Life-history comparisons between the native range and an invasive island population of a colubrid snake

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Abstract Invasive snakes can lead to the rapid extinction of endemic vertebrates on insular ecosystems, usually because snakes are an efficient and novel predator. There have been no successful (i.e. complete) eradications to date of invasive snakes on islands. In this study we assess a novel invasion on Gran Canaria in the Canary Islands. The invader, the California king snake (*Lampropeltis californiae*), arrived from California via several generations in the pet trade. King snakes are captive bred for various phenotypes, and first were detected in the wild on Gran Canaria in the 1990s. Because very little natural history data exist from within their native range, we focused on developing datasets from native habitats to compare with similar data for the introduced snakes in the Canary Islands. We found that most aspects of the snake's life history have not changed since invasion, except that there appears to be a lower level of juvenile recruitment along with an increase in the length and body mass of adult snakes on Gran Canaria. We identified environmental parameters for when capture/trapping could be completed to reduce effort and maximize success. Additionally, we show different trap success on the various life stages of the snakes. Risk assessments could be required prior to permitting pet trade or allowing captive bred snakes into regions where they are not native.

Keywords: California, Canary Islands, detection, *Lampropeltis californiae*, morphology, pet trade

INTRODUCTION

Invasive species on islands drive high levels of extinction globally (Jones, et al., 2016). No examples of eradications of invasive snakes are known from islands (DIISE, 2015). Unlike mammals, where successful methods of eradication exist and great conservation success has been achieved (Jones, et al., 2016), snakes continue to invade cryptically, often with dramatic impacts (Willson, 2017). The accidental introduction of the brown tree snake (*Boiga irregularis*) to Guam has led to the loss of almost all the bird and much of the lizard diversity of the island (Rodda & Savidge, 2007). When this invasion was recognised, major changes in the biodiversity of the island had already taken place (Savidge, 1987; Rodda & Fritts, 1992). The brown tree snake, like several other snake invaders, is poorly known biologically in its native range, and thus any biological changes to the invader during the invasion cannot be easily detected (Rodda & Savidge, 2007).

One of the main pathways for introductions of reptiles is the pet trade, which is linked to many invasive species issues globally (Krysko, et al., 2016; McFadden, et al., 2017). Little is known about the effects of having captive raised snakes released into the wild. In addition, there is little information regarding the biology (morphology, reproduction, behaviour, etc.) of non-native snakes when they are introduced to islands. California king snakes (*Lampropeltis californiae*; CKS) were originally caught and bred for the pet trade, and many are from San Diego County, California. The CKS has been a major element of the international pet trade since the 1980s (Hubbs, 2009). They have been artificially selected for certain coloration and pattern phenotypes in captivity, including albino, striped, and banded. They were originally imported to the Canary Islands as well as many other places to be bred in captivity and sold as pets. They were released accidentally or escaped into the wild and have subsequently been on the Canary Islands as an invasive species since the late 1990s, adversely affecting the native wildlife and currently occurring in two discrete populations (Cabrera- Pérez, et al., 2012; Monzón-Arguello, et al., 2015). There have been perceived morphological changes in the snakes, and their expansion could be exponential as they irrupt without competition or predation (Cabrera- Pérez, et al., 2012). When trying to compare the invasive snakes with those in their natural habitat, we found that there is little known of the life history of CKS from their native range, especially southern California, and most references cite only the regional field guides, without much primary literature to support this information. Recently for the first time, movement data, which is very useful for understanding the invasion process, has been published for this species (Anguiano & Diffendorfer, 2015).

The Canary Islands are isolated oceanic islands off the coast of West Africa. They have low biodiversity, but high endemism, with some species that have important adaptations (Rando, et al., 2008; Fernandez-Palacios, et al., 2011). These include endemic lizards, of which the lacertids (*Gallotia* spp.) are herbivorous and are important seed dispersers (Valido, et al., 2003). The islands contain no native species of snake. On the Canary Islands, the invasive CKS have become a major predator for all of the native lizard species and are therefore threatening this island's biodiversity (Cabrera- Pérez, et al., 2012; Monzón-Arguello, et al., 2015). As with other invasive species, CKS on the Canaries have gone after the most abundant prey first, so they have been preying on the native lizards primarily and then secondarily on invasive small mammals. Birds do not make up a large part of their diet yet (Cabrera- Pérez, et al., 2012), but there are endangered birds present that might become snake prey over time as other prey become exhausted (Carrascal, et al., 2017). In addition, there are limited control efforts over the spread of the snakes on the Canary Islands and potentially all of Macaronesia (Azores, Madiera, and Cape Verde Islands). This could potentially threaten the biodiversity of the entire area if they are not eradicated. The snakes appear to have no predators in the Canary Islands.

