



## ECOLOGY

# Loss of sea turtle eggs drives the collapse of an insular reptile community

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Marine subsidies are vital for terrestrial ecosystems, especially low-productivity islands. However, the impact of losing these subsidies on the terrestrial food web can be difficult to predict. We analyzed 23 years of survey data from Orchid Island to assess the consequences of the abrupt loss of an important marine subsidy. After climate-driven beach erosion and predator exclusion efforts resulted in the abrupt loss of sea turtle eggs from the terrestrial food web, predatory snakes altered their foraging habitats. This increased predation on other reptile species in inland areas, resulting in population declines in most terrestrial reptile species. Comparisons with sea turtle-free locations where lizard populations remained stable supported these findings. Our study emphasizes the cascading effects of generalist predators and the unintended consequences of single-species conservation, highlighting the importance of understanding species interconnectedness and considering potential ripple effects in marine-dependent insular ecosystems.

## INTRODUCTION

The availability of nutrients and energy is critical in shaping the community dynamics of ecosystems, and some energetic inputs derive from adjacent or nearby ecosystems (1, 2). These subsidies often come from the transport of nutrients by organisms that move between habitats, such as seabirds (2, 3), seals (3), salmon (4), and sea turtles (5). Nutrient subsidies can have notable impacts on the receiving system, influencing the distribution and abundance of organisms (2, 4, 6, 7) and food web interactions (7–10), especially in ecosystems with poor primary productivity (8, 11). If such cross-ecosystem inputs are abundant and predictable in space and time, they may support high densities of key species, despite the relatively low primary productivity within the system (8, 11), which could in turn shape a number of species interactions in the receiving ecosystem (12). Because subsidies can be mediated by one or a few critical species, human activities can readily disrupt these inputs when key organisms that transfer nutrients across systems are affected (2, 13, 14). These disruptions at the species level can have far-reaching consequences for the entire food web linked to that subsidy, analogous to the loss of dominant species in bottom-up processes or the disruption of keystone species in top-down processes, ultimately leading to severe impacts on the ecosystem as a whole.

Sea turtles provide essential links between marine and terrestrial ecosystems, transporting nutrients and energy from the ocean to the land by nesting in beach habitats (5, 13, 15). Their nests contain substantial nutrition, energy, and biomass, with a large portion remaining within the terrestrial ecosystem. For example, in 1996, loggerhead sea turtle nests on a 21-km stretch of beach contained an estimated 1.6 million eggs, but only about 27% of the energy

content within these nests returned to the ocean as hatchlings, with the remaining resources staying onshore and entering the local terrestrial ecosystem (5). This input of nutrients from sea turtles is vital for the health and functioning of inland ecosystems, supporting both animal and plant communities, and is especially important for island ecosystems with more limited availability of nutrients from other sources (15).

Unfortunately, this crucial input is currently being affected by anthropogenic activities in two different ways. The first is beach erosion, which is becoming increasingly problematic because of the effects burgeoning human populations on the coast and global climate change increasing sea levels and the frequency and severity of extreme storms (16, 17). For example, across eight monitored Caribbean islands, 33 to 93% of the beaches showed significant signs of erosion, with an average erosion speed of 0.5 m year<sup>-1</sup> since 1985 (18). This worldwide erosion means that sea turtles are losing their nesting sites. The other major anthropogenic impact on the marine subsidy derived from sea turtles comes, unexpectedly, from conservation efforts. More specifically, predator exclusion, a commonly used sea turtle conservation management strategy, can constrict the flow of nutrients from sea turtles to terrestrial ecosystems (19, 20). While predator exclusion can be effective in protecting vulnerable turtle nests from egg predators (which are often invasive species), this practice also prevents native predators that have coevolved with sea turtles from accessing eggs and thereby stops the input of oceanic nutrients into the terrestrial community. The loss of this pivotal resource may have cascading effects on other members of the inland food web, especially on small islands with low productivity and dense populations of native predators subsidized by this significant input of oceanic nutrients. Unexpectedly, despite the pivotal role of sea turtles in inland ecosystems and the widespread use of predator exclusion in sea turtle conservation, there is currently no study investigating the impacts of this lost input on the terrestrial community.

Here, we present a case study based on 23 years of monitoring ecosystems in southeast Taiwan, including a site where we were able to collect data on key members of the terrestrial community before

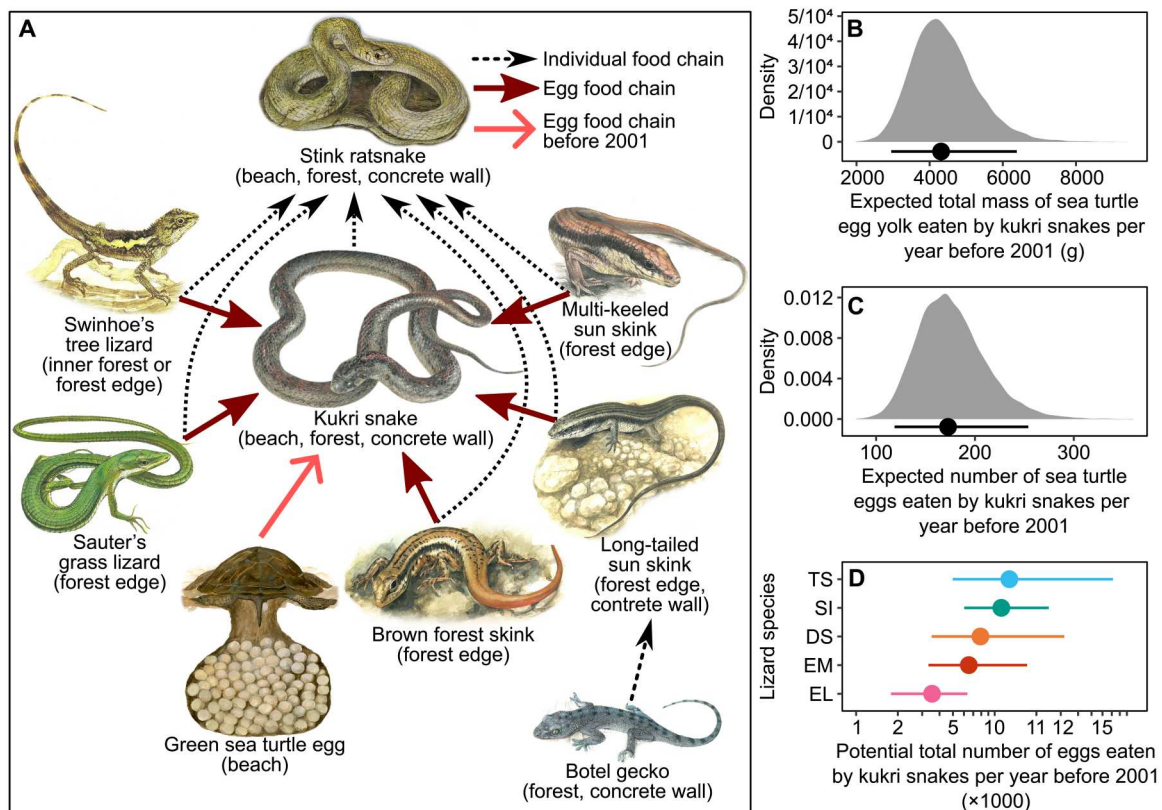
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and after the loss of sea turtle eggs as a nutrient subsidy. The reptile community on Orchid Island was primarily connected to green sea turtle (*Chelonia mydas*) eggs by two predators: the reptile egg-eating kukri snake (*Oligodon formosanus*) and the generalist predator stink ratsnake (*Elaphe carinata*, the top predator of the island community) (Fig. 1A). Sea turtle nests historically provided an abundant source of food for the flourishing kukri snake population on this small island, driving the evolution of remarkable behaviors in both prey and predator species (12, 21–23). However, because of beach erosion and predator exclusion practices meant to protect sea turtle nests, this pivotal resource has become inaccessible for both kukri snakes and stink ratsnakes. Gradual beach erosion, coupled with a series of unusually strong storms in 2001, resulted in the depletion of the larger beaches, rendering them unsuitable for sea turtle nesting. Consequently, sea turtles now only nest on one smaller beach, Badai Beach (24). Furthermore, since 1997, sea turtle nests at Badai Beach have been safeguarded using means to exclude predators. Over the course of several years, different exclusion fences were designed and deployed, leading eventually to the use of a fine-meshed plastic fencing structure surrounding each nest, which proved highly effective in preventing snakes from accessing nests. Therefore, despite their historical link to the island

