Reproductive plasticity as an advantage of snakes during island invasion

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Abstract
Most invasive species are not studied during their initial colonization of ecosystems to which they were recently introduced. Rather, research is typically performed after invasive species are well established and causing harm to the native biodiversity. Thus, novel adaptations of invasive species during their initial invasions are rarely identified. The California kingsnake (Lampropeltis californiae) is an invasive species in the Canary Islands that originated via escape or release from captive populations. Previous studies have demonstrated several morphological differences between the native California population and the invasive populations on Gran Canaria Island, particularly in regard to color pattern and body mass. In this study, we assessed the reproductive condition of 1,538 museum specimens of L. californiae from the native range, and 668 from Gran Canaria. Our results show that 57.1% of female L. californiae from Gran Canaria were gravid versus 13.4% of those from California. Moreover, average follicle size and clutch size were both greater in the invasive range (20.3 and 65%). In addition, there was a marked phenological shift in the invasive populations, among which follicles appeared 60 days sooner than in the native range. These differences can possibly be attributed to a larger body mass in the invasive populations, a lack of interspecific competition, origin from the pet trade, increased selection for large clutch sizes, and/or increased climate suitability in the invaded habitats. Overall, these reproductive and phenological attributes appear to constitute advantages for L. californiae during the invasion of this newly encountered ecosystem. The phenomenon of reproductive plasticity might generally be advantageous for rapid irruption of snakes on islands.

Keywords
California kingsnake, Canary Islands, clutch size, island invasive species, Lampropeltis californiae, pet trade, reproduction behavior
The most devastating predatory impacts of snakes have fallen not on domestic animals, however, but on wild prey that have been inadvertent victims of snakes transported by humans to new environments, especially islands. Because they do not fly or swim great distances in salt water, snakes (excluding sea snakes) are naturally absent from many remote islands, and small animals that live on such islands generally lack defense mechanisms to protect them from snake predation. When a snake is transplanted to such an island, catastrophic loss of native species may occur... (Rodda et al., 1999, p. 2)

First the snake must be stopped.
(Greene, 1997, p. 179)

1 | INTRODUCTION

Invasive species have long been documented as detrimental to native biodiversity (Kueffer & Daehler, 2009). Their effects are most apparent on islands, where they may have few to no competitors and can lack predators (Polo-Cavia, López, & Martín, 2008). This ecological release can open the door to the evolution of new physiological, behavioral, or morphological traits that can give invasive species an even greater ecological advantage over native species (Pusack, Benkwitt, Cure, & Kindinger, 2016). In addition, historically insular species often have not evolved alongside the nonnative species and thus have no natural defenses or behaviors against these invasive taxa. A disproportionate number of extinctions occur on islands, especially of critically endangered species, due in part to invasive species (Jones et al., 2016).

Research on the effects and extinctions caused by vertebrate island invasive species have disproportionately focused on mammals due to their global footprint from commensalism with humans and the availability of effective tools for mammal eradications from islands (Holmes et al., 2019; Spatz et al., 2017). The effects of other invasive vertebrate groups such as birds, reptiles, and amphibians on islands have only recently received any focus, with no current effective tools for large-scale island eradications (Blackburn, Delean, Pyšek, & Cassey, 2016; Kraus, 2009; Rodda, Fritts, Campbell, Dean-Bradley, Perry, & Qualls, 2002; Russell, Meyer, Holmes, & Pagad, 2017). This is best illustrated by looking at successful island eradications globally. The Database of Island Invasive Species Eradications (DIISE, 2021) indicates that 67 species have been eradicated from 965 islands, representing a total of 1,525 eradications. The majority are mammals, except for 17 species of birds eradicated 50 times from 40 islands. Only two species of amphibians have been eradicated from one island each, and within reptiles, one successful eradication of one lizard species is documented (DIISE, 2021).

Within reptiles, snake invasions have only recently been recognized as a potential widespread global threat for islands; historically, attention has been focused on a select few snake-invaded islands (e.g., Guam; Rodda, Sawai, Chiszar, & Tanaka, 1999). A decade ago, the list of globally invasive reptiles on islands included approximately 20 species of snakes and around 30 island invasions (not including Brahminy blindsnakes, Indotyphlops braminus), with the earliest record more than 7,000 years ago from the Mediterranean region (Kraus, 2009). Since then, the number of known snake invasions on islands has continued to increase, and to date, there are no completely successful snake eradication programs (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patino-Martínez, López-Jurado, & Rochester, 2019; Friebohle, Siers, & Montgomery, 2020; Montes, Feriche, Alaminos, & Pleguezuelos, 2020; O’Shea, Kusuma, & Kaiser, 2018; Reilly, Stubbs, Karin, Arida, Iskandar, & McGuire, 2019; Siers et al., 2020).