How snakes invade and the dynamics of the early invasion process, in particular the changes to their phenology, phenotype, and reproduction during the irruption phase, have not been previously studied. Most

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snake invasions are more mature before study. The Canary Islands offer a unique opportunity to study these issues as it is a novel environment for snakes, and the snake invading is a species from the mainland of North America where numerous museum specimens and other field data are available. Because CKS are relatively well known, developing detailed life history parameters should be more straightforward than for other poorly known tropical species of snakes, such as brown tree snakes or Burmese pythons (*Python bivittatus*). The CKS is widespread from southern Oregon, south to the tip of the Baja Peninsula in Mexico, and east to mid-Nevada, southern Utah and the majority of Arizona; throughout its range it occurs naturally with many other snake species. The goal of this paper is to use museum and field datasets to resolve critical life history traits for this species, which can help to interpret CKS invasion dynamics within the Canary Islands and may be useful for optimising eradication/control techniques and efforts (i.e. trapping timing and placement).

MATERIALS AND METHODS

To document potential biological changes in the snake's natural history during the invasion process, we sampled CKS in their native range across 22.8°N to 40°N and made comparisons with the invasive snakes. Most samples were from southern California. Data were collected from 1,538 museum specimens (California Academy of Sciences, Natural History Museum of Los Angeles, San Diego Natural History Museum, University of California, Santa Barbara Cheadle Center for Biodiversity & Ecological Restoration) and augmented with records from wild caught CKS delivered to the San Diego Zoo (electronic supplementary materials). Additionally, we used southern California field data from 778 CKS captured between 1995 and 2012 in pit-fall and snake trap arrays by USGS (methods from Fisher, et al., 2008; electronic supplementary materials). These data from southern California included all snake species caught in these traps (n=4,708) and were used to assess the capture rate ranking of the CKS species compared to the other 24 native snake species for which we had contemporary capture data from these traps. We also obtained two different field datasets from the native range for CKS. One was a citizen science dataset from HerpMapper (HerpMapper, 2017) which had 1,299 records for the snakes from which we used capture/detection dates. The second was an unpublished dataset from Brian Hinds (BH) which represented 717 detections with associated observation dates. We compared these four native-range datasets to the Canary Island dataset, which encompassed 668 snakes (hand and trap caught from 2012 to 2014) on Gran Canaria Island (28°N), all from the western of the two populations on the island.

The museum specimens of CKS were measured for snout-vent length (SVL) and tail length using measuring tapes. Adults were defined as >600 mm in SVL (Hubbs, 2009). Sex was determined either through dissection or tail length and width. Some snakes were found dead on road (DOR) and the sex could not be determined. Many of the older museum specimens were missing reproductive systems; therefore, only a subset of data was available from these. Specimens missing their organs were used for length comparisons, but not for sex or reproductive status. Dorsal patterning and evidence of tail breaks were recorded and tail breaks were documented photographically.

The pit-fall and snake trap samples were collected from the wild in the native range in southern California primarily from south of Los Angeles to the Mexican border. Individuals were sexed, weighed, measured, and released. Data for colour pattern and tail status were lacking for most specimens. We also analysed the total capture for all snake species from these traps to look at the relative capture success of CKS compared to all other snakes for which we had data in the native snake community in California. To further look at activity phenology within their native range, we used data from HerpMapper (2017) and BH to assess observations by month as a recent sample to compare against our older native range data sources. Many of these records are from active searches under artificial cover (AC), and others are from night driving. Both of these are techniques that might have high seasonal biases in detections. This is because snakes under AC could be non-active, but using the cover to environmentally thermoregulate; whereas snakes detected on roads at night would be animals that are actively moving. These behaviours would change seasonally based on climatic conditions.

Samples from Gran Canaria Island were collected by hand or by trap then euthanized and frozen for later dissection. Sex, weight, SVL, tail breaks or scarring, were recorded.