ecosystem, sea turtle eggs have been almost eliminated from the terrestrial food web since 2001.

We combined both experimental and observational approaches to determine how this loss of a critical marine subsidy may have affected the terrestrial reptile community. We used an egg-feeding experiment and short-term mark-recapture data to quantitatively estimate the biomass of sea turtle eggs consumed by kukri snakes before the loss of nesting beaches. We then used our long-term survey data to investigate whether the spatial distribution and foraging behaviors of snake predators changed after the loss of sea turtle eggs. We also used these survey data to evaluate the population dynamics of all reptile species across the island before and after the loss of sea turtle eggs. Last, to determine whether population trajectories on Orchid Island differed from regional trends, we compared survey data for two formerly common and abundant lizards on Orchid Island with data from two ecologically similar locations (another island and a site on mainland Taiwan) where sea turtle eggs were never present.



**Fig. 1. The reptile food web on Orchid Island and the importance of sea turtle eggs in the context of egg predation by kukri snakes.** (A) Trophic links between reptile species, with egg predation shown by red arrows and predation on hatched individuals shown by black arrows. For species that nest in particular habitats, nesting habitat is given parenthetically after species name. (B) Estimated mass and (C) number of sea turtle eggs consumed annually by kukri snakes from 1997 to 2000 at Tungching Beach; (D) sea turtle egg mass consumed by kukri snake expressed as the equivalent number of lizard eggs for five lizard species. DS, *Diploderma swinhonis*, Swinhoe's tree lizard; EL, *Eutropis longicaudata*, ling-tailed sun skink; EM, *Eutropis multicarinata*, multi-keeled sun skink; SI, *Sphenomorphus incognitus*, brown forest skink; TS, *Takydromus sauteri*, Sauter's grass lizard.

**RESULTS****Number of eggs consumed by kukri snakes on Orchid Island**

We recaptured a total of 28 kukri snakes that were foraging on the sea turtle nesting beach and had lost mass (i.e., had not eaten) since their initial capture 1 to 6 days prior (table S3). Using these data, we estimated the daily weight-loss rate of free-ranging kukri snakes as 1.34% [0.92 to 1.77%; Bayesian  $R^2 = 0.276$  (0.150 to 0.387)]. We used the mass gain of the 10 kukri snakes fed sea turtle eggs in captivity (table S2) to estimate an egg mass conversion ratio ( $K$ ) of 32.2% (27.0 to 37.4%). Using these values for Eq. 3 (see Materials and Methods), we estimated that the average sea turtle egg mass a snake consumed per day ( $W$ ) before 2001 was 0.321 g (0.270 to 0.3734), which was equivalent to 0.081 (0.060 to 0.105) sea turtle eggs.

Incorporating our assessment of annual number of kukri snakes found at Tungching Beach before 2001 ( $N$  in Eq. 4) and the annual length of sea turtle breeding season ( $T$  in Eq. 4), we estimated that the total mass of turtle eggs consumed by kukri snakes annually during 1997–2000 was 5.40 kg (3.6 to 7.8; Fig. 1B), which is equivalent to 120.1 sea turtle eggs (79.8 to 174.2; Fig. 1C). If the kukri snake population extracted the same amount of egg from the five soft-shelled lizard species living on Orchid Island after 2001, it would be equivalent to a total annual consumption of ~5000 to 18,000 lizard eggs (4903 long-tailed sun skink eggs, 8992 multi-keeled sun skink eggs, 15,369 Swinhoe's tree lizard eggs, 10,684 brown forest skink eggs, or 17,589 Sauter's grass lizard eggs) (Fig. 1D).