Snakes have many life history traits that make them extremely efficient predators with strong potential for collapsing and changing food webs in new locations (Greene, 1997; Rogers, Hille Ris Lambers, Miller, & Tewksbury, 2012). An example of this is the wolf snake (genus Lycodon), which has evolved specialized teeth for durophagy (the eating of hard scaled or shelled animals). This trait is specifically useful for feeding on skinks and has helped contribute to the collapse and/or extinction of as many as three species of skinks on Christmas Island in the Indian Ocean (Jackson & Fritts, 2004; Oliver, Blom, Cogger, Fisher, Richmond, & Woinarski, 2018; Smith et al., 2012). This invasive genus has continued to spread; at least two species of Lycodon (capucinus and subcinctus) have been found moving eastward across about 40 islands in the Indian Ocean, eastern Indonesia, and the Philippines (Kuch & McGuire, 2004; Leviton, 1965; Leviton, Siler, Weinell, & Brown, 2018; O’Shea, Kusuma, & Kaiser, 2018; Reilly, Stubbs, Karin, Arida, Iskandar, & McGuire, 2019). Further eastward, the island of Guam has one of the most famous cases of an invasive snake species, the brown tree snake (Boiga irregularis), which is driving food web shifts and the mass extinction of native biodiversity (Rogers, Hille Ris Lambers, Miller, & Tewksbury, 2012; Savidge, 1987; Siers et al., 2020).

There are many well-known examples in which reptiles have become established invasive species via human mediation, especially from the pet trade (Kraus, 2009).
Snakes are one of the most common animals in the herpetological and exotic pet trade, with a wide range of legal or illegal species sold (Bush, Baker, & MacDonald, 2014; Jensen, Auliya, Burgess, Aust, Pertoldi, & Strand, 2019; Kraus, 2009; Krysko, Burgess, Rochford, Gillette, CuevA, Enge, & Nielsen, 2011; Toland, Bando, Hamers, Cadenas, Laidlaw, Martinez-Silvestre, & van der Wielien, 2020). Given that certain traits and reproductive productivity are selected for by breeders, invasive animals sourced from the pet trade often have different genetics and reproductive traits than individuals sourced from wild populations (Monzón-Argüello et al., 2015; Willson, Dorcás, & Snow, 2011). With respect to snakes, human-mediated release from the pet trade is further compounded by snakes’ cryptic nature and ability to fill a variety of ecological niches; they are likely to go unnoticed by local wildlife officials and colonize new environments (McFadden, Topham, & Harlow, 2017; O’Shea, Kusuma, & Kaiser, 2018; Reilly, Stubbs, Karin, Arida, Iskandar, & McGuire, 2019; Willson, Dorcas, & Snow, 2011). There is a significant need for management efforts to focus on invasive snake species and help contain their detrimental effects on native species (Colvin, Fall, Fitzgerald, & Loope, 2005; Kraus, 2009; McFadden, Topham, & Harlow, 2017; Pitt, Vice, & Pitzler, 2005). Increased allelic diversity from outbreeding of wild animals captured in various parts of a species range can lead to changes such as increased fecundity and an increased range of climatic tolerance within invasive species (Card et al., 2018); these and other differences can give certain invasive species ecological advantages over native competitors and promote their establishment in new environments (Hunter, Johnson, Smith, Davis, Butterfield, Snow, & Hart, 2018; Jackson, Strubbe, Tollington, Pry-Jones, Matthysen, & Groombridge, 2015; Kotsakiozi et al., 2017). Studies comparing native ranges and non-native populations of invasive species can help identify aspects of their biology that inform management of these detrimental species.

The California Kingsnake, Lampropeltis californiae, is native to North America, ranging from California, southern Oregon, southwestern Nevada, Utah, Arizona, and extending into Baja California and mainland México (Hubbs, 2009). Lampropeltis californiae is a powerful constrictor and is considered one of the top reptilian predators in its native habitats. Lampropeltis californiae competes directly with other snakes in its native range for a wide variety of prey, including rodents and other small mammals, lizards, lizard eggs, snakes (including rattlesnakes), snake eggs, turtle eggs and hatchlings, frogs, salamanders, birds, bird eggs and chicks, and large invertebrates (Wiseman, Greene, Koo, & Long, 2019). Lampropeltis californiae has been documented as a new invasive species in the Canary Islands of Spain, an island ecosystem lacking native snake species (Cabrera-Pérez, Gallo-Barneto,Esteve, Patiño-Martínez, & López-Jurado, 2012; Fisher, Fisher, Alcaraz, Gallo-Barneto, Patiño-Martínez, López-Jurado, & Rochester, 2019; Monzón-Argüello et al., 2015). Unsurprisingly, L. californiae populations are having devastating effects on endemic species in the Canary Islands, especially the endemic bird and lizard species (Cabrera-Pérez, Gallo-Barneto, Esteve, Patiño-Martínez, & López-Jurado, 2012). Previous studies have shown that the two invasive L. californiae populations originated from the pet trade and subsequently escaped or were released onto Gran Canaria Island (Monzón-Argüello et al., 2015). Despite a similar body length, one population studied (Gáldar) had a heavier average body mass compared to those from the natural range in North America (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patiño-Martínez, López-Jurado, & Rochester, 2019). To date there have been over 9,000 snakes captured and removed from the wild on Gran Canaria Island, and the species is continuing to expand on the island (GesPlan, 2021). Recent modeling has shown high climatic suitability on Gran Canaria Island and the Canary Island archipelago overall, with increasing suitability under future predicted climatic conditions (Piquet et al., 2021).

