

RESEARCH ARTICLE

Dances with wolves: The demographic consequence of asymmetric competition and intraguild predation in a native-invasive skink system

Shi-Ping Huang¹ | Jhan-Wei Lin² | Chun-Chia Chou² | Chen-Pan Liao² | Jung-Ya Hsu² |
Jing-Fu Tsai² | Shao-Lun Liu³ | Wen-San Huang^{2,3,4} 

¹Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

²Department of Biology, National Museum of Natural Science, Taichung, Taiwan

³Department of Life Science, Tunghai University, Taichung, Taiwan

⁴Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan

Correspondence

Wen-San Huang
Email: wshuang.380@gmail.com

Funding information

Ministry of Science and Technology, Taiwan, Grant/Award Number: MOST 109-2621-B-178-001-MY3

Handling Editor: Jerry F. Husak

Abstract

1. Currently, we lack enough knowledge to fully explain how the impacts of species invasion on native communities are attributed to multifaceted, individual-based behavioural outcomes.
2. Here, we illustrate the long-term population dynamics of the native long-tailed sun skink (*Eutropis longicaudata*) before and after the invasion of the common sun skink (*Eutropis multifasciata*). We conducted diet investigation, morphological measurement, and a series of behavioural experiments both in the field and laboratory. We explained how the impacts of the invasive skink on the native skink can cascade towards the population level based on these individual-level behavioural data.
3. We present evidence of competition exclusion of the native skink population resulting from the invasion of the common sun skink. The drastic decline found in the native skink population was largely accounted for by low recruitment, as shown by the decrease in its clutch numbers correspondingly.
4. We also found dominance of the invasive skink in both exploitation competition and intraguild predation. Considering the highly overlapping morphological and dietary niches between the two species, our findings imply that the native skink has undergone strong food competition and predation pressure on its eggs and juveniles.
5. Interestingly, the native skink started to display parental care behaviour 2 years after the invasion event, and its clutch survival rate has recovered since then. The shift in parental care behaviour may help the native skink cope with this new predation pressure from the invasive skink.
6. Overall, the two competitive skinks showed low chances of coexisting. The negative population growth of this native skink species may be primarily derived from poor reproductive performance, given a sharp decline in its clutch numbers and its inferiority in exploitation competition, despite rebounding clutch survival rates.

Shi-Ping Huang, Jhan-Wei Lin and Chun-Chia Chou contributed equally.

© 2023 The Authors. Functional Ecology © 2023 British Ecological Society.

KEYWORDS

behaviour plasticity, competition exclusion, demographic consequences, niche overlap, species invasion

1 | INTRODUCTION

Introductions of invasive species have been recognized as one main cause of biodiversity loss (Clavero & García-Berthou, 2005; Sala et al., 2000; Vilà et al., 2011). The types (e.g. predation/competition) and modes (e.g. direct/indirect) of newly formed interactions between native and invasive species are frequently the key behavioural mechanisms determining the long-term ecological and evolutionary consequences of local communities (Mollot et al., 2017; Vilà et al., 2011). Meanwhile, the physiological ability, behavioural flexibility and capability of making adaptive responses of native species could greatly affect their vulnerabilities in a given event of biological invasion (Ruland & Jeschke, 2020; Shine, 2010; Strauss et al., 2006). For example, while the introduction of the American cane toad, *Rhinella marina*, has severely interfered with the native, large predators in Australia through toxic ingestion, other predator species able to tolerate the toxins were not even affected by this invasion event (Shine, 2010). Such multifaceted interplays between species make every event of species invasion a unique case and it is difficult to predict its consequences without comprehensive examination.

Competition with invasive species can be a major threat to the persistence of native species (Holway & Suarez, 1999; Sakai et al., 2001; Schoener, 1983); such negative impacts can be severe when the invasive species are always the superior competitors and competitiveness between native and invasive species is significantly asymmetric (Amarasekare, 2002). Two non-exclusive processes could be involved: exploitation competition and interference competition (Miller, 1967). The former focuses on the resource similarity among the competitor species and predicts that the superiors often exhibit better efficiency in resource use. Interference competition focuses on the aggressive interaction between species and predicts that the superiors often carry a larger armament (e.g. body size) that benefits them when having contests with other species. In the extreme case where these competitor species have a great difference in their body sizes (Holt & Polis, 1997; Wissinger, 1992), intraguild predation can occur (i.e. IGP, the competitors consume each other; Arim & Marquet, 2004; Polis et al., 1989). For example, the brown anole (*Anolis sagrei*) has been rapidly excluding the native green anole (*A. carolinensis*) in the southeast United States; this outcome resulted from not only their high ecological niche overlaps (diet, size, and spatial use) but also the dominance of the brown anole in aggressive contests (Edwards & Lailvaux, 2013; Gerber & Echernacht, 2000).

Behavioural changes are usually the initial response of organisms when experiencing novel environmental pressures. Native species that are able to demonstrate rapid and adaptive behavioural shifts to cope with the invasion pressure may have higher chances of survival (Sih et al., 2011; Strauss et al., 2006). Such behavioural responses are

pervasively observed across animal taxa (Ruland & Jeschke, 2020) and are likely to mediate long-term evolutionary consequences despite the fact that these shifts are not always modulated by genes (Wong & Candolin, 2015). For example, the green anole has been found to elevate its perch height (Bush et al., 2022; Edwards & Lailvaux, 2012) and increase the toepad area (Stuart et al., 2014) when sharing habitat with the invasive brown anole. Such a behavioural shift differentiated the habitat use of the two anole species and increased the chance of coexistence. Since behavioural shifts can play an important role in determining the outcome of interspecific competition, taking this behavioural perspective into account would be essential for better explaining how biological invasion impacts native populations.

There is an urgent need to elucidate how biological invasion can lead to different demographic consequences of native species and how the impacts are attributed to multifaceted, individual-based behavioural outcomes (Crystal-Ornelas & Lockwood, 2020). Existing studies addressing the impacts of biological invasion primarily consist of two categories. Some of these studies mainly investigated behavioural and/or morphological shifts in native species following invasion events (e.g. Bush et al., 2022; Edwards & Lailvaux, 2013; Stuart et al., 2014) but the ecological and evolutionary consequences of these changes were less addressed. The other studies mainly focused on the impacts of biological invasions on native species at the macro-spatiotemporal scales (e.g. population persistence, distributional shift, community structure, ecosystem functioning; Gallien & Carboni, 2017; Vilà et al., 2011). However, these latter studies typically do not consider the fundamental mechanisms that cause such large-scale impacts. Studies that bridge the two disparate knowledge dimensions are thus in high demand because they can significantly aid in determining why invasive and native species cannot coexist and how the ripple effect of biological invasion begins at the individual level and spreads to larger ecological processes.

