islands, such as simplified food webs, limited competition, and ecological naivete can render island endemics susceptible to even small changes in their environment (Blackburn et al. 2004; Fordham and Brook 2010). These traits often result in island species failing to recognise or respond appropriately to novel threats, which can result in their decline and extinction (Salo et al. 2007; Sih et al. 2010; Carthey and Banks 2014).

Invasive vertebrates are well documented agents of disturbance of island ecosystems (Jeschke and Strayer 2005; White et al. 2008), but invertebrates are also effective invaders and may have similarly serious consequences (Green et al. 2009; Kenis et al. 2009). For example, the introduction of the mosquito *Culex. quinquefasciatus* to Hawaii was responsible for large declines in forest birds due to it being a vector for avian malaria (LaPointe et al. 2012). Introduced ant species also impact native species, from deterring the Mauritius blue-tailed gecko (*Phelsuma cepediana*) from accessing food sources (Hansen and Müller 2009), to inducing ecosystem meltdown via the formation of Yellow crazy ant (*Anoploepis gracilipis*) supercolonies on Christmas Island (O'Dowd et al. 2003). Unlike predatory invasive vertebrates (Doherty et al. 2016), there is less research on how invasive invertebrates' impact native species via predation, but some anecdotal and empirical evidence exists of native spiders and centipedes consuming small vertebrates such as microbats, lizards, and amphibians (Nyffeler and Knörnschild 2013; Arsovski et al. 2014; Nordberg et al. 2018).

Centipedes are a diverse group of predatory invertebrates in the class Chilipoda that predate primarily on invertebrates. Members of the family *Scolependridae*, however, are large (up to 30 cm in length) that have been documented predating on vertebrate species exceeding their own mass including Marine toads (*Rhinella marina*), the nose-horned viper (*Vipera ammodytes*), and the microbat *Eptesicus fuscus* (Carpenter and Gillingham 1984; Arsovski et al. 2014; Lindley et al. 2017) and may represent important predators and competitors within forest food web systems. However, few studies have examined the potential negative impacts of introduced centipedes.

One study though, Anthony et al. (2007) examined for intraguild effects between the introduced centipede *Lithobius forficatus* and native juvenile red-backed salamanders (*Plethodon cinereus*) and found that salamanders and introduced centipedes avoided eachother, but found no predation of salamanders by centipedes. Despite there being no predation by centipedes in this study, centipedes are capable predators and their ability to reach large densities (Maljkovic et al. 2010) may indicate that centipedes are important intraguild competitors with smaller vertebrate groups (Pike et al. 2007), particularly in areas they are introduced and not subjected to natural population regulation by other competitors and predators.

Christmas Island has lost a substantial proportion of vertebrate biodiversity since settlement in 1888. These losses amount to four of the five endemic mammals, while four of six native reptiles are now classified as Extinct (*Emoia nativitatis*, endemic), Extinct in the Wild (*Crytoblepharus egeriae* and *Lepidodactylus listeri*, both endemic) or extirpated (*Emoia atrocostata*, native but not endemic) by the IUCN red list (James et al. 2019; Tingley et al. 2019) With the exception of the two native rodents, invasive predators are thought to be a key factor underpinning these declines. The endemic blue-tailed skink (*Cryptoblepharus egeriae*) narrowly avoided extinction. Formerly common and widespread across Christmas Island until the late 1980s, *C. egeriae* underwent rapid declines across its range and was last seen in the wild in June 2010 (Smith et al. 2012). The reason for the decline of *C. egeriae* (and other native reptiles) is unknown, but the introduced *L. capucinus* is considered the most likely candidate (Andrew et al. 2018). Native to south-east Asia, *L. capucinus* is a skink and gecko specialist (Jackson et al. 2014) and was first detected on Christmas Island in 1987 (Smith 1988) with native lizard declines being noticed shortly after in 1992 (Rumpff 1992). Fortunately, extinction was avoided thanks to successful breeding programs on Christmas Island and at Taronga Zoo in Sydney that were initiated shortly before the species disappeared (Andrew et al. 2018).

A key part of planned recovery actions for *C. egeriae* are reintroductions back onto Christmas Island. A fundamental aspect of reintroduction success is to eliminate or manage the root cause of decline in such a way that its impacts are significantly reduced (Wolf et al. 1996; Seddon et al. 2007). Hence in 2017, a trial reintroduction was undertaken with 137 *C. egeriae* released into 2600 m^2 exclosure surrounding revegetated forest, where *L. capucinus* had been removed. However, while *C. egeriae* survived well over the first few weeks, the population subsequently declined and no skinks were sighted approximately five months after release (JP Emery, unpublished data). There was no obvious cause of reintroduction failure, as mortality events were not observed, but one plausible cause for skink decline was negative impacts fromthe introduced Giant centipede (*Scolependra subspinipes*). Giant centipedes were accidentally introduced to Christmas Island around 1900, and were widespread and common by the 1930s (Waldock and Lewis 2014). Native to parts of South East Asia, *S. subspinipes* have been introduced to many islands in the Pacific and Indian Oceans (Waldock and Lewis 2014) and can attain lengths exceeding 25 cm. Centipedes occurred inside the enclosure at densities of approximately two adults per 25 m^2, and in the captive breeding facilities on Christmas Island, infrequent invasions of centipedes into exclosures have resulted in skink deaths (Brendan Tiernan & JP Emery, personal observations). Additionally, they have been observed consuming the introduced Oriental wolf snake (*Lycodon capucinus*) (JP Emery, personal observations; S1 Figure 1),. In light of these observations, interactions between *S. subspinipes* and *C. egeriae* are important to understand, as *S. subspinipes* may influence the success of future *C. egeriae* reintroductions. Additionally, the two remaining extant reptile species on Christmas Island (the Christmas Island forest gecko *Crytodactylus sadleiri* and Christmas Island blind snake *Ramphotyphlops exocoeti*) areclassified as Critically Endangered, so establishing whether *S. subspinipes* may threaten these other species is also important.