Previously, there were no studies on the differences in reproductive biology between L. californiae populations in the Canary Islands and those in their native range. We hypothesize there are differences between the clutch sizes of native and invasive L. californiae females that can be associated with the combined influences of larger body mass, lack of interspecies competition, and increased selection for larger clutch sizes in these invasive populations as a direct result of originating from the pet trade (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patiño-Martínez, López-Jurado, & Rochester, 2019). Additionally, we hypothesize that clutch size could decrease on Gran Canaria due to a shift to a lower latitude, as has been shown in the literature for squamates (Meiri et al., 2020). This study was an unusual opportunity to document and compare differences in the reproductive biology of an invasive snake species originating from the pet trade during its initial colonization stages within an unfamiliar habitat with snakes from its native range. To do this we utilized native-range museum specimens and Canary Islands invasive specimens to look at L. californiae reproductive traits and population level differences between their native and invasive ranges. This study could help guide the development of more effective management efforts, inform risk assessments for the pet trade, provide insight to the reproductive biology of invasive species early in their invasion process, and further elucidate changes in snakes between native and invaded locations.
2 | MATERIALS AND METHODS

We examined 1,538 museum specimens of *L. californiae* from their native range (from 23°N to 40°N) within the United States and Mexico, and 668 specimens from the invasive Gáldar population on Gran Canaria Island, Canary Islands, Spain. We used museum specimens from a variety of institutions (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), since they have been shown to be a useful tool for understanding the range-wide natural history of snake reproduction without the need for new mortalities (Mullin & Seigel, 2009). Museum specimens were collected by various methods between 1886 and 2013. Specimens from Gáldar, Gran Canaria Island, were collected by hand or with traps from March 2012 through September 2014, then euthanized utilizing standard veterinary procedures as part of the eradication attempt and frozen for later dissection (Cabrera-Pérez, Gallo-Barneto, Esteve, Patiño-Martínez, & López-Jurado, 2012). We did not include individuals from Telde, the second known population in Gran Canaria due to lack of access to specimens. A flexible measuring tape was used to measure snout vent length (SVL), and adult snakes were defined as any specimen with a SVL > 600 mm, as no sexually mature snakes were found below 600 mm SVL (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patino-Martinez, Lopez-Jurado, & Rochester, 2019; Hubbs, 2009; Monzón-Argüello et al., 2015). Sex was determined either through dissection or tail length and width measurements (Fitch, 1960). Some museum specimens were too damaged to sex, or were missing their reproductive systems, so these were excluded from all analyses.

The female museum specimens identified as adults were examined for enlarged follicles by cutting above the reproductive zone on the ventral side or by internal examination if the abdomen was already opened. If enlarged follicles were visible (>7 mm length), the specimen was considered gravid. Follicle number and size were documented for gravid females for both the right and left side of the reproductive system. Follicle size was measured and recorded using a measuring tape along the longest and widest axis of each follicle, and follicle sizes for females were averaged using the length data for the longest axis measured. Dates when follicles were present were used to determine breeding phenology for the invaded population and the native range.

We calculated averages, top decile, top quartile, and standard deviations (SD) for both samples to compare: percentage of females gravid, snout vent length (SVL), enlarged follicle length, and clutch size as measured by the number of enlarged follicles as relevant. We also calculated coefficient of variations (CV) for SVL and clutch size (Shine & Seigel, 1996). To determine whether differences in the proportion of gravid females were significant between the two population ranges, we performed a chi-square test. Finally, we conducted analysis of variance (ANOVA) tests to determine whether (a) SVL differed by location, (b) follicle size differed by location, (c) clutch size varied by location and SVL, and (d) clutch size varied with follicle size, and if so, did the

![Figure 1](image-url)
relationship differ among population locations. All analyses were performed using SPSS (IBM Corp, 2020). Collection dates of the specimens were used to determine if there were any shifts in breeding phenology between the invasive population and the native range.

3 | RESULTS

3.1 | Gravid females

Out of the 1,538 specimens from the native range, 209 adult female *L. californicae* met the criteria for inclusion in the study as their reproductive tracts were intact and they exceeded 600 mm in SVL. A total of 252 adult females out of 668 specimens from the Canary Islands also met these criteria. In the Canary Islands 57.14% of the females (*n* = 144) were considered gravid, versus 13.4% of the females (*n* = 28) in the native range (*χ²* = 93.47, *df* = 1, *p* < .0001). These statistics taken together mean there was a 426.5% higher chance of finding females with enlarged follicles among snakes captured in the Canary Islands than among those in the native range (Figure 1 and Table 1). The sample size of 28 gravid snakes for the native range is a relatively large sample size compared to most snake female reproductive studies (*n* = 61; 47 studies with sample size ≤28) as reported by Shine and Seigel (1996) because obtaining wild gravid snakes is generally rare.