Comparisons were made among these five study population samples for the relevant metrics and controlled for differences in sampling types. For example, the museum series is similar to the invasive population in that animals were collected by hand, trap, or opportunistically, but no comparison of weight could be completed, as the preserved weight of the museum snakes is not comparable to live weight. In contrast, live weight and length of the pit-fall and snake trap series could be compared to the invasive series, but reproductive states could not be compared, as these data were not available for the trapped and released snakes from their native range. These trap records are from snakes that are actively foraging, as they have to be moving in the landscape to encounter a trap. The last two field data sets (HerpMapper and BH) could only be used for detection/capture date comparisons with the other data sets, as they involved primarily active searches, especially under artificial cover, and not necessarily surface-active snakes. They also lacked length/weight measurements for individual snakes. We used means of the top decile to highlight comparisons between populations.

RESULTS

Snake community structure in California

Within a community of 25 native snake species captured via pit-fall and snake trap arrays in southern California, CKS was found to be the second most abundant species following the California whipsnake (*Masticophis lateralis*) and represented approximately 17% of the 4,708 captures across these species (Fig. 1). Snakes in this dataset were captured when snakes entered traps; no active searching for snakes took place. Thus, these records would be biased towards species more frequently moving over the landscape. These data indicate that within its native range the CKS is one of the most abundant snakes captured with this technique.

Trap success by size class

Using the USGS pit-fall and snake trap dataset, we were able to look at the effect of trap type on capture success by snake length, as a proxy for age (Fig. 2). We found that pit-fall trap buckets (18.9 L) buried in the ground were most successful, capturing snakes less than 500 mm in length. Wire-mesh snake traps had the greatest success with snakes exceeding 500 mm in length. Additionally, there was no trend in body size of CKS incidentally observed while conducting sampling using these traps.

Snake detections by month

We plotted the monthly detections/captures across five different datasets to assess variability across months.

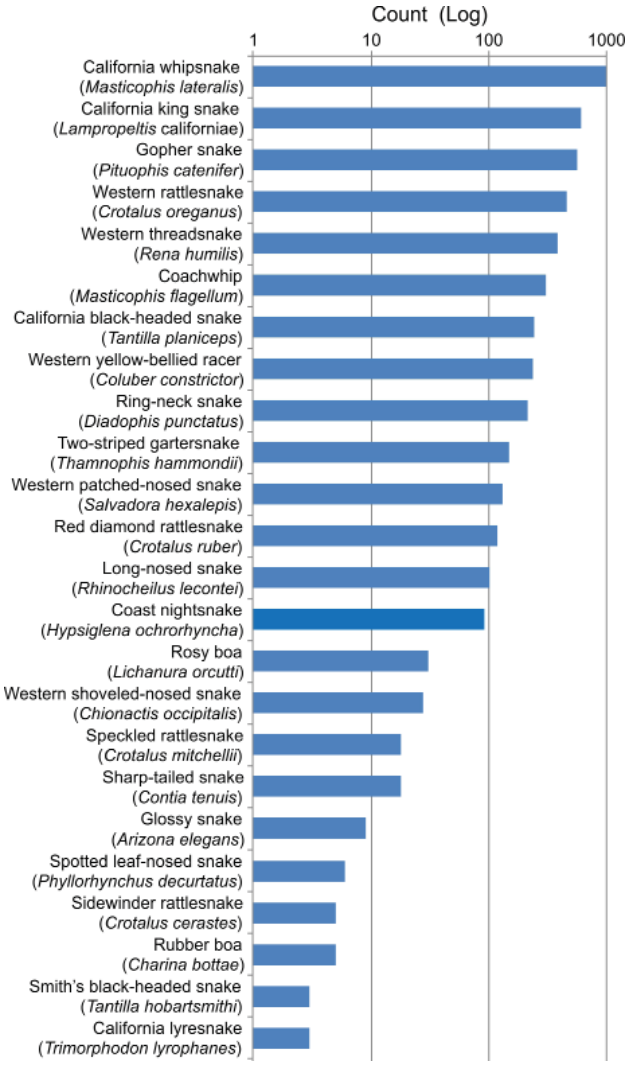


Fig. 1 All snake captures in southern California from the USGS pit-fall and snake trap study (n=4,708). *Lampropeltis californiae* is the second most common snake species captured.