Here, we constructed an integrated knowledge framework illustrating the chain reaction of how species invasion can impact native species by interfering with vital demographic processes. We provided empirical evidence of the long-term population dynamics (before and after the invasion event), niche overlap analyses, and a series of behavioural experiments of an invasive-native sun skink study system. We overcame one long-lasting constraint in invasion biology: we often lack sufficient information about the initial condition of native populations (Crystal-Ornelas & Lockwood, 2020; D'Antonio & Flory, 2017; Strayer et al., 2006) because the impacts of species invasion usually begin with subtle changes and are therefore difficult to detect in time (D'Antonio & Flory, 2017; Pergl et al., 2020). We estimated the net impacts of species invasion by comparing the population size, clutch number,

frequency of parental care, and clutch survival of a native long-tailed sun skink population before and after the invasion of the common sun skink. We measured the overlaps of the dietary and morphological niches of the two skink species and compared their relative competitiveness.

2 | MATERIALS AND METHODS

2.1 | Study system and fieldwork

The long-tailed sun skink is distributed in southern Taiwan and Orchid Island. It is oviparous and its reproductive season spans from March to August (Huang, 2006a). This species exhibits flexibility in parental care behaviour; female skinks on Orchid Island have been documented to defend their eggs against the egg predator, the Formosa kukri snake (*Oligodon formosanus*; Huang, 2006b). This behaviour has rarely been observed among other populations free from the predatory snake, suggesting that egg predation could be the main selection force driving this behavioural change (Huang et al., 2013). The common sun skink originates from Southeast Asia (Uetz, 2021). It has been inferred as an alien invasive species threatening the persistence of native skinks due to its extending population, large body size, and high aggressiveness (Lee et al., 2019). This invasive skink is viviparous and reproduces throughout the year. It was first recorded in Kaohsiung City, southwest of Taiwan in 1992 (Ota et al., 1994) and radially expanded its distribution in Taiwan as well as three nearby islands (Lee et al., 2019; Lin et al., 2019).

We conducted population surveys along a 3-km transect in Shandimen Township, Pingtung County, Taiwan (22°43'17.0"N 120°38'15.5"E) from June to August before (i.e. 2000–2002) and after the invasive event (i.e. 2011–2018). Each survey was conducted once per month by two experienced investigators and lasted for 3 days. One investigator continuously participated in the surveys throughout this project with the assistance of other members of the same research group (i.e. the second investigator). During each survey, we captured individuals, identified their species, and recorded the sex, age class, and body size (i.e. snout-vent length, SVL, and body weight). We left temporal marks on the individuals we captured using non-toxic paint to avoid repeatedly disturbing them in the same survey periods. The captured individuals were released immediately after the measurement. We illustrated the population dynamics of each species by summing up the number of individuals we captured in the same survey year.

2.2 | Investigation of clutch number and parental care behaviour

We inspected the clutch number and parental care behaviour of the long-tailed sun skink at the same study site as our population surveys. A previous study indicates that female long-tailed sun skinks prefer to nest inside plastic drainage pipes (Huang, 2006b). Eggs laid in these pipes were larger, hatched earlier and had higher hatching success

(Huang & Pike, 2011). Each pipe had an opening retained in concrete walls and allowed these mother skinks to enter and nest. This artificial nesting habitat also provided us with a great opportunity to observe the parental behaviour of these mother skinks from the pipe openings. During our population surveys, we also recorded the clutch site that each mother skink nested (i.e. the specific pipe), as well as the numbers of clutches we found in our study site. We considered that a clutch had successfully survived a reproductive season if we could still find the eggs (or egg shells after the eggs were hatched) inside the same pipe in the last survey of the year. We also recorded the presence of parental care behaviour of these mother skinks if they stayed with their clutches (Huang, 2006b; Huang et al., 2013). During the survey period of 2017–2018, we further tested if these mother skinks defended their clutches against the common sun skink by placing a common sun skink individual into the pipe. We considered that a mother skink successfully defended her clutches if the intruded skink was expelled from the pipe (Video S1).

2.3 | Experimental preparation

We captured individuals of the two skink species and collected eggs of the long-tailed sun skink for the dietary investigation and behavioural experiments. Given that the common sun skink is viviparous, we obtained its hatchlings by bringing pregnant common sun skinks back to our laboratory and waiting for them to give birth. We conducted the fieldwork in an area 2 km away from the monitored population to prevent any potential influence of this artificial removal on the population we regularly monitored. The environmental conditions, vegetation and fauna of this capture site were highly similar to the site where we conducted our population surveys. We captured a total of 56 long-tailed sun skink individuals and 83 common sun skink individuals during 2017–2018. We took them back to the laboratory, kept them individually in terrariums (36 × 17 × 20 cm), and provided them with water and food ad libitum, as well as a natural light–dark cycle.

We checked the pregnant common sun skinks twice per day and kept their hatchlings away from them once they gave birth. These hatchlings were later used in the juvenile consumption experiment. Eggs of the long-tailed sun skink were partially used in the egg consumption experiment, and some of them were incubated in the laboratory at 25°C and 45%–55% RH. Hatchlings of the long-tailed sun skink were also used in the juvenile consumption experiment. We released these adult skinks we captured back to the capture site after the laboratory experiments. We received animal use protocols to conduct these experiments and this research was approved by IACUC at the National Museum of Natural Science (licence No. NMNSIACUC2016-001).

2.4 | Diet investigation

We measured dietary overlap of the two skink species based on the food they consumed by stomach flushing the skinks (i.e. 30

long-tailed sun 175 skinks and 58 common sun skinks) in the laboratory. We held the necks of the skinks, opened their mouths with pincers, and gently inserted a silicone tube (5 mm in diameter) into their mouths until the tube reached their throats. A 10–20 mL saline solution was then slowly injected into the skinks' esophagi. We repeatedly injected the solution until there was no more food content washed out. We preserved these dietary samples using 70% alcohol before further analyses. We counted and identified the prey items we found in each of these samples to the lowest possible taxonomic level (e.g. invertebrates to class and insects to order) using an anatomic microscope (Leica EZ4).

2.5 | Behavioural experiments

We conducted three behavioural experiments using the adult skinks captured in the field. The three experiments were food competition, egg predation and hatchling predation. We ran these experiments using terrariums (120 × 60 × 45 cm) and we placed skinks (or pairs of skinks) into these terrariums. We gave the focal individual(s) 15 min to acclimate to the experimental setting in each of the trials. The trial started as soon as the food, a heterospecific egg, or a heterospecific hatchling was placed in the terrarium. Each of the trials lasted for 15 min or ended earlier when the focal skink consumed the (food) item. We recorded whether the (food) item was consumed and which species consumed it.