|                 | Canary Islands | Native range | % difference between Canary Island vs. native |
|-----------------|----------------|--------------|---------------------------------------------|
| # of adult females examined | 252            | 209          |                                             |
| # gravid        | 144            | 28           |                                             |
| % gravid        | 57.14          | 13.4         | 426.53                                      |
| Mean SVL        | 884.31         | 851.51       |                                             |
| Standard deviation SVL | 126.04        | 106.43       |                                             |
| CV of SVL       | 14.3           | 12.5         |                                             |
| Mean clutch size | 10.02          | 6.08         | 164.8                                       |
| Standard deviation of clutch size | 4.85         | 2.06         | 235.44                                      |
| CV of clutch size | 48.4           | 33.88        |                                             |
| Minimum # of enlarged follicles | 1             | 1            | 100                                         |
| Maximum # of enlarged follicles | 29            | 11           | 263.64                                      |
| Clutch size (top decile) | 21.14          | 9.33         | 226.58                                      |
| Clutch size (top quartile) | 16.9           | 8.14         | 207.62                                      |
| Mean max follicle length | 35.6           | 29.3         | 121.5                                       |
| Standard deviation of follicle length | 16.78         | 13.99        | 119.94                                      |
| Median max follicle length | 36.6           | 25.5         | 143.53                                      |

**TABLE 1** Comparisons between the native and invasive locations of *L. californicae*

![Figure 2](image.png) **FIGURE 2** The largest enlarged follicle found and recorded in female snakes, with the lines showing the mean maximum enlarged follicle length per snout vent length

3.2 | Gravid female snout-vent length

Overall, gravid *L. californicae* were of similar average SVL in both the Canary Islands and the native range. The average SVL of gravid females in the native range was 844.4 mm (*n* = 28, range = 678–1,104; SD 109.40; CV 12.5). The average SVL of gravid females from the Canary Islands was 884.3 mm (*n* = 144, range = 626–1,474; SD
There was no significant difference in average SVL between these locations ($F = 2.44, p = .120$). On average, there was a trend towards larger females having larger clutches in both locations (Figure 1) with a positive relationship between SVL and clutch size ($F = 19.08, p < .001$). Clutch sizes were significantly greater in the Canary Island sample versus that of the native range ($F = 13.12, p < .0001$). Follicle size increased as SVL increased ($F = 9.647, p = .002$), but this relationship did not differ significantly between locations ($F = 1.95, p = .164$; Figure 2).

### 3.3 Enlarged follicle size

Invasive *L. californiae* were found to have a mean maximum enlarged follicle length of 35.6 mm, versus the native range length of 29.6 mm (Table 1; $n = 25$ for native range as three gravid snakes had damaged follicles that could not be counted and measured). Therefore, follicle size within the invasive population was on average 20.3% greater than the follicle size of snakes in the native range. Increased follicle size was associated with both increased SVL of individual snakes ($F = 9.65, p = .002$) and location ($F = 1.95, p = .164$; Table 1).

### 3.4 Clutch size

*Lampropeltis californiae* from the Canary Islands also had a larger clutch size than snakes in the native range ($F = 15.8, p < .001$). The mean clutch size for invasive female snakes was 10.02 ($n = 144$) enlarged follicles, whereas the specimens from the native range had a mean clutch size of 6.08 ($n = 26$), an increase of 65% within the invasive range (Table 1). The maximum clutch size of invasive *L. californiae* was 29 follicles, and the maximum clutch size of native *L. californiae* was 11, an increase of 263%. In both locations, the minimum clutch size was 1 (Table 1 and Figure 1). The relationship between follicle size and clutch size was dependent upon location (interaction term $F = 4.41, p = .037$). In the invasive population, clutch size increased as follicle size decreased. Whereas in the native range, clutch size tended to increase as follicle size increased (Figure 3).

### 3.5 Phenology shift based on presence of enlarged follicles

There was a 2-month reproductive phenology shift in the invasive populations of *L. californiae*. Enlarged follicles appeared approximately 60 days earlier in the year in invasive *L. californiae* females than in the native range, and correspondingly, individuals stopped being gravid earlier in the year as well. More specifically, invasive *L. californiae* females started to develop enlarged follicles in March, whereas the native range females had enlarged follicles starting in May (Figure 4). Overall, in both the native range and the invasive population, there was a trend toward follicles being larger later in the year; smaller follicles found later in year may represent a second clutch (Figure 4). In the invasive Canary Island populations, no gravid females were found past July, whereas one native range female was found to be gravid in September.
This study identifies distinct reproductive differences between gravid *Lampropeltis californiae* females in the native range and those in the Canary Islands. A larger percentage of snakes were gravid in the invasive G/C19 aldar population in the Canary Islands than were gravid in the native range in North America. In addition, invasive gravid *L. californiae* from this population had larger clutch sizes and more enlarged follicles than snakes in the native range, even though SVL did not differ in the two locations. We hypothesize that the clutch size increase is due to invasive *L. californiae* having more available energy due to a heavier body mass (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patino-Martinez, López-Jurado, & Rochester, 2019), a lack of predators, an origination in the pet trade, and/or selection favoring increased reproductive output.