Overall, monthly detections across datasets were highest between March and June, with the various peaks being due to variance in detection technique used. The citizen science (HerpMapper) and BH datasets, where they were actively searching for snakes, had peaks between March and April.

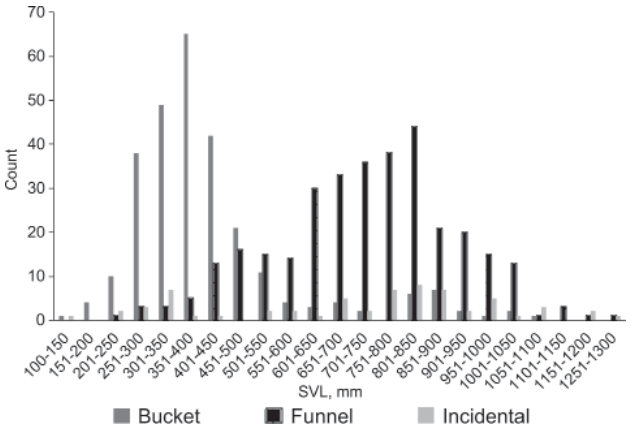


Fig. 2 Body size of *Lampropeltis californiae* by trap type for southern California. This figure has 50 mm breaks in size groups and highlights the different capture success of the two different trap types (pit-fall versus snake trap).

The museum and Canary Island datasets both had their peaks in the month of May, and these were identified using a variety of detection types, including active searching and traps. Finally, the pit-fall and snake trap dataset, with its passive traps for detections, had its peak in June. This last dataset was the only method based solely on active snakes. From August to January there was <10% per month of total snake detections across all datasets and from November to January there was <5% per month of total snake detections (Fig. 3).

Sex ratios, body size, and tail injury comparisons between California and the Canary Islands

We were able to make more detailed comparisons across three datasets, two from the native range (museum and pit-fall/snake trap) and the Canary Islands (Table 1). We found that there was a greater proportion of adults captured in the Canary Islands compared to the native range pit-fall/snake trap captures or museum specimens. There was no difference between the two native populations in the percent of juveniles, with about 49% of the samples representing juveniles; in contrast, only 22% of the invasive snakes were juveniles (Table 1). Thus, there were 2.3 times more juveniles detected in the native range than in the Canary Islands regardless of dataset used (museum or pit-fall/snake trap). For the pit-fall/snake trap and Canary Island captures, we compared the frequency by 50 mm size classes to see where this juvenile/adult bias was

Table 1 Morphological comparisons between native and invasive populations of *Lampropeltis californiae*. Differences between values of the invasive versus native populations were calculated as percentages to illustrate variance from 100%. Values in parentheses in table are sample sizes for top deciles.

	Gran Canaria Island	Southern California field	Museum specimens	Difference Gran Canaria Is. vs California
Total	668	780[a]	1,538[b]	
Total # adults (>600mm)	519	335	769	
Percent non-adults	21.9	49.6	48.4	0.44
Mean SVL (top decile) (mm)	1,071.7 (n=52)	1,069.1 (n=33)	1,032.2 (n=77)	1.00
Largest SVL (mm)	1,474	1,290	1197	1.14
Mean weight (top decile) (g)	412.8 (n=52)	334.9 (n=28)	-	1.23
Weight largest (g)	770.3	570	-	1.35
Tail break frequency	16.64	-	6.72	2.48

[a]670 with measurements that could be used
[b] except non-wild caught ~70 individuals

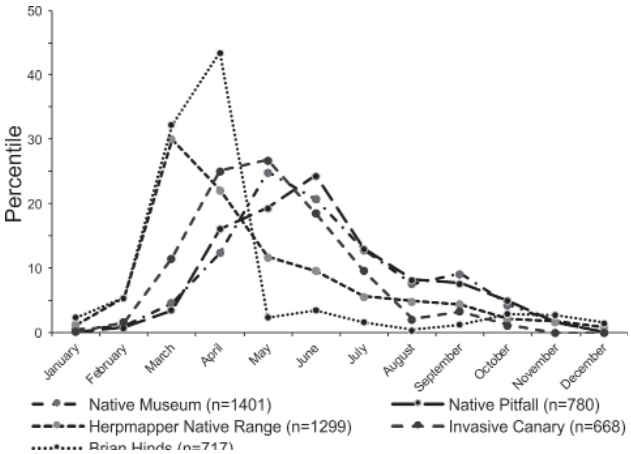


Fig. 3 Monthly percent of total detections of *Lampropeltis californiae* across the four datasets from the native range and the dataset from the invasive snakes on Gran Canaria.

the greatest. We found the native range had only one size class (351–400 mm) occurring in greater than 10% of the sample, whereas four consecutive size classes (701–900 mm) occur in greater than 10% each of the sample from the Canary Island. Thus, our data from the native range had a bimodal distribution between juvenile and adult captures compared to the Canary Island data (Fig. 4).