This study investigated whether *C. egeriae* is negatively impacted by a potential intraguild competitor; the introduced *S. subspinipes*, using experiments undertaken in open mesocosms where skinks were housed with and without *S. subspinipes* over three months. If there is intraguild competition between *C. egeriae* and *S. subspinipes,* we expect the survival and body condition of *C. egeriae* to be lower in the presence of *S. subspinipes* after three months. We attempted to represent centipede density at the time of the 2017 *C. egeriae* reintroduction trial, to retrospectively assess whether centipedes could have been influential in the failed reintroduction attempt. Further, we investigated if *S. subspinipes* predates both native and introduced reptiles on Christmas Island based on DNA barcoding of their gut contents.

MATERIALS AND METHODS

Study area

Christmas Island (105°40′E,10°30′S) is a remote Australian territory situated in the north-east Indian Ocean with a tropical environment characterised by two seasons: wet (December-May) and dry (June-November). Approximately 65% of the 135 km^2 island is covered in natural vegetation, of which 63% is National Park. The island is dominated by tall tropical rainforest on the plateau and by semi-evergreen thicket on the coastal terrace (Abbott 2006). The mesocosm experiment described below was undertaken at the Pink House, a research facility operated by Parks Australia located near the centre of the island.

Source of animals and husbandry

Adult *C. egeriae* were sourced from the captive breeding colony on Christmas Island and raised in indoor and then outdoor enclosures. Only adult males were used for the experiment as they were not needed in the breeding program. Skinks were fed three times a week on insects (mostly crickets and termites) and were toe clipped for individual identification. Additional food (largely cockroaches, spiders, and grasshoppers) was collected using large butterfly nets along the local international airport runaway. There have been some cases of *C. egeriae* escaping exclosures at the Pink House, so to avoid the unlikely event of a centipede consuming a *C. egeriae* before being placed into the exclosure, *S. subspinipes* were collected at least 500 m from the Pink House, and centipedes with a body length >100 mm were used for the experiment.

Mesocosm configuration

A 12-week experiment was undertaken in 2018 within six 5 m x 5 m mesocosms situated inside an outdoor aviary, which prevented bird predation and cage destruction by Coconut crabs (*Birgus latro*) (Fig. 1A). Habitat provided for skinks was based on existing captive breeding protocols. Each mesocosm contained a 2 m high platform of intersecting tree stumps, branches and exfoliated bark. In addition, two stacks of four tiles, two stacks of four pallets, two rock piles consisting of eight rocks, two timber piles consisting of eight pieces of timber, two artificial cover hides of closed cell foam, and two ‘Malibu huts’ (four metal droppers attached to an aluminium roof) were added to each mesocosm. In each case, one replicate of each structure was situated in full sun, and the other in part-shade. Two 5 L water bowls were also provided.

Experimental design

Experimental treatments consisted of two densities (low and high) of *S. subspinipes* and a control without centipedes (Fig. 1B). Each treatment was replicated twice with treatments randomly assigned. The control treatment had no centipedes added, the low-density treatment had two centipedes added (2 centipedes per 25 m^2), and the high-density treatment had six centipedes added (6 centipedes per 25 m^2). The lower centipede density was chosen based on estimated centipede densities during the 2017 reintroduction trial, whereas the high-density treatment was chosen as an arbitrary higher density that might have a greater impact on skinks. Although we consider a density of six *S. subspinipes* per 25 m^2 to be unlikely in most habitats on Christmas island, scolopendrid centipedes are capable of reaching very high densities (e.g. Maljkovic et al. (2010) recorded 12 adult *Scolependra abnormis* per m^2 on Round Island in the Mascarenes).

Prior to release, all skinks were weighed to the nearest 0.01 g using an electric balance (Mettler Toledo, model;ME204) and measured (snout-vent length and tail length, mm) using digital callipers (Craftright 150 mm digital caliper), and it was noted if each individual had an original or regenerated tail. Fifteen skinks were randomly assigned to each enclosure on July 3 2018 and were allowed five days to become familiar with their new environment. Centipedes were added to the high and low centipede density treatments on July 8, and the experiment concluded on October 1. An individual *L. capucinus* infiltrated a control exclosure in the first week of the experiment and consumed seven skinks. We were able to individually identify deceased skinks in the wolf snake's stomach through toe clip identification, and we therefore replaced these skinks with seven new individuals.