Within the two Canary Island populations examined by Monzón-Argüello et al. (2015), 39.4 and 34.8% of the snakes had prey in their gut year-round, whereas 91% of prey consumption in specimens from the native range was between April and September (Wiseman, Greene, Koo, & Long, 2019). For approximately 6 months out of the year in the native range, only 9% of snakes were found with food, which might prevent them from investing in a large second clutch or might delay their breeding time until the following spring (Sun, Shine, Zhao, & Tang, 2002; Wiseman, Greene, Koo, & Long, 2019). The literature shows that clutch size in snakes may increase with prey availability (Seigel & Ford, 1991), but variability (CV) in clutch size often remains the same (Shine & Seigel, 1996). Within the invasive population, there was a doubling of the SD of clutch size and an increase in CV, which is not consistent with the expectations, and contrasts what we found for SVL (Table 1) (Seigel & Ford, 1992; Shine & Seigel, 1996). It has been shown that lizards tend to have larger clutch sizes at higher latitudes, not lower ones (Meiri et al., 2020; Sinervo, 1990). We failed to find support for the hypothesis that lower latitudes would lead to lower clutch size. One reason for this could be the extreme climate suitability of Gran Canaria for this invasive species (Piquet et al., 2021).

Previous studies with wild caught *L. californiae* snakes from the Central Valley in California showed a mean clutch size of 6.3 (10 clutches; range 3–9 eggs) (Hansen, 1982). This is in line with the mean clutch size of 6.08 follicles that we found for native range snakes in our study (26 clutches; range 1–11). Data for captive, laboratory-bred females show mean clutch sizes of 6.3 follicles (13 clutches; range 2–9) and 8.4 follicles (8 clutches; range 6–10) (Zweifel, 1980). The invasive populations from our study had a mean clutch size of 10.02 follicles (144 clutches; range 1–29). We suggest that the increase in mean clutch size from native range to invasive population may be due in part to selection favoring increased reproductive output.
specimens from the native range (Figure 4). This type of shift is consistent with the “silver spoon” effect, as the hatchlings have a longer growth period by hatching earlier in the year (Madsen & Shine, 2000). When snakes have higher food availability during their first year, they maintain a faster growth rate through to adulthood (Madsen & Shine, 2000). We hypothesize that this, in addition to a lack of interspecific competitors, may further increase the population size in the Canary Islands, as snakes would reach reproductive size faster than those in the native range. This could also possibly explain the reduction in juvenile snakes documented in the invasive range compared with the native population (Fisher, Fisher, Alcaraz, Gallo-Barneto, Patino-Martínez, López-Jurado, & Rochester, 2019). Not only are the invasive populations of *L. californiae* able to breed and become gravid earlier in the year, but they can carry more enlarged follicles as well. There are serious negative implications for the endemic prey species in the Canary Islands through the continual increases in predation pressure. Furthermore, any increases in the *L. californiae* population on Gran Canaria Island would increase the possibility that these snakes disperse to other islands in the archipelago as well.

Increased allelic diversity due to multiple introductions from the pet trade may further help to explain the differences in the Canary Island and native snakes’ reproductive biology (Card et al., 2018; Montes, Feriche, Ruiz-Sueiro, Alaminos, & Pleguezuelos, 2020; Nania, Flecks, & Rodder, 2020). It is possible that *L. californiae* in the invasive population may have a heterozygosity advantage that results from range-wide genetic diversity (Monzón-Argüello et al., 2015), resulting in more reproductive plasticity than if they had come from one singular native locality (Ji & Wang, 2005). Furthermore, the two populations of *L. californiae* in the Canary Islands were shown to have different genetic histories and currently are isolated from each other geographically; if they merge, this could create even greater local genomic diversity within the zone of overlap, with unknown reproductive and environmental consequences (Monzón-Argüello et al., 2015). Recently, there has been a significant shift away from wild-caught reptiles to captive-bred and ranched individuals in the pet trade (Robinson, Griffiths, St. John, & Roberts, 2015). As a result, selection on the traits discussed above could be occurring in captivity, though we are not aware that this has been documented. It is generally difficult to determine what reproductive behaviors of specific invasive species may have been artificially selected by breeders, compared to environmental selection from their native distributions.

The reproductive plasticity exhibited by snakes is generally absent from other island invasive groups, such as mammals and birds, because of the need for natal care (Stearns, 1976) and many lizard lineages that have fixed clutch sizes (i.e., anoles, some agamids, and most geckos; Shine & Seigel, 1996). Thus, it is a novel challenge to manage snake invasions, as snakes may be better able to adjust to new conditions and environment (Rodda, Fritts, Campbell, Dean-Bradley, Perry, & Qualls, 1999). Knowledge about snakes’ baseline probability of establishment could inform selective trade restrictions on islands and perhaps reduce invasion potential (Kraus & Cravalho, 2001). This is important, since our work here suggests that invasive snakes sourced from the pet trade may have increased reproductive potential, and thus an increased rate of irruption.

Snakes become part of the global spread of invasive reptiles by stowing away and other human mediated processes (Capinha, Marcolin, & Reino, 2019). When tied with snakes’ cryptic behavior, their ability to survive for long times without food, and their ability to deal with broad environmental conditions, snakes’ ability to stow away greatly increases the risk that live snakes will arrive in new ecosystems through cargo and other inadvertent transit. The best data on this process comes from New Zealand, where over 50 species of snakes have arrived unintentionally over an 85-year period (Chapple, Knegtmans, Kikillus, & Van Winkel, 2016). This suggests that other suitable islands within the Canary Islands, as well as other locations in Macaronesia (e.g., Azores and Madeira) may be at risk of *L. californiae* invasion (Piquet et al., 2021). Ultimately, we hope this study further highlights snakes as invasive species that are under-appreciated as major threats to insular ecosystems (Kraus & Cravalho, 2001).