In the food-competition experiment where pairs of skinks participated in the trials ($N = 13$), we put the two skink individuals of each pair beside the two short sides of rectangular terrariums. Each pair was composed of one native skink and one invasive skink, both of the same sex and similar SVL. The two individuals were segregated by a non-transparent plastic board during the 15-min acclimation. Thereafter, we placed three mealworms (carried by a petri dish) in the centre of the terrarium and removed the partition at the same time. We recorded the species that consumed the mealworms first as the winner. In the egg predation experiment ($N = 23$), we put one egg of the long-tailed sun skink into each of the terrariums after the common sun skink individuals had acclimated inside these terrariums for 15 min. We recorded whether they consumed the eggs within the 15-min experimental period. We performed the same procedure but replaced the provided item with hatchlings of either the native or invasive skink in the hatchling predation experiment ($N = 14$).

2.6 | Statistical analyses

To illustrate population dynamics of the two skink species, we performed segmented Poisson regression (R package 'segmented', Muggeo, 2017) using data from the two survey periods (2000–2002 and 2011–2018). We fitted amounts of each skink species we recorded in the same survey years. We allowed 0–2 breakpoints to occur along the fitted population dynamics. This breakpoint

estimation method was proposed by Muggeo (2003); its algorithm can automatically search for possible breakpoints and iteratively improve the breakpoint estimate to minimize the residual deviance. This method provided us information about whether and when the population size of the native skink changed dramatically. We presented our results based on the model with the lowest Akaike information criterion (AIC) value, and we also reported the result of the likelihood ratio test of this model.

We compared the SVL, body mass, and clutch size of adults of the two skinks we collected during 2017–2018 by using exact Wilcoxon rank sum tests. We also performed permutation tests to examine morphological niche overlaps between the two species. Based on the information of their SVLs and body masses, we computed four morphological hypervolumes (i.e. two sexes two skink species) using the R package 'hypervolume' (Blonder, 2022) with Gaussian estimates. For each sex, we further created a null hypothesis based on 5000 permutations. We generated these permuted samples based on the two hypervolumes of the two species and the assumption that all samples were from the same population. With this null hypothesis, we tested (1) whether their hypervolume sizes significantly differed from each other, and (2) whether the two hypervolumes were statistically separated from each other (i.e. small overlap, based on the Jaccard similarity index).

We analysed the diet breadths of the two skink species and their diet overlap using several methods. First, we estimated the dietary niche breadths of the two species based on Levin's index and performed a permutation test to test whether their dietary breadths were different. Second, to detect the dietary dissimilarity between the two species, we performed a principal coordinate analysis (PCoA) based on the Jaccard's dissimilarity index using the R package "ape" (Paradis & Schliep, 2019). Third, we compared the prey richness of the two species by depicting their prey richness accumulation curves (the Arrhenius model in the R package "vegan", Oksanen et al., 2020). Each curve was formulated as

$$Y \sim kX^z,$$

where Y denoted the expected number of prey categories consumed by a skink species, X denoted the numbers of individuals of a skink species, k was a scaling parameter estimating the numbers of prey categories we found when sampling each skink individual, and z estimated the steepness of the curve. We performed permutation tests to examine whether the two estimated parameters, k and z , in the two accumulation curves differed significantly (a null hypothesis was generated by 5000 permuted samples based on the prey categories we observed in the two skink species). Finally, we examined the niche overlap of the two species based on their diet compositions. We adopted the Pianka niche overlap index (Pianka, 1973) as below,

$$O_{jk} = \frac{\sum_i^n (p_{ij} p_{ik})}{\sqrt{\sum_i^n (p_{ij}^2) \sum_i^n (p_{ik}^2)}}.$$

This index's values O_{jk} can range from zero to one, whereby a value closer to one represents a larger overlap between the dietary niches of the two species. There were a total of n prey categories consumed by the two skink species, j or k ; p_{ji} and p_{jk} denote the prey proportions in the diets of the two species respectively (i.e. prey category i consumed by the skink species j or k). Given that this index is applicable to comparisons at the species level, we obtained values representing prey proportions in a skink's diet by averaging the prey proportions we observed in the diets of individuals of the same species. We tested whether the dietary niches of the two species overlapped using a permutation test (R package "EcoSimR" version 0.1, "ra3" algorithm, Gotelli et al., 2015). We simulated 10,000 null models based on the average prey proportions we obtained from the diets of the two species.

We examined the propensities of IGP of the two skink species by performing Firth's logistic regression (R package "logistf"; Heinze et al., 2020). In this model, the probabilities of the observed IGP were treated as the response variable and sex was treated as the explanatory variable. To examine changes in parental care behaviour and clutch survival rate in the native skink after the invasion of the common sun skink, we employed segmented logistic regression models using the R package 'segmented' (Muggeo, 2017). We treated the proportions of the survived clutches and the proportions of the mother skinks that displayed parental care behaviour as the response variables in two respective models. Survey years (i.e. 2014 to 2018) were treated as the explanatory variable. Given that we did not observe parental care behaviour in the native mother skinks before 2012, we fitted a logistic regression only using data recorded after 2012 in the parental care behaviour model. We allowed 1–2 breakpoints to occur in this model over our survey years. For the two regression models, we reported the results of likelihood ratio tests based on the models with the lowest AIC values. We also employed a binomial exact test to examine if the native mother skinks could successfully protect their clutches from the common sun skink. All analyses were performed using R version 4.1.0.

3 | RESULTS

3.1 | Dynamics of population and clutch number

We detected a significant decline in the population size of the long-tailed sun skink in 2012 ($\chi^2 = 19.5$, $df = 2$, $p < 0.001$, $\Delta AIC = -14.9$). Before 2012, the population size of the long-tailed sun skink was stable (-0.4% per year, $p = 0.717$; Figure 1a), and none of the common sun skink individuals were found in the field. In 2012, we found the first common sun skink individual; its population size has been growing dramatically (40% per year, $p < 0.001$), and this has accompanied an apparent decline in the population size of the long-tailed sun skink (-20% per year, $p < 0.001$; Figure 1a). Meanwhile, we also detected a drastic change in clutch numbers of the native skink since 2012 ($\chi^2 = 28.5$, $df = 2$, $p < 0.001$, $\Delta AIC = -24.5$). Despite a gradual decrease in clutch numbers prior to the invasion of the common sun