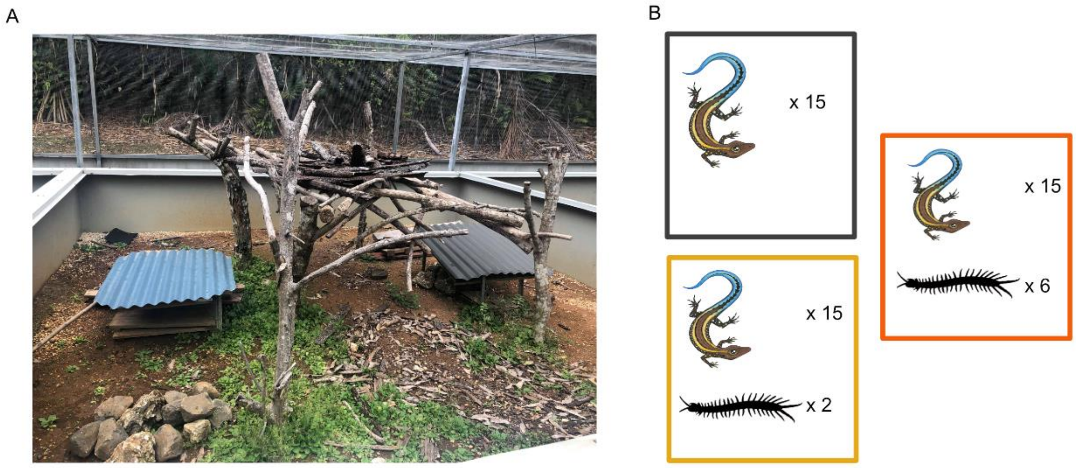

Fig. 1 A). Image of an experimental mesocosm showing the configuration of habitat. B) Schematic of the three treatments; a control (no centipedes), low density (2 centipedes) and high density (6 centipedes). Each treatment was replicated twice.

Mesocosm surveys

Daily observations were undertaken between 08:30 and 11:00 hrs throughout the experiment. Observations were the primary means of identifying any reductions in population sizes between weekly census counts (see below), that might indicate a *L. capucinus* incursion. Observations were undertaken for 5 minutes in each exclosure. A weekly census (on day 7 of each week) involving the capture of skinks was also undertaken, where each recaptured skink was weighed and released immediately after processing.

Centipedes were also captured during each weekly census. If any skinks were missing from a mesocosm that contained centipedes, all centipedes within that mesocosm were euthanised by decapitation and stored in 100% ethanol for DNA analysis (see below), and replaced with new centipedes. Further, to reduce the possibility that centipedes became accustomed to skinks, centipedes were replaced every two weeks, even if no skinks were missing from a mesocosm.

Collection of *S. subspinipes* for gut content analysis

To investigate if *S. subspinipes* predate on native and introduced reptile species on Christmas Island, 70 centipedes were collected from three spatially-separated sites: 20 at South Point in the south-east of the island, 30 at the Pink House and 20 at Phosphate Hill in the northeast of the island. These areas have high densities of centipedes and support populations of the last remaining native reptile, *C. sadleiri* and two introduced gecko species (*Hemidactylus frenatus* and *Geyhra mutiliata*) and one introduced lizard (*Subdolups bowringii*, formally

Lygosoma bowringii) (JP Emery, unpublished observations). Centipedes were captured during nocturnal surveys, euthanised as described above, and stored in 100% ethanol. We extracted DNA from the gut content of each centipede and used Polymerase chain reaction (PCR) amplification and subsequent DNA sequencing to identify components of their diet (see below).

DNA extraction and PCR amplification

Gut-content samples were extracted from 98 centipedes; the 70 specimens described above, and 28 centipedes removed from experimental mesocosms. Centipede guts were sampled across the fore, middle and hindgut to maximise the chance that the DNA of ingested items could be amplified. DNA of each gut content sample was extracted using a DNeasy blood and tissue kit (QIAGEN, Hilden, Germany), as was the DNA of one *C. egeriae* reference specimen. DNA was sequenced at an approximately 200 base pair fragment of the Cytochrome c oxidase subunit I (COI) gene using primers GeckoF2 and IslGeckoR1 (Y. Hitchen, unpublished). Each 25µl PCR contained 0.25 µM of forward and reverse primer, 0.2 mM each dNTP, 0.75 mM $MgCl_2$, 1 x PCR buffer, 0.4mg/ml BSA (Fisher Biotec, Wembley, WA, Australia) 0.05U Platinum® *Taq* DNA Polymerase (Thermo Fisher Scientific, USA) and 5µl of DNA. Amplification was performed using an Eppendorf MasterCycler *epgradient S* (Eppendorf, Hamburg, Germany) with the following cycling conditions: initial denaturing of 15 min at 95 °C; 40 cycles of 30 s at 94 °C, 1 min 30 s at 56 °C and 30 s at 72 °C; followed by a final elongation cycle of 30 min at 60 °C. Unpurified PCR products were sequenced by the Australian Genome Research Facility (AGRF) on an AB 3730*xl* using BDT v3.1 reaction mix (Applied Biosystems, USA). Sequences were then edited using the GENIOUS software (Drummond et al. 2011). Extraction and PCR negative and positive controls were employed to confirm that cross-contamination did not occur. All sequences were analysed using the NCBI BLAST tool, which utilises GenBank to identify potential species matches. Confidence levels in the identification were dependant on the match percentages, with a minimum requirement of 99% to assign species. Where this requirement could not be met, Genus or Family was the highest order assigned.