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
S. R. Fisher: Conceptualization; data collection; analysis; writing – editing and review. R. N. Fisher: Conceptualization; funding support; data collection; analysis; writing – editing and review. S. Alcaraz: Conceptualization; data collection; analysis; writing – editing and review. L. F. López-Jurado: Conceptualization; data collection; analysis; writing – editing and review. A. Cabrera-Pérez: Conceptualization; funding acquisition; project administration; review. M. Á. Cabrera-Pérez: Conceptualization; data collection; editing and review. L. F. López-Jurado: Conceptualization; funding acquisition; project administration; review. J. L. Grismer: Writing – editing and review.

DATA AVAILABILITY STATEMENT
Any researchers that request the data will have it made available to them.

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REFERENCES
Blackburn, T. M., Delean, S., Pyšek, P., & Cassey, P. (2016). On the Island biogeography of aliens: A global analysis of the richness of plant and bird species on oceanic islands. Global Ecology and Biogeography, 25, 859–868.

Bush, E. R., Baker, S. E., & MacDonald, D. W. (2014). Global trade in exotic pets 2006–2012. Conservation Biology, 28(3), 663–676.

Cabrera-Pérez, M. Á., Gallo-Barneto, R., Esteve, I., Patiño-Martínez, C., & López-Jurado, L. F. (2012). The management and control of the California kingsnake in Gran Canaria (Canary Islands): Project LIFE+ Lampropeltis. Aliens: The Invasive Species Bulletin, 32, 20–28.

Capinha, C., Marcolín, F., & Reino, L. (2019). Human-induced globalization of insular herpetofaunas. Global Ecology and Biogeography, 29, 1328–1349.

Card, D. C., Perry, B. W., Adams, R. H., Schield, D. R., Young, A. S., Andrew, A. L., ... Castoe, T. A. (2018). Novel ecological and climatic conditions drive rapid adaptation in invasive Florida Burmese pythons. Molecular Ecology, 27, 4744–4757.

Chapple, D. G., Knechtmans, J., Kikillus, H., & Van Winkel, D. (2016). Biosecurity of exotic reptiles and amphibians in New Zealand: Building upon Tony Whitaker’s legacy. Journal of the Royal Society of New Zealand, 46(1), 66–84.

Colvin, B. A., Fall, M. W., Fitzgerald, L. A., & Loope, L. L. (2005). Review of brown tree snake problems and control programs: Report of observations and recommendations (USDA National Wildlife Research Center – Staff Publications 631). Lincoln, NE: University of Nebraska–Lincoln.

DIISE. (2021). The database of island invasive species eradications, developed by Island Conservation, Coastal Conservation Action Laboratory UCSC, IUCN SSC Invasive Species Specialist Group, University of Auckland, and Landcare Research New Zealand. Retrieved from http://diise.islandconservation.org

Fisher, S. R., Fisher, R. N., Alcaraz, S. E., Gallo-Barneto, R., Patino-Martinez, C., López-Jurado, L. F., & Rochester, C. J. (2019). Life-history comparisons between the native range and an invasive Island population of a colubrid snake. In C. R. Veitch, M. N. Clout, J. C. Russell, & C. J. West (Eds.), Island Invasives 2017: Scaling up to meet the challenge. Proceedings of the International conference on island invasives 2017 (pp. 326–331). Gland, Switzerland: IUCN.

Fitch, H. S. (1960). Criteria for determining sex and breeding maturity in snakes. Herpetologica, 16, 49–51.

Friebohle, J., Siers, S. R., & Montgomery, C. E. (2020). Acetaminophen as an oral toxicant for invasive California kingsnakes (Lampropeltis californiae) on Gran Canaria, Canary Islands, Spain. Management of Biological Invasions, 11(1), 122–138.

GesPlan. (2021). Biological invasions in the Canary Islands, Canary Islands. Retrieved from invasionesbiologicas.blogspot.com

Greene, H. W. (1997). Snakes: The evolution of mystery in nature. Berkeley, CA: University of California Press.

Hansen GE. (1982). Life history of the California kingsnake (Lampropeltis getulus californiae) at a southern Sacramento Valley, California locale (MS thesis). California State University Sacramento, Sacramento, CA, 110 pp.

Holmes, N. D., Spatz, D. R., Oppel, S., Tershby, B., Croll, D. A., Keitt, B., ... Wegmann, A. (2019). Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. PLoS One, 14(3), e0212128.

Hubbs, B. (2009). Common kingsnakes: A natural history of Lampropeltis getula. Tempe, AZ: Tricolor Books.

Hunter, M. E., Johnson, N. A., Smith, B. J., Davis, M. C., Butterfield, J. S., Snow, R. W., & Hart, K. M. (2018). Cytonuclear discordance in the Florida Everglades invasive Burmese python (Python bivittatus) population reveals possible hybridization with the Indian python (P. molurus). Ecology and Evolution, 8(17), 9034–9047.