The invasive group of CKS did not have greater mean of the top decile compared to snakes in their native range (Table 1). The longest snake in the Canary Islands was 1,474 mm, 14% longer than the longest snake in the California sample (1,290 mm) and 21% longer than the next longest snake in the Canary Islands (1,217 mm). The invasive snakes had 23% greater average mass within the top decile compared to the USGS pit-fall/snake trap captures (Table 1). The heaviest snake in the Canary Islands was 770 g, 35% greater than the heaviest snake within the California sample (570 g).

One of the natural history traits we looked at was the frequency of tail breaks or scarring, as a proxy for predation risk. In the museum dataset, 6.7% of the snakes had broken tails, whereas 16.6% of the CKS on the Canary Islands had broken tails (2.48 times higher frequency of tail breaks compared with snakes in the native range) (Table 1). There was no noticeable association between tail break and colour pattern for either of these datasets.

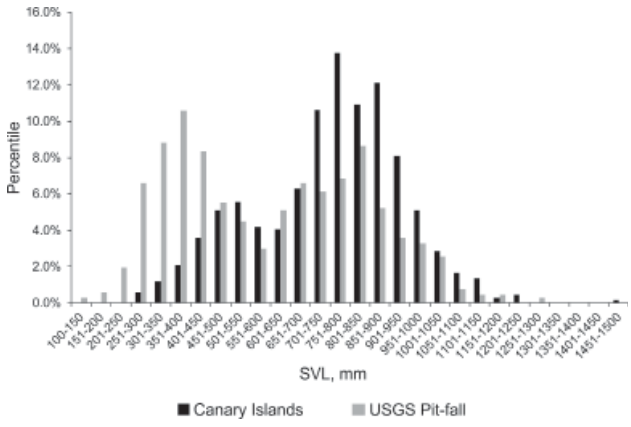


Fig. 4 Comparison of *Lampropeltis californiae* by percentage of size class between the USGS pit-fall snake trap dataset and the Canary Islands dataset. This graph highlights the lack of smaller size classes in the Canary Islands and the greater frequency of the larger size classes.

DISCUSSION

Since 2009, field work on control and eradication of the invasive CKS in the Canary Islands has resulted in the removal of over 4,500 snakes from the invaded habitats (<www.lifelampropeltis.com>). There was one population on Gran Canaria when the snakes were discovered, but now there are at least three populations on the island, indicating they are still spreading even with the control activities. We were able to compare various life history traits for native range CKS to the invasive range in the Canary Islands. Overall, we compiled records for 4,404 CKS for various aspects of their biology from the native range across four different data sources. These data were compared to 668 records for snakes from the Canary Islands. Below, we make comparisons on their biology and then suggestions on how they might be controlled or managed as an invasive species.

Snake community structure in California

We found that CKS was the second most captured species across the 25 species detected by the USGS pit-fall and snake trap sampling in California (Fig. 1). This sampling is based on the species actively entering the traps, and since the traps are passive, they only detect snakes when the snakes are active. Klauber (1931), using primarily road-riding for eight years (1923–1930), found that CKS were the third most detected snake species in his sample. They comprised 14% of the total record of 6,231 snakes across 24 species he detected for San Diego County, following the gopher snake (*Pituophis catenifer*) and the two-striped garter snake (*Thamnophis hammondii*). As our data were collected 70 years after his, this difference could represent actual changes in the abundance of the snakes due to habitat shifts over time, but it most likely represents the different sampling techniques. Both studies found CKS to be in the top three most captured snakes in the region across habitat types, indicating that even in a diverse snake community, CKS is one of the dominant species. This suggests that as an invasive species, it possibly could be successful even in regions with native snake communities, such as mainland Europe. Within the Canary Islands, it appears to have the ability to broadly utilise the habitats present on these islands.