Data analysis

Skink body condition

Body condition indices are used as proxy indicators of energy stores and have been linked to fitness (Hoare et al. 2006), so we investigated whether co-habitation with *S. subspinipes* affected the body condition of *C. egeriae* within the mesocosms. While there has been debate over interpreting body condition indices in ecological studies, particularly when using mass to length relationships (Green 2001), body condition indices provide an informative and non-lethal technique for assessing changes in condition if assumptions undergo stringent testing (Bradshaw et al. 2000). Here, we calculated body condition using the residuals of the regression equation of body mass to snout-vent length (Rodríguez-Prieto, 2010). Each variable was first checked for normality using a Levene's test and then log transformed. Body condition indexes for skinks normally exclude individuals with regenerated tails, however due to captive conditions a high proportion of adult males available for this study (~80%) had regenerated tails. However, we only generated body condition indices for skinks that: (1), survived for 12 weeks, and (2), without additional tail loss.

A linear mixed effects analysis was undertaken in the statistical program R (R Core Team 2013) using the *lme4* package (Bates et al. 2014) to investigate if the body condition of *C. egeriae* differed at the beginning and end of the experiment. We used treatment and time as fixed effects with an interaction term. A random intercept for mesocosm ID was included as a random effect in the model. In addition to visual inspection of the of residual plots for normality, we also undertook a Levene's test to test the assumption of equal variances. To obtain p-values, we used a likelihood ratio test of the full model (with interaction) against the model without the effect (no interaction). Finally, we undertook pairwise Tukey honest significant (HSD) comparisons with Bonferroni correction between centipede density and time, using the *glht* function in the package *multcomp* (Hothorn et al. 2008) to compare body condition between treatments at the start and end of the experiment.

Skink survival

Survival analyses use survivorship data to investigate time-to-event outcomes using a specified time of origin and a specified endpoint or event of interest (Batson et al. 2016). We undertook univariate survival analysis using nonparametric Kaplan-Meir plots to test for differences in *C. egeriae* survival probabilities at different centipede densities. We then used log-rank tests with Bonferroni correction to examine pairwise differences in the survival probability between treatments. Kaplan-Meir estimates can only examine differences between treatments and cannot account for additional explanatory variables that can influence survival (Bewick et al. 2004). Hence to examine the potential effect of covariates on survival, we used Cox proportional hazards models. The Cox proportional hazard model is a semi-parametric model equivalent to a multiple regression model, and can incorporate fixed and random effects (Bewick et al. 2004; Batson et al. 2016). We used a Cox proportional hazard model with starting body condition and treatment as fixed effects, and mesocosm ID as a random effect to investigate their effects on survival.To obtain the p value of the best model, we used a likelihood ratio test of the full model (with interaction) against the model without the interaction. We then report the p values for each variable from the best model with their coefficients, standard errors and z values. Hazard ratios measure the magnitude of an explanatory variable (both positive and negative) on the dependent variable (survival). We pooled the data across the two mesocosms within each treatment (Clulow et al. 2018; Sswat et al. 2018). Any differences between mesocosms were accounted for using the cox proportional hazard model with mesocosm ID as a random effect. Survival analyses were undertaken in the survival package using the *survfit, coxph, cox.zph and coxme* functions in R, with statistical significance assumed at $p < 0.05$ (Therneau 2015).

RESULTS

Influence of centipedes on skink survival

The survival of *C. egeriae* was significantly reduced by both low and high densities of *S. subspinipes* after 12 weeks (Fig 2). Survival was 93% in control mesocosms, whereas survival was 63% and 49% in low and high-density centipede treatments respectively. The log rank test indicated a significant difference in the survival curves ($x^2 = 13.5$, df = 2, $p = 0.001$). Pairwise comparisons revealed a significant difference between the control and low and high centipede density treatments on skink survival ($p = 0.013$ and $p < 0.001$ respectively), but there was no difference between low and high centipede density treatments ($p = 0.917$). From the Cox proportional model, we found no significant interaction between treatment and initial body condition on survival ($x^2 = 0.515$, df = 2, $p = 0.772$). However, initial body condition did influence survivorship ($p = 0.037$; Table 1), and the coefficient was large ($\beta = -10.145$, se = 4.85) suggesting that body condition had a positive effect on survival. In contrast, centipedes affected skink survival at low ($\beta = 1.815$, $p = 0.021$) and high densities ($\beta = 2.318$, $p = 0.002$; comparison relative to controls). High positive coefficients (Table 1) indicated that survival decreases from the control to low centipede density treatment, and further decreases when contrasting the control and high centipede density treatment (Fig 2). Cox proportional models require that the proportional hazard remains constant over time, and this assumption was met ($x^2 = 2.571$, $p = 0.463$).

Table 1. Results from the Cox proportional hazard model of skink survival, with significant effects in bold.

	Coefficient (*β)**	Se	Z value	P value
Low centipede density	1.815	0.771	2.32	**0.021**
High centipede density	2.318	0.754	3.08	**0.002**
Initial body condition	-10.145	4.865	-2.09	**0.037**

* positive values indicate a negative effect on survival, and negative coefficients a positive effect on survival.