IBM Corp. (2020). IBM SPSS statistics for windows, version 27.0. Armonk, NY: Author.

Jackson, H., Strubbe, D., Tollington, S., Prys-Jones, R., Matthysen, E., & Groombridge, J. J. (2015). Ancestral origins and invasion pathways in a globally invasive bird correlate with climate and influences from bird trade. Molecular Ecology, 24(16), 4269–4285.

Jackson, K., & Fritts, T. H. (2004). Dentitional specialisations for durophagy in the common wolf snake, Lycodon aulicus capucinus. Amphibia-Reptilia, 25, 247–254.

Jensen, T. J., Auliya, M., Burgess, N. D., Aust, P. W., Pertoldi, C., & Strand, J. (2019). Exploring the international trade in African snakes not listed on CITES: Highlighting the role of the internet and social media. Biodiversity and Conservation, 28, 1–19.

Ji, X., & Wang, Z. W. (2005). Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese cobra (Naja atra). Biological Journal of the Linnean Society, 85(1), 27–40.

Jones, H. P., Holmes, N. D., Butchart, S. H. M., Tershby, B. R., Kappes, P. J., Corkery, I., ... Croll, D. A. (2016). Invasive
mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 4033–4038. https://doi.org/10.1073/pnas.1521179113

Kotsakiozi, P., Richardson, J. B., Pichler, V., Favia, G., Martins, A. J., Urbanelli, S., ... Caccone, A. (2017). Population genomics of the Asian tiger mosquito, *Aedes albopictus*: Insights into the recent worldwide invasion. *Ecology and Evolution*, 7(23), 10143–10157.

Kraus, F. (2009). *Alien reptiles and amphibians: A scientific compendium and analysis* (Vol. 4). Berlin, Germany: Springer.

Kraus, F., & Cravalho, D. (2001). The risk to Hawai‘i from snakes. *Pacific Science*, 55(4), 409–417.

Krysko, K. L., Burgess, J. P., Rochford, M. R., Gillette, C. R., Cueva, D., Enge, K., & Nielsen, S. V. (2011). Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages. *Zootaxa*, 3028(1), 1–64.

Kuch, U., & McGuire, J. A. (2004). Range extensions of *Lycodon capucinus* Boie, 1827 in eastern Indonesia. *Herpetozoa*, 17, 191–193.

Kueffer, C., & Daehler, C. C. (2009). A habitat-classification framework and typology for understanding, valuing, and managing invasive species impacts. In J. A. Drake (Ed.), *Management of invasive weeds* (Vol. 5, pp. 77–101). Dordrecht, the Netherlands: Springer.

Leviton, A. E. (1965). Contribution to a review of Philippine snakes. VIII. The snakes of the genus *Lycodon* Boie. *Philippine Journal of Science*, 94, 117–140.

Leviton, A. E., Siler, C. D., Weinell, J. L., & Brown, R. M. (2018). Synopsis of the snakes of The Philippines a synthesis of data from biodiversity repositories, field studies, and the literature. *Proceedings of the California Academy of Sciences*, 64, 399–568.

Madsen, T., & Shine, R. (2000). Silver spoons and snake body sizes: Ecology and Evolution, 7(23), 10143–10157.

Mullin, S. J., & Seigel, R. A. (2009). *Snakes: Ecology and conservation*. Ithaca, NY: Cornell University Press.

Nania, D., Flecks, M., & Rodder, D. (2020). Continuous expansion of the geographic range linked to realized niche expansion in the invasive mourning gecko *Lepidodactylus lugubris* (Dumeril & Bibron, 1836). *PLoS One*, 15(7), e0235060. https://doi.org/10.1371/journal.pone.0235060

O’Shea, M., Kusama, K. L., & Kaiser, H. (2018). First record of the Island wolf snake, *Lycodon capucinus*, from New Guinea, with comments on its widespread distribution and confused taxonomy, and a new record for the common sun skink, *Eutropis multicincta*. *IRCF Reptiles and Amphibians*, 25, 70–84.

Oliver, P. M., Blom, M. P. K., Cogger, H. G., Fisher, R. N., Richmond, J. Q., & Woinarski, C. Z. (2018). Insular biogeographic origins and high phylogenetic distinctiveness for a recently depleted lizard fauna from Christmas Island. *Australia. Biology Letters*, 14, 20170696. https://doi.org/10.1098/rsbl.2017.0696

Piquet, J. C., Warren, D. L., Bolaños, J. F. S., Rivero, J. M. S., Gallo-Barneto, R., Cabrera-Pérez, M. Á., ... Nogales, M. (2021). Could climate change benefit invasive snakes? Modelling the potential distribution of the California Kingsnake in the Canary Islands. *Journal of Environmental Management*, 294, 112917.

Pitt, W., Vice, D., & Pitzler, M. (2005). Challenges of invasive reptiles and amphibians. *Wildlife Damage Management Conferences Proceedings*, 84, 112–119.

Polo-Cavia, N., López, P., & Martín, J. (2008). Interspecific differences in responses to predation risk may confer competitive advantages to invasive freshwater turtle species. *Ethology*, 114(2), 115–123.