**Shifts in prey and foraging habitat of snakes on Orchid Island**

Our segmented Poisson model estimates revealed that the frequency of lizard clutches attacked by kukri snakes increased significantly around the time of the loss of the sea turtle nesting beach in 2001 (3- to 19-fold, depending on species) before slowly declining over the subsequent years (Fig. 2). Accompanying this shift in behavior was a shift in habitat use (Fig. 3). Kukri snakes present on the beach decreased significantly since 1997 [−26% (−23 to −30%) per year] and stayed low in subsequent years (Fig. 3A). Although the estimated breakpoint is not 2001, the number of snakes on the beach dropped from ~20 individuals in years before 2001 to less than 5 in the years after 2001 (Fig. 3A). During the same time period, models showed significant increases in the abundance of kukri snakes present at concrete retaining walls [+28% (17 to 40%) per year around 2003; Fig. 3B], as well as in the forest habitat [+61% (17 to 120%) per year around 2003; Fig. 3C]. Following this increase, kukri snake abundance in the forest habitat remained constant [−2.4% (−5.9 to 1.2%) per year; Fig. 3C] but declined at the retaining wall [−37% (−30 to −43%) per year; Fig. 3B]. The number of stink ratsnakes on the beach and concrete retaining wall habitats similarly declined after 2003 [−42% (−25 to −56%) per year, beach; Fig. 3D] and 2006 [−50% (−22 to −68%) per year, concrete; Fig. 3E] but remained constant in the forest habitat [+2% (−2 to 6.1%) per year; Fig. 3F].

**Population trends of snakes and lizards on Orchid Island**

Our models estimating population trends for snakes and lizards on Orchid Island revealed widespread declines across this food web.

Populations of kukri snake and stink ratsnake were estimated to have declined by −12% (−10 to −13%) and −8.3% (−5.7 to −11%) per year, respectively, from 1997 to 2020 (Fig. 4, A and B). With the exception of geckos, our model estimates for lizard species on Orchid Island also indicated significant declines ranging from −11 to −25% per year (Fig. 4, C to G). Models for Sauter's grass lizards and long-tailed sun skinks showed consistent decline similar to the snakes, whereas Swinhoe's tree lizards, brown forest skinks, and multi-keeled sun skinks showed populations stabilizing at low levels after steep initial declines (Fig. 4, C to G).

Our Poisson regression models predict that counts for kukri snakes, stink ratsnakes, Sauter's grass lizards, long-tailed sun skinks, and multi-keeled sun skinks could drop to zero within a few decades (see the estimated boundary when the observed counts are predicted to drop below five and one; Fig. 4, A to D and G). Swinhoe's tree lizards and brown forest skinks are predicted to maintain low population sizes (Fig. 4, E and F). In contrast to other reptiles, the abundance of the Botel's geckos, which are not susceptible to kukri snake predation because of their hard-shelled eggs, increased significantly across 1997–2020, with a positive annual growth rate of 9.3% (6.8 to 12%) (Fig. 4H).

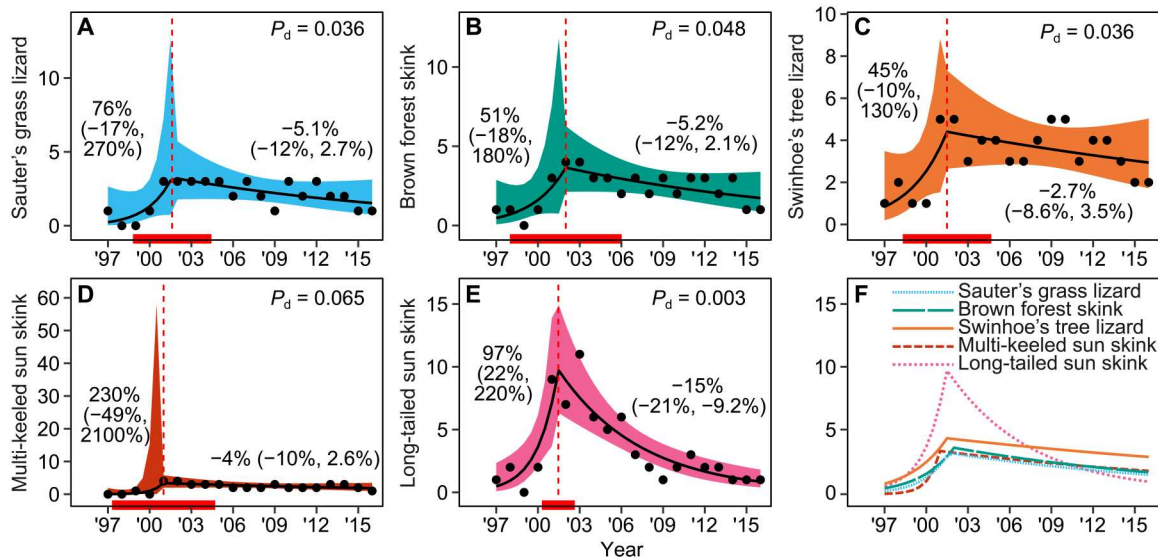
**Population trends of lizards on nearby locations**

To provide context for Orchid Island, we compared our survey data for long-tailed sun skinks and Swinhoe's tree lizards on Orchid Island to survey data and population estimates from nearby Green Island and Pintung County (mainland Taiwan), restricting comparisons for these models to the habitat types that were found at all three sites (concrete retaining walls for skinks and forest habitats for tree lizards). The population trends of long-tailed sun skinks were similarly stable for all three locations before 2002 (−3 to 1.9%; Fig. 5, A to C). However, the abundance of the long-tailed sun skink on Orchid Island declined markedly after 2002, with models estimating a significant negative annual growth rate [−32% (−27 to −36%) per year; Fig. 5A]. No breakpoints for the long-tailed sun skink population growth rates were observed for Green Island and Pintung, with models estimating modest declines at these sites [−2.1% (−0.087 to −4.1%) per year Green Island, −3% (−1.1 to −4.8%) per year Pintung; Fig. 5, B and C].

Similarly, Swinhoe's tree lizard growth rates on Orchid Island were significantly negative [−16% (−11 to −21%) per year] between 1997 and 2004, after which they remained low but stable [−2.8% (−1.5 to 7.3%); Fig. 5D], whereas Swinhoe's tree lizard population estimates for Green Island and Pintung remained stable across the sampling period, with no breakpoints [−0.11% (−1.4 to 1.2%) and −0.78% (−2.3 to 0.74%) per year, respectively; Fig. 5, E and F].