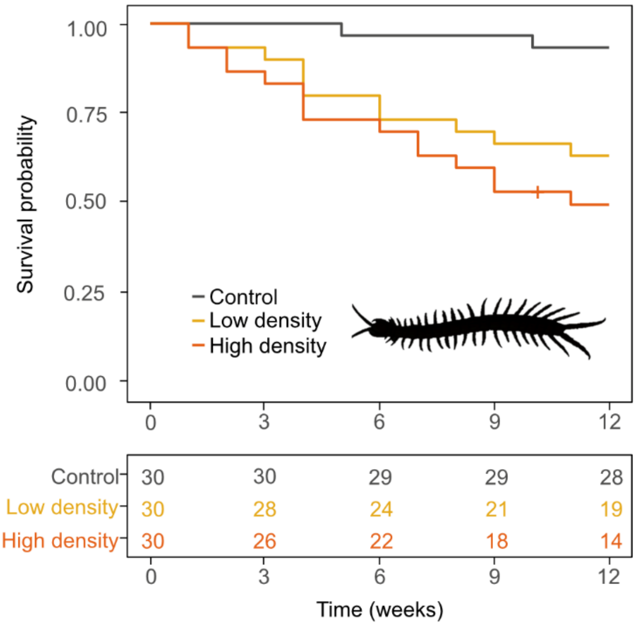

Fig. 2. The survival probability of adult male *C. egeriae* in experimental mesocosms over 12 weeks (top) and the numbers of surviving skinks at each time point (bottom). One *C. egeriae* from a high centipede density mesocosm was removed at week 10 (indicated with a +) due to a possible bacterium infection (*Enterococcus sp*) and was not included in survival probability calculations.

Influence of centipedes on *C. egeriae* body condition

A total of 45 *C. egeriae* (18 control, 15 low density, 12 high density) were used in body condition analyses. We found a significant interaction between treatment and time on *C. egeriae* body condition (x^2 =7.874, df = 2, p = 0.019). Tukey post hoc tests (S1 Table 1) confirmed there were no differences in skink body condition across treatment groups at the start of the experiment, but body condition was significantly lower between the control and both low and high-density centipede treatments after 12 weeks (Fig 3). Skinks from the high and low centipede density treatments had similar body condition at the conclusion of the experiment (Fig 3).

DNA-based evidence of reptile consumption by centipedes

Eight of 28 samples of gut contents extracted from centipedes used in the mesocosm experiment amplified sufficient DNA for sequencing, and all returned a 100% match for *C. egeriae*. Notably, all samples that returned positive for *C. egeriae* were collected immediately after a skink disappeared from a mesocosm. As expected, our positive control also returned 100% positive for *C. egeriae*, but one negative control (a centipede collected ~1 km from the Pink House) had gut contents that were a 98.9% match for *Lycodon capucinus*.

Gut contents of six of the 70 centipedes collected across Christmas Island amplified sufficient DNA for sequencing (S1 Table 2). The samples amplified dietary DNA from two introduced cockroaches species (1) (*Pycnosceius sp*; 99.5%), and (2) the introduced American cockroach *Periplaneta americana* (99.5%), the invasive gecko species *Hemidactylus frenatus* (99.1%), and a centipede from the Family *Scolopendridae* (best match *Scololependra subspinipes;* 92.5%). Non-dietary identifications included amplification of *Homo sapiens* DNA (100%) and a bacterium species from the Genus Citrobacter (best match *Citrobacter werkmanii* strain; 96.2%). Both these amplifications were likely due to contamination associated with dealing with degraded samples.

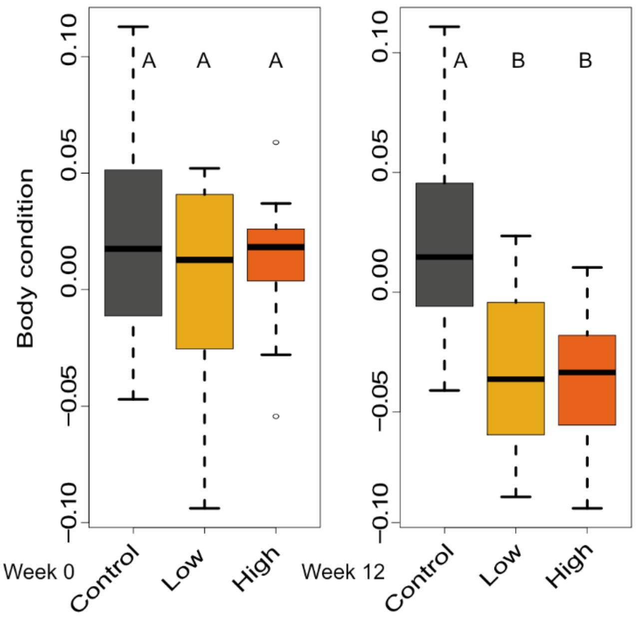

Fig. 3. Body condition of adult male *C. egeriae* at the beginning and the end of the experiment for three centipede treatments: a control (no centipedes); low density (2 centipedes) or high density (6 centipedes). Boxes represents the interquartile range with the middle line representing the median value, whiskers show the minimum and maximum body condition, and open circles represent outliers. Capital letters indicate statistical differences between treatments and at both week 0 and week 12, where $p < 0.05$.