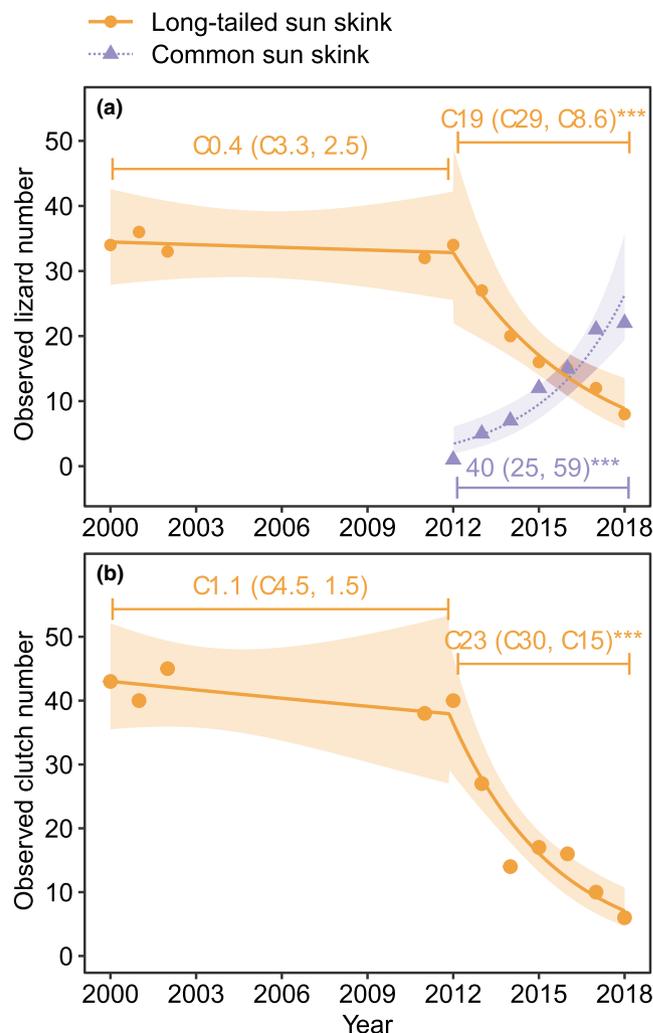


FIGURE 1 The observed numbers of the native long-tailed sun skink (*Eutropis longicaudata*; orange circles and solid lines) and the invasive common sun skink (*E. multifasciata*; purple triangles and dotted lines) (a), and the observed clutch numbers of the native skink (b) from 2000 to 2018. Regression lines and grey areas represent the expected skink numbers and 95% confidence bands respectively. The estimates and 95% confidence intervals (i.e. numbers in brackets) of the growth rates of the native and invasive skink populations are labelled. *** $p < 0.001$.

skink (1.1% per year; $p = 0.560$), a significant decrease in clutch numbers occurred after 2012 (23% per year, $p = 0.001$; Figure 1b).

3.2 | Clutch predation and parental care behaviour in the long-tailed sun skink

The proportion of the native mother skinks displaying parental care behaviour has increased significantly since 2012 (Figure 2a). The clutch survival rate of the native skink changed significantly in 2013 and 2015 (Figure 2b). Clutch survival of the native skink had been stable before 2013 ($\sim 70\%$), but it dropped significantly from 2013 to 2015 ($\sim 30\%$ in 2015) and started to rebound after 2015 (100% in 2018, Figure 2b). Correspondingly, we found that 92% (11 in 12)

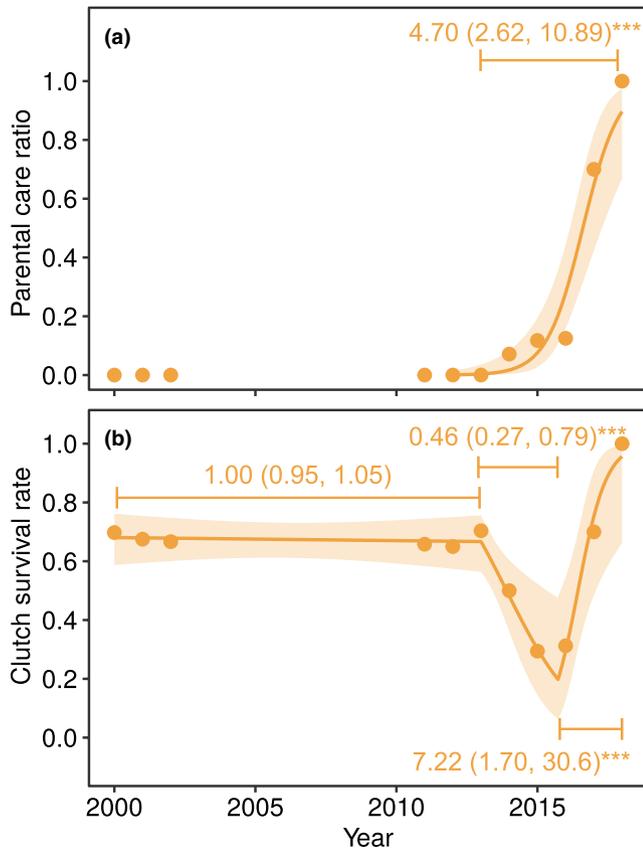


FIGURE 2 Parental care ratios (i.e. proportion of the mother skinks displaying parental care behaviour) (a) and clutch survival rates (b) of the long-tailed sun skink. The two regression lines depict the expected probabilities according to logistic model regressions, and the two filled stripes depict 95% confidence bands. We also reported the odds ratios (i.e. numbers in front of the brackets, \exp [regression coefficient]) and 95% confidence intervals (i.e. numbers in the brackets). *** $p < 0.001$.

of these mother skinks successfully protected their eggs by chasing away the common sun skink individuals we experimentally introduced (95% CI = 61.5–99.8, $p = 0.006$).

3.3 | Niche overlap

3.3.1 | Morphology and reproductive characteristics

Males of the two skink species showed no significant difference in their SVLs and body weights, whereas in females, the long-tailed sun skink was significantly larger (4.3%) and heavier (22%) than the common sun skink (Table 1). The two sun skink species had similar sizes with respect to their morphological hypervolumes (Table 1; Figure 3). The morphological hypervolumes of the two species highly overlapped and their morphological niches were not significantly partitioned (females, Jaccard similarity = 0.485, $p = 0.098$; males, Jaccard similarity = 0.454, $p = 0.074$; Figure 3).

The clutch size of the long-tailed sun skink was significantly larger than that of the common sun skink (Table 1). We found that the common sun skink is viviparous and can reproduce throughout the year, whereas the long-tailed sun skink is oviparous and can only reproduce in summer (Table 1).

3.3.2 | Diet composition

There was no significant difference in the dietary breadth between the common sun skink and the long-tail sun skink (Levins' breadth index, 13.29 vs. 12.28, $p = 0.124$; Table 1). Compared with the long-tailed sun skink's dietary breadth, the dietary breadth of the common sun skink encompassed a slightly larger area (based on the PCoA ordination result, Figure 4a). However, the two skink species showed no significant difference in either the estimated numbers of prey categories they consumed (i.e. k , $p = 0.102$) or the steepness of their prey accumulation curves (i.e. z , $p = 0.304$). Overall, their diets highly overlapped (Pianka niche overlap metric = 0.853, $p < 0.001$, Figure 4b).

3.4 | Food competition and IGP

In the food competition experiment, it was always the common sun skink individuals initiating the consumption of the mealworms we provided in the trials ($N = 13$, marginal 95% CI = 67.7–97.9, $p < 0.001$). Sex had no significant effect on the competition outcome as we continuously observed the same trend among these focal skink pairs regardless of their sexes ($\chi^2 = 0.022$, $df = 3$, $p = 0.999$).