**DISCUSSION**

In this study, we illuminate the consequences of the loss of a vital oceanic subsidy, sea turtle eggs, within the reptile community of a small island. Between 1997 and 2001, as sea turtles were losing their large nesting beach and their nests were becoming protected at the smaller beach, we documented substantial shifts in kukri snake foraging behavior and habitat use. Kukri snakes were observed less often on beaches, and more often in forest habitats and concrete retaining walls (Fig. 3), where they were observed more frequently



**Fig. 2. The frequency of lizard clutches attacked by kukri snakes.** Panels represent the number of attacks observed on egg clutches of (A) Sauter's grass lizard (*T. sauteri*), (B) brown forest skink (*S. incognitus*), (C) Swinhoe's tree lizard (*D. swinhonis*), (D) multi-keeled sun skink (*E. multicaudata*) and (E) long-tailed sun skink (*E. longicaudata*) and (F) predictions for above five species, respectively. Percentages indicate the estimated annual rate of increase of attack and the corresponding 95% confidence intervals. Vertical dashed red lines and horizontal red lines indicate breakpoints and 95% confidence intervals estimated by segmented Poisson regressions.  $P_d$  represents the  $P$  value corresponding to the comparison of attack rates before and after breakpoints.

predating lizard egg clutches (Fig. 2). Ratsnakes exhibited a parallel shift in habitat preference to that of kukri snakes (Fig. 3, D and E).

Although the demographic trends we documented across lizard species on the island are complex (Fig. 4), the general patterns of decline reflected their relative susceptibility to kukri snakes. Geckos, which lay eggs that are not predated by kukri snakes, showed increasing population sizes across the study period. The three lizard species most susceptible to kukri snakes—the Swinhoe's tree lizard, brown forest skink, and multi-keeled sun skink—displayed sharp declines during the period in which sea turtle eggs were being lost, and then continually low population sizes in subsequent years. These species lay relatively larger eggs (table S1) in open and exposed soil beneath the forest canopy and lack parental care behaviors. Long-tailed skinks and grass lizard populations declined more gradually across the study period (Fig. 4). These species are less susceptible to kukri snake egg predation as the long-tailed skink exhibits parental care behavior specifically adapted to defend clutches against kukri snakes (21), and the grass lizard typically lays only two small eggs (table S1) in soil within dense grassland and among grass roots.

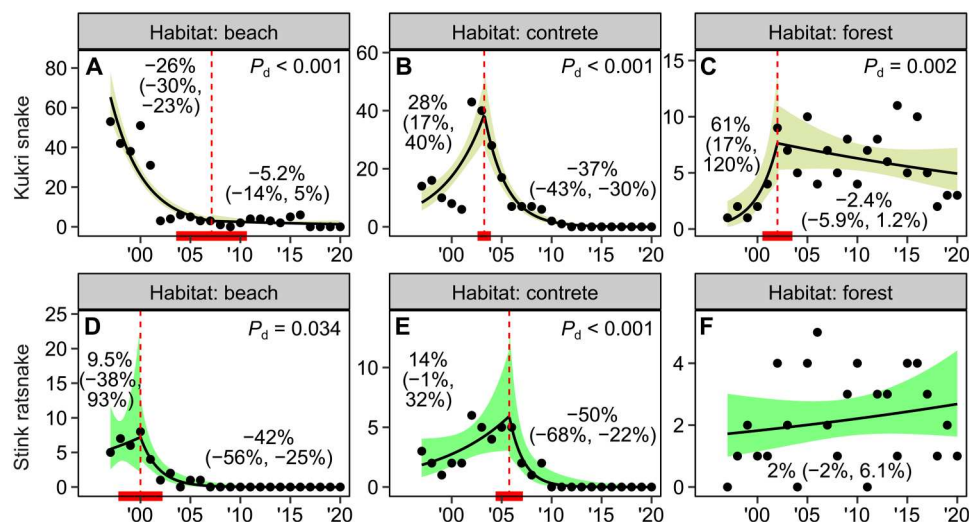
Although these findings represent compelling evidence for the loss of sea turtle eggs causing a shift in snake predatory behavior that subsequently drove steep declines in populations of lizards, the data are correlational, and a variety of other factors could also result in the patterns we documented. This region is susceptible to increasing human development (24), more frequent and intense storms driven by climate change (25), rising sea levels (26), and invasive species such as rats (27), and more intensive monitoring or more empirical studies would be needed to definitively demonstrate a causal relationship between kukri snake egg predation and lizard population declines. Nevertheless, the fact that populations of these lizards that occur in nearby areas that lack large kukri snake populations were stable across this same time frame (Fig. 5) also supports

the hypothesis that the lizard declines on Orchid Island are driven primarily by the loss of a pivotal marine food resource that had supported a large population of kukri snakes.

### The oceanic subsidy-generalist predator effect

Our study suggests that sea turtle eggs provided a critical subsidy to the terrestrial ecosystem of Orchid Island, supporting large populations of kukri snakes and stink ratsnakes, and when this subsidy was removed, these snakes shifted into other habitats for alternative prey (Figs. 2 and 3), perhaps driving the widespread decline of those lizard species vulnerable to egg predation (Fig. 4).

Our data on kukri snake egg consumption indicates that a shift in foraging behavior of this predator could have major consequences for egg-laying lizards, as we found that a substantial amount of sea turtle egg biomass was consumed by kukri snakes before 2001 (Fig. 1, B and C)—an energy resource that supported an abundant population of this specialist egg predator. When sea turtles were able to nest on the island, their nesting season largely overlapped the reproductive season of the island lizard community, likely easing predation pressure on lizards from kukri snakes (fig. S3) (12). After kukri snakes were deprived of sea turtle eggs, as they are obligate predators of reptile eggs, the large number of snakes increased egg predation across the lizard community, likely negatively affecting populations of every other soft-shelled egg-laying species. We also found evidence that the island's top generalist predator, the stink ratsnake, shifted habitat use away from the beach during the time sea turtle nests were being lost, which could have further exacerbated population declines of the lizard species that would then become its primary prey. Thus, almost all lizard species on Orchid Island likely experienced a major increase in predation pressure on both eggs and adults after the loss of sea turtle nesting beaches.



**Fig. 3. Abundance of kukri snake (*O. formosanus*) and stink ratsnake (*E. carinata*) in beach, concrete, and forest habitats.** (A to C) and (D to F) present the abundances of kukri snakes (*O. formosanus*) and stink ratsnakes (*E. carinata*) in beach [(A) and (D)], concrete [(B) and (E)] and forest [(C) and (F)] habitats. Percentages indicate the annual growth rate and the corresponding 95% confidence intervals. Vertical dashed red lines and horizontal red lines indicate breakpoints and their 95% confidence intervals, respectively.  $P_d$  represents the  $P$  value corresponding to the comparison between growth rates before and after breakpoints. A panel without red lines indicates that no breakpoint was favored by Bayesian information criteria.