DISCUSSION

Scolopendrid centipedes have long been documented as opportunistic predators of vertebrates (Carpenter and Gillingham 1984; Arsovski et al. 2014). Here we show using experimental mesocosms that giant centipedes (*S. subspinipes*) significantly reduce the survival of a highly threatened skink species (*C. egeriae*). Further, centipedes elicited a significant reduction in the body condition of surviving skinks over 12 weeks of exposure. We also showed that *S. subspinipes* consumes other reptile species on Christmas Island, including an introduced gecko and snake. Collectively these results suggest that *S. subspinipes* is likely an intraguild competitor with *C. egeriae* an potentially underappreciated predator within the Christmas Island ecosystem. Importantly, the direct and indirect impacts of *S. subspinipes* on *C. egeriae* demonstrated here suggest that attempts to reintroduce *C. egeriae* to Christmas Island will benefit from centipede control or exclusion; assuming that *L. capucinus* has also been excluded.

DNA barcoding of gut contents is becoming increasingly useful for investigating the prey consumed by both vertebrate and invertebrate predators (Sheppard and Harwood 2005), however amplification of a particular species does not prove predation (Sheppard et al. 2005). As we did not observe any predation events of *C. egeriae* by *S. subspinipes*, we cannot rule out the scavenging of at least some *C. egeriae* individuals by *S. subspinipes*. However, in our snapshot landscape analysis of the gut contents of 70 centipedes we found additional evidence of consumption of reptiles including *L. capucinus* and *H. frenatus* (S1 Table 2). On Christmas Island, the high abundance of red crabs and coconut crabs means that any dead animal matter is likely consumed before a centipede finds them, and as such this implies that centipedes likely predated L. capucinus, H. frenatus and *C. egeriae* before consumption. Several factors may have contributed to the low amplification rates of DNA in the landscape samples, including time since feeding, size of prey species, meal size, and abiotic factors such as temperature and storage post collection (Sheppard et al. 2005; Hosseini et al. 2008). But if predation of free-ranging reptiles by *S. subspinipes* can be proven via further observations (e.g. S1 Figure 1), it would provide strong evidence that *S. subspinipes* predate on at least three of the reptile species on Christmas island (*C. egeriae*, *L. capucinus* and *H. frenatus*) and may also exert pressureon the remaining endemic reptiles (*C. sadleiri* and *R. exocoeti*), particularly where *S. subspinipes* occur at high densities. Our findings build upon other examples of scolopendrid centipedes consuming vertebrates such as amphibians (Forti et al. 2007), microbats (Molinari et al. 2005; Lindley et al. 2017), lizards (Nordberg et al. 2018) and snakes (Smart et al. 2010; Arsovski et al. 2014).

Island species often display ecological naiveté as a result of low predation pressures over evolutionary time-periods (Carthey and Banks 2014; Gérard et al. 2014). Ecological naivete can range from (1) the complete inability to recognise a predator, (2) recognising a predator but failing to respond appropriately, or (3) recognising a predator, employing antipredator defences, but still being outcompeted by a superior predator (Sih et al. 2010; Carthey and Banks 2014). We observed that *C. egeriae* avoided sharing refuges with *S. subspinipes*, to the extent that some skinks slept exposed on the aluminium roofs of the Malibu huts within the centipede exclosures. This suggests that *C. egeriae* recognise *S. subspinipes* as a predator, as similar behaviours have been observed in juvenile velvet geckos (*Oedura lesueurii*) and redback salamanders (*Plethodon cinereus)*, which avoid sharing retreats with native and introduced predatory scolopendrid's (Anthony et al. 2007; Pike et al. 2010). Such avoidance behaviours are likely to be energetically and physiologically costly. For instance, a common response to predation risk in reptiles is the release of glucocorticoids hormones, which if sustained over long time periods result in high parasite loads, reproductive inhibition and a loss in body condition (Rodríguez-Prieto et al. 2010; Anson et al. 2013).

We documented a significant reduction body condition of skinks co-housed with *S. subspinipes.* This may have: 1) been a stress response, as alluded to above, 2) reflected competition for limited food, or 3) the presence of centipedes may have affected how *C. egeriae* foraged. The second explanation is unlikely as daily inspections of mesocosms consistently revealed excess food. Hence, behavioural changes as a result of intraguild competition is more likely. The predator-sensitive foraging hypothesis predicts that the presence of predators will restrict foraging efficiency or increase predator vigilance (Lima and Dill 1990; Lima and Bednekoff 1999). So, while skinks have distinctly different foraging periods to *S. subspinipes* (diurnal vs nocturnal respectively), they could have been actively avoiding areas with *S. subspinipes* scent, constraining how or where they foraged, leading to reduced body condition.

In reptiles, low body condition may compromise an individual's ability to defend against disease and parasites, or mount effective anti-predator defences (Amo et al. 2006; Rodríguez-Prieto et al. 2010). Our mesocosm data supported this pattern, as *C. egeriae* with higher initial body condition had higher survivorship, even in the presence of centipedes. These result suggests that S. subspinipes are an interspecific competitor with C. egeriae. However, it is still possible that due to a reduction in body condition by factors such as increased stressed and exposure that some *C. egeriae* died prior to consumption by S. subspinipes. Further, direct observations of *C. egeriae* with S. subspinipes, and/or experiments using chemical cues from centipedes, will be required to test if *C. egeriae* recognise centipedes /or alter their behaviour in their presence. A longer experiment which included an analysis of the effects of *S. subspinipes* on adult females *C. egeriae* will be required to see if low body condition leads to a reduction in other fitness traits such as fecundity (Rodríguez-Prieto et al. 2010).