Regarding the two IGP experiments, six males (85%) and all females of the common sun skink consumed the long-tailed sun skink's eggs (marginal 95% CI = 67.2–99.0, $p = 0.002$; Figure 5a). There was a significant difference in whether the two skink species depredated juveniles of the other skink species (OR = 150, $p < 0.001$; Figure 5b). We found that six females (83%) and six males (100%) of the common sun skink consumed the long-tailed sun skink's juveniles but none of the native skink adults (female, $N = 6$; male, $N = 6$) consumed the invasive skink's juveniles.

4 | DISCUSSION

We present evidence of competitive exclusion of a population of the native, long-tailed sun skink after the invasion of the common sun skink. The two skink species have highly overlapping morphological and dietary niches. Additionally, the invasive skink was able to secure its food resources (i.e. mealworms, eggs and juveniles of the native skink) even though it was exposed to a novel experimental environment. These characters may greatly account for why this invasive skink could have successfully invaded southern Taiwan and expanded its spatial distribution rapidly within an extremely short time span. We also found that the native mother skinks adjusted

	<i>E. longicaudata</i>	<i>E. multifasciata</i>	<i>p</i>
SVL (mm)	Male: 108.7 ± 7.8 (N = 38) Female: 107.8 ± 7.0 (N = 41)	Male: 106.1 ± 11.0 (N = 45) Female: 103.4 ± 9.4 (N = 40)	0.481 ^a 0.020 ^a
Body mass (g)	Male: 36.72 ± 6.19 (N = 38) Female: 37.00 ± 6.64 (N = 41)	Male: 37.22 ± 9.69 (N = 45) Female: 30.74 ± 7.67 (N = 40)	0.492 ^a <0.001 ^a
Morphological hypervolume	Male: 873.1 Female: 877.4	Male: 1760.0 Female: 1198.0	0.093 ^b 0.311 ^b
Reproductive mode	Oviparity	Viviparity	—
Clutch size	7.000 ± 1.214 (N = 39)	6.318 ± 1.211 (N = 22)	0.043 ^a
Reproductive cycle	March to August	Whole year	—
Levins' niche breadth	12.28 (N = 30; 95% CI = 8.69–12.6)	13.29 (N = 58; 95% CI = 10.6–14.3)	0.124 ^a

^aExact Wilcoxon test.

^bPermutation test.

TABLE 1 Comparisons of body sizes, body masses, reproductive traits, and niche breadths (Levins' *D*) between the native long-tailed sun skink (*Eutropis longicaudata*) and the invasive common sun skink (*E. multifasciata*). Average ± SD of SVL, body mass and clutch size were reported.

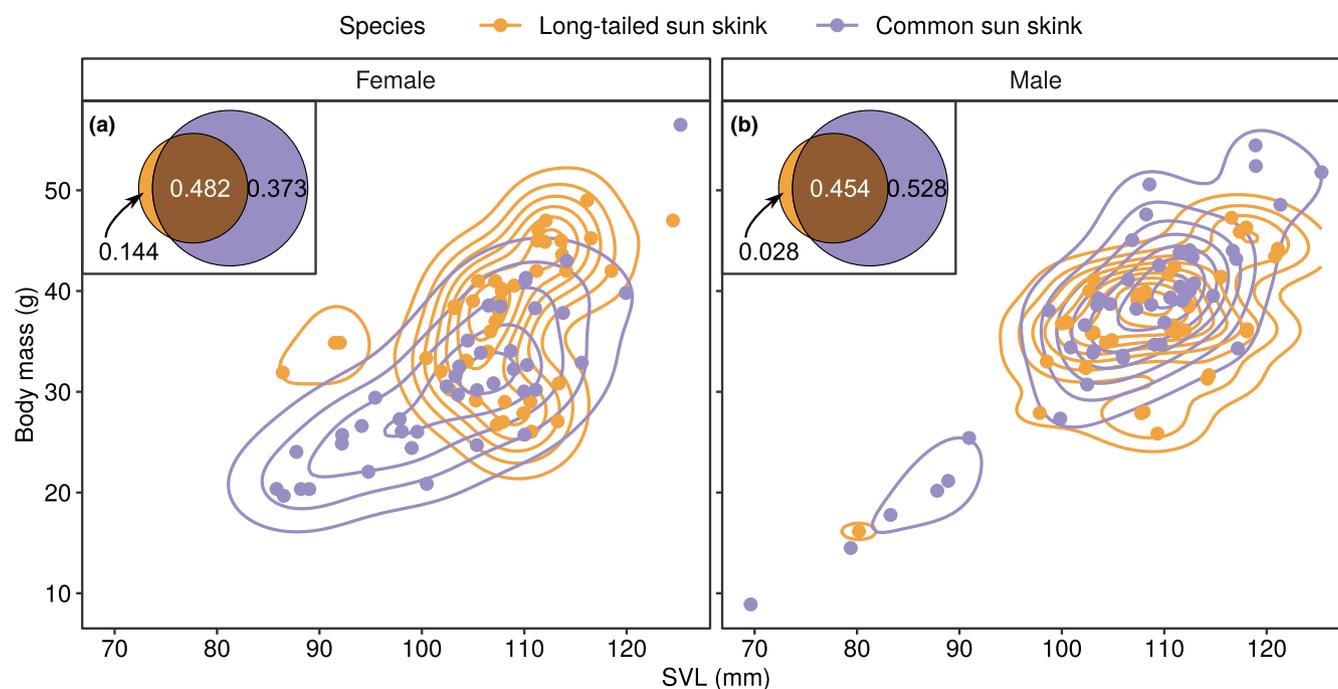


FIGURE 3 Comparisons of two morphological traits (i.e. snout-vent length [SVL] and body mass) between the two skink species in either sex (long-tailed sun skink: orange circles and lines; common sun skink: purple triangles and lines). Distributions of the two morphological traits of either sex of the two species were plotted using two-dimensional kernel density estimation based on the observed SVLs and body masses. Numbers in the Venn diagrams show the overlap proportions of the two hypervolumes.

their parental care behaviour after the invasion of the common sun skink. This behavioural shift may have greatly improved the native skink's clutch survival against the IGP on its eggs. By aligning multifaceted behavioural outcomes with long-term population demographics of the two skink species, we illustrate how species invasion could catalyse impacts on native species in nature.