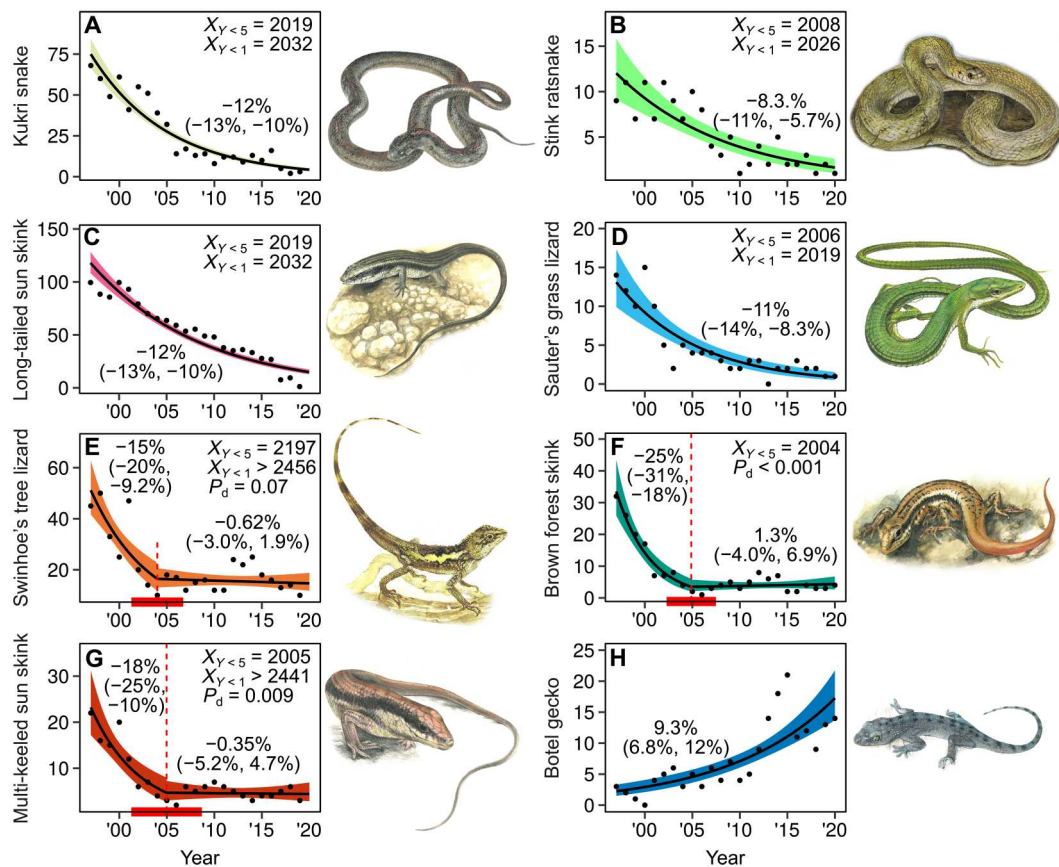
Sea turtle eggs represent a significant nutrient subsidy from marine ecosystems into terrestrial island communities (5, 13, 15). Cross-ecosystem nutrient subsidies usually operate as bottom-up processes in the recipient community, with subsidies becoming primary production, or being taken up initially by primary producers and then integrated into higher levels of the food chain (3, 4, 28–31). However, in the Orchid Island community, sea turtles acted as pivotal prey that influenced the foraging behavior and abundance of keystone snake predators, and the loss of this subsidy appears to have induced a strong top-down effect on other members of the food web. Similar effects have been documented in studies that manipulate subsidies (9, 10). In the case of Orchid Island, numerous species were affected due to their general susceptibility to the top snake predators. These top-down effects operating through the interaction between marine subsidies and generalist predators may be more widespread in nature than is generally appreciated [e.g., (6–8, 11)]. For instance, a recent study showed that the proliferation of wolves because of previously unavailable marine prey (sea otters) drove the extinction of terrestrial ungulates on an island (7). Our case illustrates that the marine subsidy-generalist predator interaction can significantly affect not just single prey species but can actually destabilize an entire community through the trophic network. Opportunistic predators that forage in a wide range of habitats, like stink ratsnakes and kukri snakes, often transfer resources from coastal areas to inland habitats (7, 32) and can become lynchpins within the terrestrial trophic networks, particularly on islands (11). They are typically thought to stabilize food webs because of the diverse and relatively weak connections to multiple prey species (33, 34). Nevertheless, when a large population of such predators is sustained by a cross-ecosystem subsidy, if the subsidy is lost, the subsequent shift in predatory behavior can unexpectedly destabilize a whole community. Because human modifications to oceanic ecosystems can affect the magnitude, quality, and spatial and temporal patterning of marine subsidies (14), understanding the

relationships between those subsidies and generalist predators is critical for comprehensively assessing the potential anthropogenic impact on insular ecosystems.

### The trade-offs in sea turtle conservation

Conservation efforts often prioritize the protection of individual species, but our study underscores the importance of taking a more comprehensive approach that considers how conservation actions will affect interspecific relationships, particularly in cases involving cross-ecosystem interactions. Our findings suggest that the conservation of sea turtle eggs from egg-eating snakes on Orchid Island may have contributed to the collapse of the island lizard community. It is important to protect green sea turtles, as this species has suffered severe population declines (24) and only one small beach (Badai Beach) remains suitable for nesting on Orchid Island. However, predator exclusion has been conducted on this beach for more than 20 years, effectively removing the sea turtles from the terrestrial island community for an extended period. Thus, when a series of storms and rising sea levels rendered the other nesting beach (Tungching Beach) unusable by sea turtles, within a few years the marine subsidy supporting kukri snakes and stink ratsnakes was lost, with severe consequences for the lizard community across the island.