We recognise some caveats in interpreting our results beyond our mesocosm experiment. Firstly, we used adult male *C. egeriae*, and when evaluating survivorship and population persistence there are often significant differences in survival between sexes and among age groups (Lindenmayer et al. 1993). Further, survival outside captivity is affected by other factors including competition (both interspecific and intraspecific), the presence of other predators, and resource availability, and each factor may act additively or non-additively (Doherty et al. 2015). However, the survival of male *C. egeriae* in the Christmas Island captive breeding facility is the highest amongst age cohorts and between sexes (Parks Australia, unpublished data), and males had high survival rate (~ 88% over three months) in a population reintroduced to a 2600 m^2 exclosure in 2018 where centipedes were excluded (JP Emery, unpublished data). As this is a similar time frame to our mesocosm experiment, translating our mesocosm survival rates (30-44% lower than the control) to the larger exclosure suggests that relative survival would be between 49-62% if centipedes had not been excluded [88-(88*.44) or 88-(88*.3)]. Undoubtedly this would greatly reduce the viability of a reintroduced *C. egeriae* population, without taking into account the potential for indirect effects associated with lower body condition.

Conclusion

Using outdoor mesocosms and DNA barcoding, we have built a case that centipedes are important reptile predators and are capable of reducing survival of *C. egeriae*, at least within small exclosures. To our knowledge this is the first study to show that scolopendrid centipedes are potential drivers of reptile declines, and more broadly, our study highlights the importance of considering all potential threats prior to reintroduction, even when there is little prior evidence implicating them. On Christmas Island, explicitly stating the uncertainty around *S. subspinipes* as a threat to *C. egeriae* could have led to specifically focusing on centipede-skink interactions in the 2017 reintroduction, reducing a potential need for retrospective mesocosm experiments, such as the one performed here.

The evidence collected from this study indicates that the threats posed to *C. egeriae* by *S. subspinipes* and its presumed major threat *L. capucinus* are different; and as such potential conservation management strategies going forward. The wolf snake is a reptile specialist and direct predator of lizards (including *C. egeriae*), whereas we found that *S. subspinipes* acts as an intraguild competitor whereby its reduces survival directly by opportunistic predation and/or indirectly by lowering body condition potentially caused by altering *C. egeriae* behaviour (eg. foraging or exclusion from favourable habitat). Whilst these effects were important, they are likely to take more time to manifest themselves compared to *L. capucinus*. Indeed, the inadvertent intrusion of a *L. capucinus* into a control exclosure resulted in the death of seven skinks in <2 days, which was the same loss as at low centipede densities in one mesocosm exclosure over 12 weeks highlights this. However, both threats have the potential to affect reintroduction success.

Wolf snake control within the landscape is impossible (eg. control of Brown tree snakes *Boiga irregularis* in Guam), so for the foreseeable future any reintroductions of *C. egeriae* are going to occur in large exclosures where *L. capucinus* can be excluded. To date; large erected aluminium fences (> 1m) have proved effective in keeping out *L. capucinus*, however not *S. subspinipes*. Manual removal of centipedes by spot lighting and pitfall lines after the exclosure is erected requires a substantial amount of time and effort and is unlikely to guarantee the removal of all centipedes as they are very cryptic (J emery pers observations). Insecticide within exclosures prior to *C. egeriae* introduction is possible, but poses additional risks as to our knowledge they are no insecticides that or poison baits that can be used to target centipedes and would result in reduced food availability for *C. egeriae*. If invertebrate biomass would be restored naturally (allow time for invertebrates to restore) or be manually replenished, then perhaps careful use of insecticide prior to reintroduction could be used. The latter is currently being trialled in a second reintroduction attempt of *C. egeriae* on Christmas Island.

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Compliance with ethical standards

The research was approved by the Taronga Conservation Society Australia: AEC protocol 4b/12/17 and by Parks Australia (permit number CINP_2017_07)The authors declare they have no conflict of interest.

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Appendix S1: Supporting figure and tables

Survival of an Extinct in the Wild skink from Christmas Island is reduced by an invasive centipede: implications for future reintroductions

Biological Invasions

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Table S1: Results from Tukey HSD tests with Bonferroni correction comparing the body condition of *C. egeriae* between the control, low density and high-density centipede treatments between the start and end of the experiment. Significant differences are shown in bold with statistical significance set at P <0.05.

Tukey HSD with Bonferroni correction	Estimate	Standard error	Z value	Pr(>Z)
Control start- Low density start	-0.014	0.014	-0.982	0.922
Control start- High density start	-0.006	0.015	-0.446	0.997
Low density start, High density start	0.007	0.016	0.475	0.996
Control start, control end	-0.000	0.012	-0.022	1.000
Control end, Low density end	**-0.052**	**0.014**	**-3.571**	**0.004**
Control end, High density end	**-0.055**	**0.015**	**-3.595**	**0.004**
Low density end, High density end	-0.003	0.016	-0.189	0.999
Low density start, Low density end	**0.038**	**0.013**	**2.867**	**0.046**
High density start, High density end	**0.048**	**0.014**	**3.280**	**0.012**

Table S2 Results from a landscape analyses of the diet of introduced giant centipedes (*Scolependra subspinipes*) on Christmas Island to investigate whether centipedes consume reptiles in the wild.