Species that share the same ecological niches are less likely to coexist since they frequently compete for identical resources in the environment (Hardin, 1960). We reveal high similarities in

the two skinks' body sizes and diet compositions, suggesting high overlaps in their morphological and dietary niches (Tables 1 and 2; Figures 3 and 4). Meanwhile, the invasive skink always acquired the food we provided during our experiments. This may result from it being either better at food access, or bolder and/or more explorative in a novel environment. Indeed, invasive animals could benefit from being more active, bold, aggressive, and/or explorative as these behavioural traits enhance their ability to exploit environmental resources (Chapple et al., 2011; Pintor et al., 2009; Short &

FIGURE 4 The results of (a) the principal coordinate analysis (PCoA) and (b) species accumulation curves based on the diets of the long-tailed sun skink (orange circles and solid lines) and the common sun skink (purple triangles and dotted lines). The area depicted by the orange solid line illustrates the native skink's diet breadth and the area depicted by the purple dotted line illustrates the invasive skink's diet breadth. EL, long-tailed sun skink; EM, common sun skink. $p_{\Delta k}$ and $p_{\Delta z}$ indicate the p -values testing the scaling parameter k and steepness parameter z , respectively.

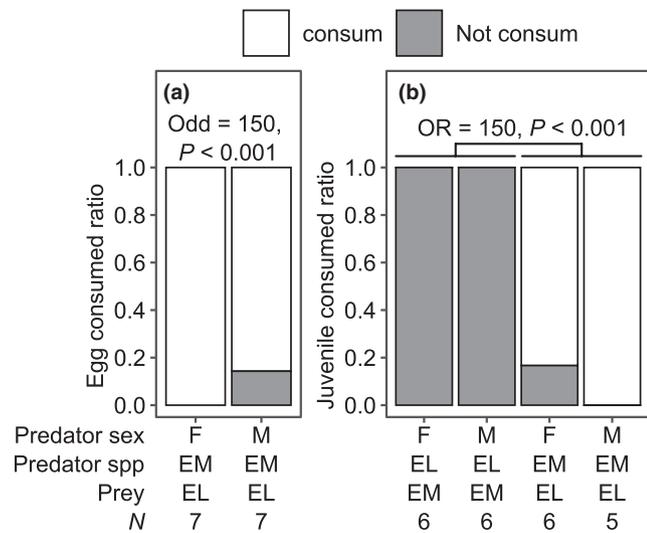
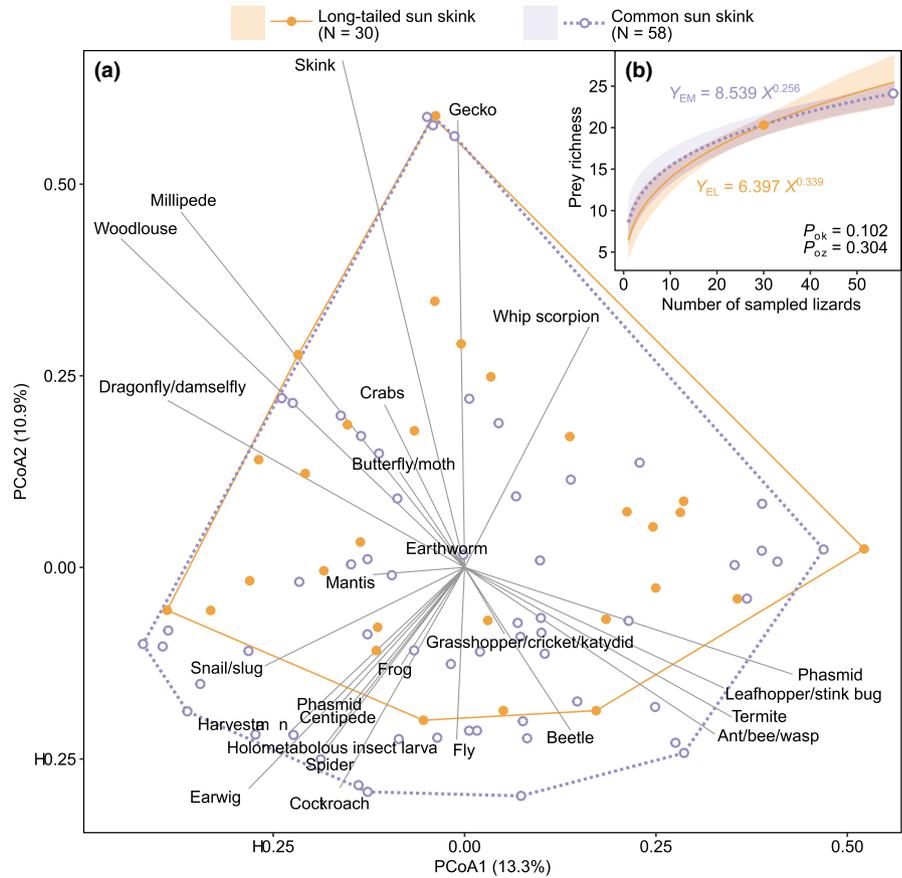


FIGURE 5 The ratios of eggs (a) and juveniles (b) the other skink species consumed in the behavioural experiments. EL, long-tailed sun skink; EM, common sun skink; F, female; M, male; OR, odds ratio.

Petren, 2008). This behavioural trait may also help us explain why we found slightly more prey categories in the invasive skink's diet. Our findings thus encourage further investigation of whether different personalities between the two skink species can act as one major behavioural mechanism determining their competitive dominancy.

We also hypothesize that this behavioural trait may amplify the asymmetry of exploitation competition between the two skink species, further leading to the exclusion of the native skink.

The other pathway that this invasive skink could have interfered with the persistence of the native skink population is through direct IGP. We found that the common sun skink consumed eggs and juveniles of the long-tailed sun skink, but the native skink did not consume any juveniles of the invasive skink (Figure 5). Again, we cannot exclude the possibility that the native skink was too shy to consume the invasive skink's juveniles in an artificial environment since it did eat other skink species in nature based on our dietary analyses (Table 2). Nonetheless, our results still suggest a high level of IGP by the invasive skink. Moreover, the identities of the IG predator (i.e. the invasive common sun skink) and IG prey (i.e. the native long-tailed sun skink) remain consistent in the two early ontogenetic stages (i.e. egg and juvenile stage). This could interrupt the recruitment process of the native skink species and explain why its clutch numbers (Figure 1b) and clutch survival rate (2012–2015; Figure 2b) decreased significantly after the invasion event. This unstable IGP system (Holt & Polis, 1997; Mylius et al., 2001) in conjunction with the sharp declines we observed in the population size and clutch numbers of the native skink suggests that the two skink species may have low chances of coexisting in the same environment.