The significant decline in almost all members of the lizard community on Orchid Island highlights the potential for unintended consequences resulting from conservation efforts focused on a single species. Similar examples exist in other systems (7, 35, 36). For instance, the conservation of wolves in Yellowstone National Park led to the recovery of willow trees and the return of beavers, which in turn drastically affected stream ecosystems (35). On island systems, such as in the case of the sea otter–wolf relationship (7), the consequences can be severe and drive the relatively small local populations to near extinction, as seen in our study. Therefore, management actions that are meant to conserve a specific species



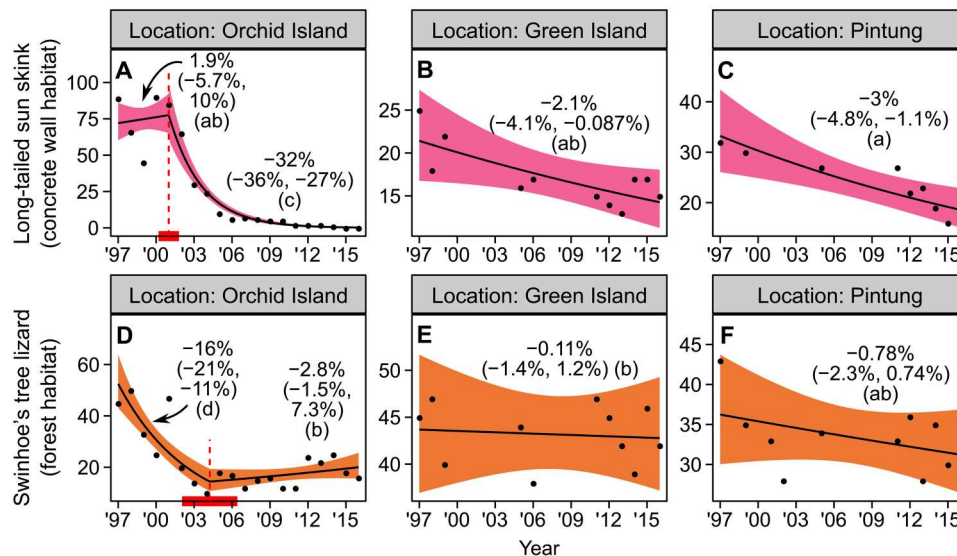
**Fig. 4. Population trends of the eight terrestrial reptile species native to Orchid Island.** Annual changes in abundance of eight reptile species, (A) kukri snake (*O. formosanus*), (B) stink ratsnake (*E. carinata*), (C) long-tailed sun skink (*E. longicaudata*), (D) Sauter's grass lizard (*T. sauteri*), (E) Swinhoe's tree lizard (*D. swinhonis*), (F) brown forest skink (*S. incognitus*), (G) multi-keeled sun skink (*E. multicarinata*), and (H) Botel gecko (*G. kikuchii*). Percentages indicate the estimated annual growth rates and the corresponding 95% confidence intervals. Vertical dashed red lines and horizontal red lines indicate breakpoints and their 95% confidence intervals, respectively.  $P_d$  represents the  $P$  value corresponding to the comparison between growth rates before and after breakpoints. A panel without red lines indicates no breakpoint favored by Bayesian information criteria.  $X_{Y < 5}$  and  $X_{Y < 1}$  indicate the boundaries when the observed counts will decrease to fewer than 5 and 1, respectively, as predicted by the model.

need to be carefully assessed to determine how interactions with other species will be affected (37). Despite the long-standing recognition of the importance of sea turtle eggs as a nutrient subsidy (5, 13, 15), there is a surprising lack of studies examining the consequences of severing this link between ecosystems. Our study demonstrates that protecting the conservation flagship, *C. mydas*, could lead to severe cascading effects on the terrestrial community.

On Orchid Island, the green sea turtle population is still threatened by beach erosion and human disturbance (24). Protecting both sea turtles and the sensitive terrestrial reptile community is a dilemma, especially given the precarious situation of both on this small island. However, the number of sea turtle nests has remained stable at the remaining nesting site, Badai Beach, over the past two decades (38). Meanwhile, the terrestrial reptile community is in urgent need of protection because our data indicate that many species are in danger of local extirpation.

Most sea turtle conservation studies use predator exclusion to reduce predation pressure from invasive species such as foxes, dogs, or rats (20), but there is currently no evidence of invasive species consuming sea turtle eggs on Orchid Island (27). We suggest that not excluding kukri snakes from the nesting beach,

while also implementing long-term population monitoring for all species, could provide more balance between conserving sea turtles and protecting the local reptile community. Allowing kukri snakes access to sea turtle nests again could repair the historical link between the ocean and the terrestrial community on this small island, and alleviate predation pressure on the island lizard community. Exclusion fences with holes large enough to allow for passage of the relatively slender kukri snake pass may be a suitable alternative to the fine-meshed plastic fence being currently used to exclude all predators. The impact of kukri snakes on sea turtle populations is likely to be minimal. Kukri snakes territorially exclude each other from sea turtle nests, and a single snake can consume only a small number of the dozens of eggs present in a nest before they hatch (27). In addition, sea turtles exhibit classic "type III" survivorship, with extremely high mortality of eggs and hatchlings, and past studies have shown that conservation efforts targeting adults are more effective than those protecting eggs (39). Ultimately, preserving the delicate balance between marine and island ecosystems is crucial to ensure the survival of not only individual species but also the additional members of the community linked to those managed species.



**Fig. 5. Comparisons of population trends of two lizard species common to three regional localities.** (A to C) Abundance of long-tailed sun skink (*E. longicaudata*) found in concrete wall habitats and (D to F) Swinhoe's tree lizard (*D. swinhonis*) in forest habitats on [(A) and (D)] Orchid Island, [(B) and (E)] Green Island, and [(C) and (F)] Pintung County. Percentages indicate annual growth rates and the corresponding 95% confidence intervals. Vertical dashed red lines and horizontal red lines indicate breakpoints and their 95% confidence intervals, respectively. Lowercase letters in parentheses indicate the results of the post hoc comparisons among growth rates, with the absence of a common letter for growth rates indicating a significant difference. A panel without red lines indicates that no breakpoint was favored by Bayesian information criteria.

## MATERIALS AND METHODS

### The reptile community on Orchid Island

We reconstructed the trophic relationships among the nine reptile species living on Orchid Island based on 23 years of field surveys and observations, as well as published studies [e.g., (21, 22, 40, 41)]. The nine reptile species native to Orchid Island include two predatory snakes (*E. carinata* and *O. formosanus*), the green sea turtle (*C. mydas*), two arboreal or grass-living lizards (*Diploderma swinhonis* and *Takydromus sauteri*), three skinks (*Eutropis multicarinata*, *Eutropis longicaudata*, and *Sphenomorphus incognitus*), and a gecko (*Gekko kikuchii*). The trophic interactions involving eggs of these species are substantially different than the trophic interactions among hatched individuals (Fig. 1, see more details in the Supplementary Materials). The eggs of most lizard species and the green sea turtle are preyed upon by the specialist egg predator, *O. formosanus* (kukri snakes) (22, 40). However, kukri snakes do not consume the rigid-shelled eggs of the Botel gecko (*G. kikuchii*), and the eggs of long-tailed sun skinks (*E. longicaudata*) are frequently protected from kukri snake predation by their mothers (12, 21). Once eggs hatch, individuals of all smaller species are preyed by stink ratsnakes (*E. carinata*), the top generalist predator on the island. In addition, the larger-sized long-tailed skinks consume Botel geckos that use the same concrete habitat (41). Green sea turtle eggs were available in large numbers at Tungching Beach, Orchid Island from 1997 to 2000 (12), but no sea turtle or sea turtle nest has been recorded there since 2001. This drastic reduction in turtle nests stems from ongoing beach erosion from rising sea levels as well as the destruction of beach habitat caused by unusually frequent and successive typhoons. Previous studies have shown how the loss of turtle eggs as a food source altered the habitat use and behavior of the kukri snake (12). To explore the impact of the loss of a vital cross-ecosystem subsidy on the terrestrial reptile community, we conducted a combination of