Trap success by size class and lack of juvenile snakes in the Canary Islands

It was a quite striking find that juveniles are not detected in high numbers in the Canary Islands yet the snake is clearly expanding its range every year. This is very difficult to explain. The juvenile detection could be affected by several factors, including trapping technique, foraging distances and activity, growth rate, etc., but with the data we have to date we cannot determine the source of this issue. We know that sampling techniques to detect snakes vary in their effectiveness. We found a distinctive pattern of smaller snakes (<500 mm) being detected primarily by bucket traps (Fig. 2). This indicated there was a size bias in the sampling, with the buckets being necessary to capture the smaller snakes (<500 mm) and the mesh wire snake traps having greater success with the larger snakes (>500 mm) (Fig. 2). In the Canary Islands bucket traps are not being used (Cabrera- Pérez, et al., 2012; Monzón-Arguello, et al., 2015), and this could possibly explain the lack of juveniles being collected in the invasive range (Table 1). However, the museum specimens from animals captured in the wild in California include juvenile snakes, suggesting their absence could be due to something implicit in the Canary Islands. It could be there is some increased predation within the Canary Islands targeting juveniles, but if that was the case, the population might not be expanding as rapidly as it appears to be spreading.

It is likely there is a greater abundance of naïve prey in the Canary Islands reducing the need for juvenile snakes to move long distances to forage, thus limiting their exposure for detection or as prey. Abundant food resources might also increase their growth rate so that detecting individuals while they are still juveniles would be more difficult. When prey presence in captured snakes was evaluated for 270 individuals in the Canary Islands, 36% of these snakes had at least one prey item in their digestive tract (Monzón-Arguello, et al., 2015). In contrast, within their native range, a recently published study found only about 8% of the snakes assessed contained prey items in their digestive tract (Wiseman, et al., 2019). This suggests that the invasive snakes are finding prey at four times the rate of snakes within their native range, which could be a proxy for increased prey abundance in the Canary Islands.

Another possible explanation for lower detection rates of juveniles might be their activity levels compared to adults. Juveniles might only be active when foraging and under cover items between foraging bouts, while adults are active while foraging and also when searching for mates for reproduction, thus even though foraging exposure might be reduced for adults in the Canary Islands, they are still exposed for capture during mating season. Overall this could result in the lower detection of juveniles in the invasive range versus the native range, because the high food availability which could lead to rapid growth rate in the Canary Islands might limit detection probability (Pike, et al., 2008).

Snake detections by month

The effectiveness of detection tools varied with the time of year. Active searches under artificial cover (HerpMapper and BH) were more effective early in the year (March and April) before snakes were fully active as they used cover to thermoregulate (Fig. 3). We found that pit-fall and snake traps which are dependent on active snakes to enter the traps were more effective in May and June. Overall, focused field effort with various sampling techniques from March to July would maximise the detection success for CKS versus other months of the year. November, December, and January had the lowest detection rates across all five datasets, indicating that lowering field efforts during that period of time would be justified.

Body size and tail injury comparisons between California and the Canary Islands

We found no difference in mean SVL of the top decile between snakes in the invasive range versus the native range (Table 1). This result indicates that there has not been a population shift to longer body size within the invasive range, although the maximum length of the largest snake in the Canary Islands was 14% longer than any California snake, and 21% longer than the next largest snake in the Canary Islands. This snake was an outlier, as it was greater than three standard deviations longer than the next longest snake in the Canary Islands. As this snake was the second heaviest snake we don't think this resulted from measurement or recording error. This lack of population shift in body size contrasts with what has been observed in other invasive species, some of which have been shown to grow larger within their invasive range (Rodda & Savidge, 2007), but this outlier snake indicates that this pattern could change as the age since invasion gets longer. We did find that the invasive snakes were 23% heavier for the top decile, and the heaviest invasive snake was 35% larger than the heaviest snake from the California trap study (Table 1). Increased weight in invasive snakes is most likely tied to their increased predation success on naïve prey.

We observed a higher percentage of tail breaks and scarring of the snakes in the Canary Islands. This could be due to incomplete predation from cats (*Felis catus*) or other predators, from defensive wounds of their prey (e.g. *Gallotia stehlini*), or possibly some other unknown process (Medina & Nogales, 2009; Santos, et al., 2011). Increased frequency of tail breaks does not necessarily affect body condition, for some species (Pleguezuelos, et al., 2013). Within the snakes' native range, predators may be more efficient resulting more often in complete predation, especially by raptors, leaving fewer individuals with incomplete predation scars.