Pusack, T. J., Benkwitt, C. E., Cure, K., & Kindinger, T. L. (2016). Invasive red lionfish (*Pterois volitans*) grow faster in the Atlantic Ocean than in their native Pacific range. *Environmental Biology of Fishes*, 99(6–7), 571–579.

Reilly, S. B., Stubbs, A. L., Karin, B. R., Arida, E., Iskandar, D. T., & McGuire, J. A. (2019). Recent colonization and expansion through the Lesser Sundas by seven amphibian and reptile species. *Zoologica Scripta*, 48(5), 614–626.

Robinson, J. E., Griffiths, R. A., St. John, F. A. V., & Roberts, D. L. (2015). Dynamics of the global trade in live reptiles: Shifting trends in production and consequences for sustainability. *Biological Conservation*, 184, 42–50.

Rodda, G. H., Fritts, T. H., Campbell, E. W., III, Dean-Bradley, K., Perry, G., & Qualls, C. P. (2002). Practical concerns in the eradication of Island snakes. In *Turning the tide: The eradication of invasive species* (Occasional Paper of the IUCN Species Survival Commission No. 27, pp. 260–266). Gland, Switzerland and Cambridge, England: IUCN.

Rodda, G. H., Sawai, Y., Chiszar, D., & Tanaka, H. (1999). *Problem snake management: The habu and the brown tree snake* (534 pp.). Ithaca, NY: Cornell University Press.

Rogers, H., Hille Ris Lambers, J., Miller, R., & Tewksbury, J. J. (2012). “Natural experiment” demonstrates top-down control of spiders by birds on a landscape level. *PLoS One*, 7(9), e43446. https://doi.org/10.1371/journal.pone.0043446

Russell, J. C., Meyer, J. Y., Holmes, N. D., & Pagad, S. (2017). Invasive alien species on islands: Impacts, distribution, interactions, and management. *Environmental Conservation*, 44, 359–370.
Savidge, J. A. (1987). Extinction of an Island forest avifauna by an introduced snake. *Ecology, 68*, 660–668.

Seigel, R. A., & Ford, N. B. (1991). Phenotypic plasticity in the reproductive characteristics of an oviparous snake, *Elaphe guttata*: Implications for life history studies. *Herpetologica, 47*, 301–307.

Seigel, R. A., & Ford, N. B. (1992). Effect of energy input on variation in clutch size and offspring size in a viviparous reptile. *Functional Ecology, 6*, 382–385.

Shine, R., & Seigel, R. A. (1996). A neglected life-history trait: Clutch-size variance in snakes. *Journal of Zoology, 239*(2), 209–223.

Siers, S. R., Eisemann, J. D., Pitt, W. C., Clark, L., Goetz, S. M., Gosnell, R. J., … Coon, W. G., (2020). Automated aerial baiting for invasive brown tree snake control: System overview and program status. In D. M. Woods (Ed.), *Proceedings 29th vertebrate pest conference* (7 p.). Lincoln, NE: University of Nebraska–Lincoln.

Sinervo, B. (1990). The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution, 44*(2), 279–294.

Smith, M. J., Cogger, H., Tiernan, B., Maple, D., Boland, C., Napier, F., … Smith, P. (2012). An oceanic Island reptile community under threat: The decline of reptiles on Christmas Island, Indian Ocean. *Herpetological Conservation and Biology, 7*(2), 206–218.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H., Genovesi, P., Ceballos, G., … Croll, D. A. (2017). Globally threatened vertebrates on islands with invasive species. *Science Advances, 3*(10), 1603080. https://doi.org/10.1126/sciadv.1603080

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Quarterly Review of Biology, 51*, 3–47.

Sun, L. X., Shine, R., Zhao, D. B., & Tang, Z. R. (2002). Low costs, high output: Reproduction in an insular pit-viper (*Gloydius hedaoensis, Viperidae*) from north-eastern China. *Journal Zoolology, 256*, 511–521.

Toland, E., Bando, M., Hamers, M., Cadenas, V., Laidlaw, R., Martinez-Silvestre, A., & van der Wielen, P. (2020). Turning negatives into positives for pet trading and keeping: A review of positive lists. *Animals, 10*(12), 2371. https://doi.org/10.3390/ani10122371

Tolxen, B. W. (1984). Additional instances of multiple egg-clutch production in snakes. *Transactions of the Kansas Academy of Science, 87*(3/4), 98–104.

Willson, J. D., Dorcas, M. E., & Snow, R. W. (2011). Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in southern Florida. *Biological Invasions, 13*, 1493–1504.

Wiseman, K. D., Greene, H. W., Koo, M. S., & Long, D. J. (2019). Feeding ecology of a generalist predator, the California kingsnake (*Lampropeltis californiae*): Why rare prey matter. *Herpetological Conservation and Biology, 14*, 1–30.

Zweifel, R. G. (1980). Aspects of the biology of a laboratory population of kingsnakes. In J. B. Murphy & J. T. Collins (Eds.), *Reproductive biology and diseases of captive reptiles* (pp. 141–152). Oxford, Ohio: Society for the Study of Amphibians and Reptiles.

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