Behaviours are often the initial response of organisms to changing environments (Sih et al., 2011; Wong & Candolin, 2015). By adjusting their behaviours adequately, organisms may gain more time

		Average \pm SD of diet percent and total count of food items	
Prey category		<i>E. longicaudata</i> (N = 30)	<i>E. multifasciata</i> (N = 58)
(a)	Centipede	0.94 \pm 2.97 (3)	2.44 \pm 7.54 (20)
	Phasmid	1.07 \pm 4.7 (2)	0.01 \pm 0.09 (1)
	Mantis	2.07 \pm 6.03 (4)	0.76 \pm 4.46 (3)
	Beetle	2.75 \pm 7.37 (6)	10.54 \pm 17.73 (58)
	Whip scorpion	2.78 \pm 8.57 (3)	1.37 \pm 7.3 (3)
	Cockroach	3.09 \pm 7.83 (9)	3.92 \pm 8.2 (26)
	Earwig	3.40 \pm 9.64 (9)	7.22 \pm 18.21 (85)
	Skink	4.00 \pm 18.50 (2)	4.89 \pm 19.44 (6)
	Fly	4.44 \pm 13.79 (3)	5.55 \pm 11.13 (36)
	Holometabolous insect larva	7.63 \pm 21.63 (10)	4.66 \pm 10.93 (53)
	Butterfly/moth	7.97 \pm 19.62 (11)	1.31 \pm 5.5 (4)
	Snail/slug	9.51 \pm 17.02 (24)	7.44 \pm 11.5 (37)
	Ant/bee/wasp	9.68 \pm 22.54 (97)	11.32 \pm 19.03 (77)
	Spider	10.67 \pm 14.13 (20)	12.90 \pm 18.52 (68)
	Grasshopper/cricket/katydid	12.03 \pm 21.09 (19)	6.91 \pm 11.9 (33)
	Leafhopper/stink bug	12.51 \pm 20.05 (25)	8.22 \pm 16.21 (31)
Subtotal	94.53 \pm 19.36 (247)	89.46 \pm 22.71 (541)	
(b)	Jumping bristletail	0 (0)	0.13 \pm 1.01 (1)
	Frog	0 (0)	0.57 \pm 2.68 (3)
	Crab	0 (0)	1.25 \pm 5.25 (4)
	Earthworm	0 (0)	1.40 \pm 5.55 (5)
	Woodlouse	0 (0)	1.64 \pm 12.51 (40)
	Dragonfly/damselfly	0 (0)	2.51 \pm 10.84 (9)
	Termite	0 (0)	3.04 \pm 13.28 (143)
	Subtotal	0 (0)	10.54 \pm 22.71 (205)
(c)	Harvestman	0.20 \pm 1.07 (1)	0 (0)
	Millipede	1.94 \pm 7.48 (2)	0 (0)
	Gecko	3.33 \pm 18.26 (1)	0 (0)
	Subtotal	5.47 \pm 19.36 (4)	0 (0)

TABLE 2 Percentages of different preys the long-tailed sun skink (*Eutropis longicaudata*) and the common sun skink (*E. multifasciata*) consumed (based on the total prey masses we measured in their stomach flush samples). Prey categories were separated into three panels: (a) preys in both species' stomach, (b) preys only in common sun skink's stomach and (c) preys only in long-tailed sun skink's stomach. Numbers inside parentheses indicates how many prey individuals we found in this skink species belonged to certain prey categories. We identified in total 26 prey categories from the stomach flush samples of the two species. Sixteen of which were consumed by both species, occupying 98.4% and 72.5% of the total prey categories in the long-tailed sun skink and the common sun skink, respectively. There were three categories only consumed by the long-tailed sun skink (1.6%) and seven categories only consumed by the common sun skink (27.5%).

to adapt to novel environmental conditions and thus mitigate the impacts of environmental changes. Here, we observed a shift in parental care behaviour in the native mother skinks following the invasion of the common sun skink. This behavioural shift seems to alleviate the novel ecological threat—IGP from the invasive skink—because the native skink improved its clutch survival soon after it started to defend its clutches (Figure 2). Two previous studies have reported the same parental care behaviour in the native skink on Orchid Island and suggested that this behaviour may have helped the skink cope with strong egg predation from an egg-eating snake (*Oligodon formosanus*; Huang, 2006b; Huang et al., 2013). Currently, it is not clear whether this behavioural shift is a kind of behavioural flexibility subject to clutch predation or whether the native skink has possessed such behavioural plasticity in response to novel

environmental threats. It is also not clear whether this behavioural shift is adaptive and can catch up with the rapid expansion of the invasive skink even though the native skink can effectively defend its clutches against the invader (see Video S1). These knowledge gaps thus urge more studies to investigate the role of behavioural flexibility and plasticity in influencing the ecological and evolutionary consequences of native species in changing environments.

Currently, the two competitive skinks show low chances of co-existence as the population size and clutch numbers of the native skink continuously declined after species invasion (Figure 1). These two decreasing trends continued even though the native mother skinks started to defend their clutches and the clutch survival rate started to rebound (Figure 2). Taking together our findings regarding the population demographics and niche overlaps between the two

skink species, we are concerned about whether the native skink will be able to maintain its productivity when undergoing strong food competition and low food accessibility after the species invasion (e.g. how many female skinks can acquire sufficient food/energy for reproduction). The local government may wish to mitigate the impacts of species invasion through relaxing interspecific competition (e.g. through removing the invasive species or increasing available resources in the environment). Additionally, continuous monitoring is required to assess how efficiently the change in parental care behaviour in the native skink can decelerate the speed of range expansion of the invasive skink.

AUTHOR CONTRIBUTIONS

Wen-San Huang conceived the idea, designed the experiment and initiated this long-term program. Shi-Ping Huang contoured the manuscript and conducted all laboratory experiments and the fieldwork during 2017–2018. Jhan-Wei Lin and Chun-Chia Chou chiefly constructed and wrote the manuscript based on the draft of Shi-Ping Huang. Chen-Pan Liao did all formal analyses, wrote the results, and revised most of the methods. Jung-Ya Hsu assisted the fieldwork and laboratory experiments. Jing-Fu Tsai inspected the food items in dietary investigation. Jhan-Wei Lin, Chun-Chia Chou, Shao-Lun Liu and Wen-San Huang revised the manuscript.

ACKNOWLEDGEMENTS

We are grateful to Mr. CH Chang for the sample collection in the wild. We are also grateful to all members of WSH's lab for their help in both the laboratory and field work. This long-term study was supported and funded by several projects in National Museum of Natural Science and Ministry of Science and Technology (MOST 109-2621-B-178-001-MY3).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad repository <https://doi.org/10.5061/dryad.gb5mkkwtj>, Huang (2022).