experimental and observational approaches. All of the collection and husbandry followed the Wildlife Conservation Act and Animal Protection Act of Taiwan. The animal use protocols were strictly reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) in the National Museum of Natural Science (license nos. NMNSIACUC108001 and NMNSIACUC109002).

### Field surveys

We studied the nine native reptile species (one species of sea turtle, six lizards, and two snakes) from early July to late August 1997–2020 on Orchid Island, Taiwan (46 km<sup>2</sup>; 22°02' N, 121°34' E; fig. S1A). We use standardized visual encounter surveys at Tungching Beach (the former nesting site for green sea turtles) and the adjacent terrestrial habitats to sample species. Surveys were conducted by two experienced investigators, one who continuously participated in surveys throughout this project with the assistance of other members of the same research group. Upon first capture, we marked all reptile individuals for permanent identification. We marked individuals of the large-sized reptiles (kukri snakes, stink ratsnakes, and long-tailed skinks) by injecting passive integrated transponder (PIT) tags between the skin and muscle at the belly (42) and marked smaller reptiles (tree lizards, grass lizards, brown forest skinks, multi-keeled skinks, and Botel geckos) with toe clips. In addition to permanent marks, we also left temporary marks for short-term identification using nontoxic paint at the outset of each field season to avoid repeatedly disturbing individuals during the same survey periods. The individuals were released at the capture sites immediately after processing.

During surveys at Tungching Beach, we also recorded the presence of sea turtles and their nests. The beach is bordered by a sand dune, with patches of mixed false pineapple (*Pandanus odoratissimus*) that are interspersed with silver grass (*Miscanthus floridulus*)

and saddle vine (*Ipomoea pescaprae*). This beach is approximately 300 m in length and 18,000 m<sup>2</sup> in area (fig. S1B) and was initially (1997–2000) covered by more than a meter of sand in which the turtles buried eggs during nesting periods, frequently attracting both kukri snakes and ratsnakes. We implemented surveys between 19:00 and 00:00 at night and again between 5:00 and 6:00 in the morning before sunrise every day to check sea turtle and two snakes. We identified the nest sites based on the large tracks left in the sand and by the visual confirmation of the presence of eggs. All snakes on the beach were captured and measured and then marked and released.

For the other terrestrial habitats on Orchid Island, we conducted surveys along 2- to 3-m-wide transects covering both sides of the major trail across Orchid Island and the trail of the southeast forest (fig. S1B). These trails bisect all major terrestrial habitat types found on the island. The surveyed area of the major trail was 7.2 km in length and contained both forest edge habitat and concrete retaining walls with holes. The 1.4-km southeast forest trail contained mainly forest as the major habitat type. All eight terrestrial species could be found in specific habitats they preferred adjacent to these trails (Fig. 1). We surveyed trails twice weekly between the hours of 8:00 to 11:00 and 14:00 to 17:00 for each week from early July to late August from 1997 to 2020.

During visual encounter surveys, we frequently observed kukri snakes foraging in habitats preferred by other egg-laying reptiles, including the beach (used by sea turtles before 2000), near the concrete retaining wall (used as an oviposition site by long-tailed sun skinks), in the forest (Swinhoe's tree lizards), and along the forest edge (multi-keeled sun skink and brown forest skinks). We used observations between 1997 and 2016 to document the overall frequency of lizard clutches attacked by kukri snakes in those habitats. When we observed egg clutches being attacked (fig. S2), we removed the kukri snakes for processing and dug the eggs out to determine the species to which the clutch belonged. The eggs of each species were identified by species-typical size, shape, and microhabitat (table S1).

We contextualized surveys on Orchid Island by also conducting surveys from 1997 to 2016 for the two lizard species (Swinhoe's tree lizard and long-tailed sun skink) that are native to two other locations in the region, Green Island and Pintung County (fig. S1A). These sites were chosen because they are nearby and ecologically similar to Orchid Island, but their beaches have never been used by green sea turtles for nesting. On Green Island, a 1.84-km forest trail was surveyed for tree lizards, and a 2-km trail with concrete retaining wall with holes was surveyed for long-tailed skinks. At our Pintung site, a 2.2-km forest trail was surveyed for Swinhoe's tree lizards, and a 2.3-km trail with concrete retaining walls was surveyed for long-tailed sun skinks. The survey duration, frequency, marking methodology, and number of field workers in these two locations were the same as described for Orchid Island.

### Total number of turtle eggs consumed by snakes annually

We calculated the mass of sea turtle egg required to fuel growth of free-ranging snakes by combining data from a captive feeding experiment (table S2) with mark-recapture data (tables S4 and S5). We captured and maintained 10 kukri snakes in captivity for at least 7 days and examined the relative mass gain of adult males, adult females, and juveniles when offered a known quantity of green sea turtle egg. Eggs for this experiment were collected from

nests that had been destroyed by other nesting turtles at the study site. Four males, four females, and two juveniles that ranged in size from 33 to 56 cm snout-vent length (SVL) and 33 to 160 g body mass were maintained under identical conditions on Orchid Island. Snake enclosures were housed outdoors to accommodate natural temperature fluctuations. Snakes were housed individually in 35 cm × 25 cm × 30 cm (*l* × *w* × *h*) glass containers containing 5 cm of beach sand, a shelter, and water ad libitum. Each snake was offered a single turtle egg of known mass and allowed to eat until satiated (pilot trials revealed that kukri snakes ignore extra eggs for several days after satiation, and no snake could eat an entire turtle egg within a 12-hour period). The uneaten egg portion was removed the following morning. We recorded the mass of egg yolk consumed by the snakes to the nearest 0.1 g by calculating the total egg mass minus the combined mass of unconsumed egg and eggshells. Snakes were weighed before eating, immediately after eating, and 1 week later to estimate the increase in steady-state body mass due to feeding (table S2).