Trophic cascades

A major concern with novel invasive species is that their removal of highly specialised endemic species with unique roles in the island ecosystems may result in unexpected downstream changes in biodiversity and in the landscape. The Canary Islands have a small but unique and ancient biodiversity that could be highly susceptible to perturbations from invasive species (Fernandez-Palacios, et al., 2011). One example is the endemic *Gallotia* lizard which is an essential part of the trophic cascade/feedback loop that enables the dispersal of trees on the Canary Islands (Valido, et al., 2003). The lizards eat the fruit off the trees and shrubs, effectively spreading the seeds of the endemic flora. The invasive CKS are consuming these lizards at a high rate, with complete removal of juveniles in areas where snakes have invaded, and over time will impede the proliferation of these native trees and shrubs, altering the biodiversity and native habitat (Cabrera- Pérez, et al., 2012; Monzón-Arguello, et al., 2015). Published examples of trophic cascades tied to snake invasions include the relationship between spiders and birds in Guam now caused by the snake irruption, and the dynamics of python and mid-sized mammals in Florida (Rogers, et al., 2012; Willson, 2017).

The CKS has a varied diet in its native range, including venomous snakes and juvenile birds (Morrison & Bolger, 2002). Because there are currently no birds recorded in the diet of the invasive snakes (Monzón-Arguello, et al., 2015), initiating intensive sampling of birds in areas with and without snakes to get an assessment of bird density and recruitment may be valuable. From the literature it seems clear that these snakes could target birds, many of which are endemic and some are currently endangered, as prey as they exhaust the lizards and rodents present (Morrison & Bolger, 2002; Carrascal, et al., 2017). This may also be valuable because the published diet data are five years old, and there might already be a change in their diet if there is a depletion of the main reptile and rodent prey.

If it looks like the snakes are going to achieve an island-wide distribution, then one approach is to pre-emptively safeguard various biologically intact areas around the island at different elevations. This approach could preserve biodiversity and create reservoirs of native animals in the event that the snake control/eradication fails.

Pet trade and captive breeding/selection and then released into wild

The invasive CKS has a unique history as it came from several generations of selection in captivity for various colour morphs and albinism, in addition to rapid growth and reproduction. Their release to the wild in the Canary Islands is concerning as this selection might provide some reproductive advantage versus the release of wild animals not subjected to selection in captivity. This trade of potential invasive species is concerning as more and more reptile species become bred for sale globally in the pet trade (Robinson, et al., 2015).

Considerations for snake management in the Canary Islands

Looking at CKS published movement data suggests that placing snake traps with sterile female snakes, or proxies,

less than every 150 m apart may be effective for snake management. This distance may be appropriate because the literature indicates that 98% of the males and 100% of the females radio-tracked do not move farther than this (Anguiano & Diffendorfer, 2015). Having a grid of traps in closer proximity across the snake-occupied parts of the island would be optimal for a snake removal programme.

There are large ecological and monetary costs to invasive animals, and costs of control and/or eradication often exceed the available funding. We suggest (1) stronger controls on snakes in the pet trade, (2) rapid response to prevent spread when detection first occurs, and (3) use of citizen science as a tool to detect early invasions.

CONCLUSION

Our results show that data from the native range of the snake can inform management and control for CKS within their invasive range. Also, we found that they flourish within a diverse native snake community; they have a high natural abundance, both historically (Klauber, 1931) and currently (Fig. 1).

We suggest that the continued use of a variety of traps in addition to active surveys be used to maximise detection of snakes of all sizes, especially within the months of March through July. We also suggest that managers consider protection of natural areas with critical biodiversity on Gran Canaria from invasion by CKS. In addition, managers may wish to consider increased controls to prevent spread to other areas in the Canary Islands.

There is no literature on where the CKS lays its eggs in its natural habitat or in the Canary Islands. A comparison of this and other reproductive characteristics may be important as well as a better understanding of how to detect juveniles within the invasive range. Greater support for risk assessments of species, within the pet trade in particular, could help to identify species of greatest concern which would help reduce these types of invasions elsewhere.

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