Sampling location	Collection date	Description of gut contents	DNA extraction date	PCR notes	Species amplified
Phosphate Hill	23/04/2019	Something in upper stomach, brown, green stringy	11/06/2019	Poor sequence	
Phosphate Hill	23/04/2019	Something brown upper stomach, sandy middle	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Green stringy material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Lots of brown material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Green stringy material, little sandy material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Sandy and green stringy material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Sandy and green stringy material	11/06/2019	Amplified	*Homo sapiens* (98.58%)
Phosphate Hill	23/04/2019	Sandy and green stringy material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Sandy and green stringy material	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Green stringy stuff	11/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Little brown material, mostly green/sandy material/eggs	13/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Little brown material, mostly green/sandy material/eggs	13/06/2019	Failed to amplify	
Phosphate Hill	23/04/2019	Lots of brown material, recently eaten, eggs	13/06/2019	Failed to amplify	

Phosphate Hill	23/04/2019	Green stringy material, eggs, little bit of brown material	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Lots of mushy sandy material	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Lots of gritty green and brown material	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Lots of brown material, looks like eaten centipede (centipede scales)	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Lots of green stringy material	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Little bit of brown material in upper stomach, middle dark material and looks like recently eaten	13/06/2019	Failed to amplify	
Phosphate Hill	24/04/2019	Mushy green material, brown like shells in middle stomach that looks like insect	13/06/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Smaller specimen, blue-green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Smaller specimen, light green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, pale brown	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, pale blue/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	

Pink House	11/3/2019	Stringy, fibrous, brown/green	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green, yellowy liquid	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, brown/green, mid-sized	28/3/2019	Failed to amplify	
Pink House	11/3/2019	Stringy, fibrous, dark brown/green	28/3/2019	Failed to amplify	
Pink House	20/3/2019	Pale green, stringy content	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Pale green, stringy content, red sticky bits	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Small specimen, green-blue content	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Pale yellow-brown	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Pale green/blue, stringy	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Pale green	4/4/2019	Failed to amplify	
Pink House	20/3/2019	Pale green, stringy content	4/4/2019	Failed to amplify	
Pink House	22/04/2019	Not much in stomach- stringy	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Not much in stomach- stringy	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Lots of sandy material	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Not much, stringy	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Lots of brown material, upper gut	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Not much, stringy	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Not much, stringy	22/04/2019	Failed to amplify	

Pink House	22/04/2019	Not much, stringy	22/04/2019	Failed to amplify	
Pink House	22/04/2019	Lots of brown material in stomach	22/04/2019	Amplified	Pycnosceius sp (99.48)
Pink House	22/04/2019	Not much, stringy	22/04/2019	Failed to amplify	
South Point	24/04/2019	Not a lot, little bit of brown material	18/06/2019	Failed to amplify	
South Point	24/04/2019	Lots of brown in upper stomach	18/06/2019	Failed to amplify	
South Point	24/04/2019	Not a lot, some sandy material	18/06/2019	Failed to amplify	
South Point	24/04/2019	Not a lot, some sandy material	18/06/2019	Failed to amplify	
South Point	24/04/2019	Bit of brown and sandy material	18/06/2019	Failed to amplify	
South Point	24/04/2019	Little bit of material in upper stomach	18/06/2019	Failed to amplify	
South Point	24/04/2019	Lots of brown material, pungent	18/06/2019	Failed to amplify	
South Point	24/04/2019	Lots of brown material in upper and middle track	18/06/2019	Failed to amplify	
South Point	24/04/2019	Lots of brown material, eggs	18/06/2019	Amplified	*Citrobacter werkmanii* strain (96.24%)
South Point	24/04/2019	Lots in upper stomach, brown material	18/06/2019	Failed to amplify	
South Point	24/04/2019	Not a lot of material	19/06/2019	Amplified	*Hemidactylus frenatus* (99.07%)
South Point	24/04/2019	Not a lot of material	19/06/2019	Failed to amplify	
South Point	24/04/2019	Lots of material in upper and middle stomach	19/06/2019	Amplified	*Scolopendra subspinipes* (92.52%)

South Point	24/04/2019	Lots of material in upper and middle stomach	19/06/2019	Amplified	*Periplaneta americana* (99.51%)
South Point	25/04/2019	Lots of material in upper and middle stomach	19/06/2019	Failed to amplify	
South Point	25/04/2019	Not a lot of material	19/06/2019	Failed to amplify	
South Point	25/04/2019	Lots of brown material in upper stomach	19/06/2019	Failed to amplify	
South Point	25/04/2019	Lots of brown material in upper stomach	19/06/2019	Failed to amplify	
South Point	25/04/2019	Not a lot of material	19/06/2019	Failed to amplify	

Figure S1 Example of a Giant centipede dissection to extract gut contents for DNA extraction. Photo credit: Yvette Hitchen.

Figure S2 A giant centipede (*Scolependra subspinipes*) consuming a juvenile wolf snake (*Lycodon capucinus*) on Christmas Island near the research station in the islands centre. Photo credit: JP Emery.