To estimate the total mass and the total number of sea turtle or lizard eggs consumed during the sea turtle breeding season, we used a series of Bayesian estimations to make the following calculations. We assumed that a kukri snake without any food intake loses a constant proportion of its body weight per day

$$m_2 = m_1(1 - D)^t \quad (1)$$

where  $m_1$  and  $m_2$  denote the body mass of a kukri snake at first capture and recapture between  $t$  days, respectively, and  $D$  denotes the daily weight-loss rate of a snake. After transposing  $m_1$  and applying a natural logarithm function on both sides, we obtained a linear formula

$$\log\left(\frac{m_2}{m_1}\right) = t \times \log(1 - D) \quad (2)$$

which allowed us to estimate  $D$  (posterior median = 1.34%, 95% credible interval (CrI) = 0.92 to 1.77%; table S3) by using a linear regression model, which regressed  $\log(m_2/m_1)$  against  $t$  without the intercept term. For this equation, we used data from 28 field snakes captured at the beach and then recaptured several days later (recapture period less than 1 week; table S3) without consuming food (i.e., did not gain mass) between captures.

We used the 6-day change in body mass of kukri snakes that consumed sea turtle eggs to estimate the average mass loss of an egg consumed by a snake ( $M$ , posterior median = 24.98 g, 95% CrI = 23.83 to 26.13 g; table S2), the average of snake body mass gained ( $m_6 - m_0$ ; posterior median = 8.1 g, 95% CrI = 6.8 to 9.3 g; table S2), and the egg mass conversion ratio ( $K$ , posterior median = 32.2%, 95% CrI = 27.0 to 37.4%; table S2) as

$$K = \frac{m_6 - m_0}{M} \quad (3)$$

where  $m_0$  denotes snake body mass before consuming a sea turtle egg,  $m_6$  denotes the snake body mass 6 days after consuming a sea turtle egg, and  $M$  denotes the mass of egg consumed.

We then used  $D$  and  $K$  values, along with our field data on body mass of recaptured snakes ( $n = 50$ ; table S4), to estimate the average

egg mass a kukri snake consumed per day ( $W$ )

$$W = \frac{1}{n} \sum_{i=1}^n \frac{m_{i2} - m_{i1}}{Kt} = \frac{1}{n} \sum_{i=1}^n \frac{m_{i2} - m_{i1}(1-D)^t}{Kt} \quad (4)$$

where  $n$  denotes the sample size ( $= 50$ ),  $m_{i1}$  and  $m_{i2}$  denote the body mass of the  $i$ th kukri snake at first capture and last recapture between  $t_i$  days, and  $m_{i2}$  represents the expected body mass at the last recapture assuming that the  $i$ th kukri snake intakes nothing since the first capture based on Eq. 2.

Last, we estimated the total mass ( $U$ ) of egg consumed by kukri snakes during the sea turtle breeding season (15 May to 15 September; 120 days; fig. S3) and converted this mass to the total number of eggs consumed assuming that those eggs were from either sea turtles or each of the specific lizard species ( $E_i$ ) by calculating

$$U = W \cdot T \cdot N$$

$$E_i = U \cdot R_i / M \quad (5)$$

where  $T$  (120 days) denotes the period length,  $N$  (12.40, 95% CrI = 9.29 to 16.13; derived by table S4) denotes the annual number of kukri snakes found at Tungching Beach before 2001, and  $R_i$  (consumption ratio) denotes the ratio of consumed mass of a sea turtle egg ( $M$ ) over the whole egg mass of species  $i$  (table S1). We estimated  $R$  for sea turtle eggs as 55% (95% CrI = 51 to 60%) because kukri snakes usually only consumed the yolk of sea turtle eggs, and we assumed  $R = 100\%$  for lizard eggs because kukri snakes swallow lizard eggs whole. Because we excluded the effort exerted by snakes to search for lizard eggs (e.g., travel distance) and assumed that kukri snake completely digested lizard eggs, our estimates are conservative (i.e., underestimates) for egg mass ( $W$  and  $U$ ) and quantity of sea turtle/lizard eggs ( $E_i$ ) consumed by kukri snakes.

### Statistical analyses

To explore how the loss of sea turtle eggs potentially affected lizards, we compared the annual rates of lizard clutches attacked by kukri snake during 1997–2000 to the years 2001–2020 with Poisson regressions. We also used Poisson regressions to estimate annual changes in species abundances from our counts of unique individuals for each year, from 1997 to 2020. For each species, the total number of unique individuals counted or total number of times a specific behavior was observed each year were considered. We separately fitted these count data using a Poisson regression against year and a segmented Poisson regression with the R package “segmented” (43). Both types of models allowed us to incorporate species abundance, and the segmented Poisson regression allowed us to estimate the yearly breakpoint (the years at which the relationship between regressed variables changed). We opted for Poisson regression to model these processes for several reasons. A Poisson regression approach accommodates density-dependent processes when observed counts remain at relatively low levels, accurately describing the situation on Orchid Island. In addition, as we lacked the information required to determine the carrying capacity of each species because of the declines they are exhibiting, we chose Poisson models to strike an appropriate balance between model complexity and explanatory power. Last, our modeling approach was intentionally designed to detect density-dependent trends, focusing on identifying breakpoints in demographic patterns that

offer insights into changes in density-dependent regulation. We restricted the breakpoints ranging from 2000 to 2015 to avoid a segment fewer than 5 years. The 95% confidence intervals of the breakpoints were determined with a 5000-iteration bootstrap. We used Akaike’s second-order corrected information criterion (AICc) to evaluate alternative models and retained the model with the lowest AICc. We also used regressions to estimate the year when the observed number of individuals was expected to be fewer than five and one, respectively. Post hoc comparisons of growth rates were performed by using a Wald test, and the  $P$  values were adjusted using the Holm-Bonferroni method to control for the family-wise type I error rate. Unless stated otherwise, parenthetical values following model estimates are 95% CrIs (Bayesian models) or confidence intervals (Poisson models).

### Supplementary Materials

This PDF file includes:

Supplementary Text  
Figs. S1 to S3  
Tables S1 to S4  
References

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## Loss of sea turtle eggs drives the collapse of an insular reptile community

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