ORCID

Wen-San Huang  <https://orcid.org/0000-0003-0073-3557>

REFERENCES

- Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 2541–2550.
- Arim, M., & Marquet, P. A. (2004). Intraguild predation: A widespread interaction related to species biology. *Ecology Letters*, 7, 557–564.
- Blonder, B. (2022). *Hypervolume: High dimensional geometry, set operations, projection, and inference using kernel density estimation, support vector machines, and convex hulls*. R package Version 3.0.1. <https://CRAN.R-project.org/package=hypervolume>
- Bush, J. M., Ellison, M., & Simberloff, D. (2022). Impacts of an invasive species (*Anolis sagrei*) on social and spatial behaviours of a native congener (*Anolis carolinensis*). *Animal Behaviour*, 183, 177–188.
- Chapple, D. G., Simmonds, S. M., & Wong, B. B. M. (2011). Know when to run, know when to hide: Can behavioral differences explain the divergent invasion success of two sympatric lizards? *Ecology and Evolution*, 1, 278–289.
- Clavero, M., & Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, 20, 110.
- Crystal-Ornelas, R., & Lockwood, J. L. (2020). The 'known unknowns' of invasive species impact measurement. *Biological Invasions*, 22, 1513–1525.
- D'Antonio, C., & Flory, S. L. (2017). Long-term dynamics and impacts of plant invasions. *Journal of Ecology*, 105, 1459–1461.
- Edwards, J. R., & Lailvaux, S. P. (2012). Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. *Ethology*, 118, 494–502.
- Edwards, J. R., & Lailvaux, S. P. (2013). Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *A. sagrei*. *Biological Journal of the Linnean Society*, 110, 843–851.
- Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, 40, 335–352.
- Gerber, G. P., & Echternacht, A. C. (2000). Evidence for asymmetrical intraguild predation between native and introduced *Anolis* lizards. *Oecologia*, 124, 599–607.
- Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015). *EcoSimR: Null model analysis for ecological data*. R package Version 0.1.0. <http://github.com/gotellilab/EcoSimR>
- Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292–1297.
- Heinze, G., Ploner, M., & Jiricka, L. (2020). *logistf: Firth's bias-reduced logistic regression*. R package Version 1.24. <https://CRAN.R-project.org/package=logistf>
- Holt, R. D., & Polis, G. A. (1997). A theoretical framework for intraguild predation. *The American Naturalist*, 149, 745–764.
- Holway, D. A., & Suarez, A. V. (1999). Animal behavior: An essential component of invasion biology. *Trends in Ecology & Evolution*, 14, 328–330.
- Huang, W.-S. (2006a). Ecological characteristics of the skink, *Mabuya longicaudata*, on a tropical east Asian Island. *Copeia*, 2006, 293–300.
- Huang, W.-S. (2006b). Parental care in the long-tailed skink, *Mabuya longicaudata*, on a tropical Asian Island. *Animal Behaviour*, 72, 791–795.
- Huang, W.-S. (2022). Dances with wolves: The demographic consequence of asymmetric competition and intraguild predation in a native-invasive skink system. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.gb5mkkwtj>
- Huang, W.-S., Lin, S.-M., Dubey, S., & Pike, D. A. (2013). Predation drives interpopulation differences in parental care expression. *Journal of Animal Ecology*, 82, 429–437.
- Huang, W.-S., & Pike, D. A. (2011). Climate change impacts on fitness depend on nesting habitat in lizards. *Functional Ecology*, 25, 1125–1136.
- Lee, K.-H., Chen, T.-H., Shang, G., Clulow, S., Yang, Y.-J., & Lin, S.-M. (2019). A check list and population trends of invasive amphibians and reptiles in Taiwan. *ZooKeys*, 829, 85–130.
- Lin, T.-E., Chen, T.-Y., Wei, H.-L., Richard, R., & Huang, S.-P. (2019). Low cold tolerance of the invasive lizard *Eutropis multifasciata* constrains its potential elevation distribution in Taiwan. *Journal of Thermal Biology*, 82, 115–122.
- Miller, R. S. (1967). Pattern and process in competition. In J. B. Cragg (Ed.), *Advances in ecological research* (pp. 1–74). Academic Press.
- Mollot, G., Pantel, J. H., & Romanuk, T. N. (2017). The effects of invasive species on the decline in species richness: A global meta-analysis. In D. A. Bohan, A. J. Dumbrell, & F. Massol (Eds.), *Advances in ecological research* (pp. 61–83). Academic Press.
- Muggeo, V. M. (2003). Estimating regression models with unknown break-points. *Statistics in Medicine*, 22, 3055–3071.
- Muggeo, V. M. R. (2017). Interval estimation for the breakpoint in segmented regression: A smoothed score-based approach. *Australian & New Zealand Journal of Statistics*, 59, 311–322.

- Mylius, S. D., Klumpers, K., de Roos, A. M., & Persson, L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *The American Naturalist*, *158*, 259–276.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community ecology package*. R package Version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Ota, H., Chang, H.-W., Liu, K.-C., & Hikida, T. J. Z. S. (1994). A new record of the viviparous skink, *Mabuya multifasciata* (Kuhl, 1820) (Squamata: Reptilia), from Taiwan. *Zoological Studies*, *33*, 86–89.
- Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.
- Pergl, J., Pyšek, P., Essl, F., Jeschke, J. M., Courchamp, F., Geist, J., Hejda, M., Kowarik, I., Mill, A., Musseau, C., Pipek, P., Saul, W.-C., von Schmalensee, M., & Strayer, D. (2020). Need for routine tracking of biological invasions. *Conservation Biology*, *34*, 1311–1314.
- Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, *4*, 53–74.
- Pintor, L. M., Sih, A., & Kerby, J. L. (2009). Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. *Ecology*, *90*, 581–587.
- Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, *20*, 297–330.
- Ruland, F., & Jeschke, J. M. (2020). How biological invasions affect animal behaviour: A global, cross-taxonomic analysis. *Journal of Animal Ecology*, *89*, 2531–2541.
- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., & Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, *32*, 305–332.
- Sala, O. E., Stuart Chapin, F. I., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M. N., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.
- Schoener, T. W. (1983). Field experiments on interspecific competition. *The American Naturalist*, *122*, 240–285.
- Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology*, *85*, 253–291.
- Short, K. H., & Petren, K. (2008). Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Animal Behaviour*, *76*, 429–437.
- Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*, 367–387.
- Strauss, S. Y., Lau, J. A., & Carroll, S. P. J. E. I. (2006). Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecology Letters*, *9*, 357–374.
- Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, *21*, 645–651.
- Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., & Losos, J. B. (2014). Rapid evolution of a native species following invasion by a congener. *Science*, *346*, 463–466.
- Uetz, P. (2021). *The reptile database*. <http://www.reptile-database.org>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708.
- Wissinger, S. A. (1992). Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology*, *73*, 1431–1444.
- Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*, 665–673.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Video S1. When the invasive *Eutropis multifasciata* enters the hole and tries to eat the eggs, the mother of the native species, the *E. longicaudata*, attacks the intruder violently to protect her eggs.

How to cite this article: Huang, S.-P., Lin, J.-W., Chou, C.-C., Liao, C.-P., Hsu, J.-Y., Tsai, J.-F., Liu, S.-L., & Huang, W.-S. (2023). Dances with wolves: The demographic consequence of asymmetric competition and intraguild predation in a native-invasive skink system. *Functional Ecology*, *37*, 614–624. <https://doi.org/10.1111/1365-2435.14276>