ECOLOGY

When males live longer: Resource-driven territorial behavior drives sex-specific survival in snakes

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Phylogenetic analysis has shown that males' propensity to engage in aggressive encounters is associated with females having greater longevity. Here, we confirm the causal link between aggression and reduced longevity by looking at an egg-eating snake (*Oligodon formosanus*) in which females defend territories in the presence of sea turtle eggs. We monitored aggressiveness and survival at two sites: a control site with a stable supply of turtle eggs, and a second site where we collected data before and after a storm that eroded the beach on which turtles nested, thus leading to a loss of territoriality. We show that territoriality was the driver behind higher injury rates in females. Territorial females also had lower survival and decreased longevity compared with the nonterritorial males, but these differences disappeared when females were not territorial. Our study demonstrates how resource availability can influence the evolution of sex-specific patterns of survival across vertebrates.

INTRODUCTION

In most animal clades, males have lower survival than conspecific females and thus live shorter lives [e.g., mammals (*1–3*), birds (*4*), amphibians (*5*), fish (*6*), and insects (*7*); but see (*8–13*) for some exceptions]. The need to compete for access to females has been argued to be a major driver of this asymmetry in survival, with males in many species growing faster (with consequentially greater resource requirements during development) and suffering injuries and stress as a consequence of aggressive interactions (*1*, *6*, *14*). For example, in a long-term study of social rank–related stress in a natural population of savannah baboons (*Papio cynocephalus*), the highest-ranking males had higher testosterone and glucocorticoid levels (stress hormone), suggesting that being at the very top may be more costly than being a low-ranking male (*15*). In a study of nonhuman primates, six of seven species showed intense male-male competition for mates, and the males of these species had shorter life spans than conspecific females (*16*). Muriquis (*Cebus capucinus*) were the only species with both sexes having equivalent life spans, presumably because of low male-male competition in this species (*16*).

A constraint of most studies trying to test the role of costly competition as a driver of increased mortality is that they have to rely on comparative data, since strategies within a species tend to be relatively inflexible. While it is possible to correct for phylogenetic non-independence, quantifying differences in lifestyle between different species that might also affect survival can be challenging.

Here, we present a detailed study of a territorial snake species (*17*), the kukri snake (*Oligodon formosanus*), which provides an ideal sys-

tem to investigate the relationship between competition and survival. The species is a specialist predator on small reptile eggs, mostly from lizards and other snake species; at our study site, however, the kukri snakes also consume sea turtle eggs (*17*). At both study sites, it is females rather than males that defend and compete for eggs as resource, leading to the prediction that survival should be male biased. To rigorously test the role of territoriality, we used a natural phenomenon that occurred when a severe storm eroded the beach where turtles nested at one of our study sites, leading to a loss of territorial behavior; we were thus able to compare the two sites before the storm (when female defended turtle eggs at both locations) to the sites after the storm (when turtle eggs, and the associated territorial behavior, was only present at one location). We confirm that turtle eggs are an important resource driving population densities at both study sites. We also confirm that, as a result of their territorial behavior, females have higher growth rates than males when eggs are available but that territoriality leads to higher injury rates and, ultimately, lower survival and shorter life span.

RESULTS

The role of turtle eggs in determining the numbers of kukri snakes

We captured and marked 476 kukri snakes (274 adult males, 139 adult females, and 63 juveniles; Fig. 1A), with 919 recaptures in Little Paiday (1997–2007); in Tungching (1997–2012), we marked 509 kukri snakes (302 adult males, 172 adult females, and 35 juveniles; Fig. 1B), followed by 632 recaptures. The numbers of both adults [mean = 83.75 ± 20.8 (1997–2000) and mean = 21.83 ± 9.5 (2001–2012)] and juveniles [mean = 5 ± 3.3 (1997–2000) and mean = 1 ± 0.9 (2001–2012); Fig. 1B] decreased significantly at Tungching following a storm that destroyed the beach where turtles nested [adult: estimated decline ratio = 0.261, $z = -4.003$, $P < 0.001$ (table S1); juvenile: estimated decline ratio = 0.186, $z = -3.300$, $P = 0.005$ (Fig. 1B and table S2)]. We can be confident that this decrease was a direct consequence of the change in resources because we do not observe a similar change at our other

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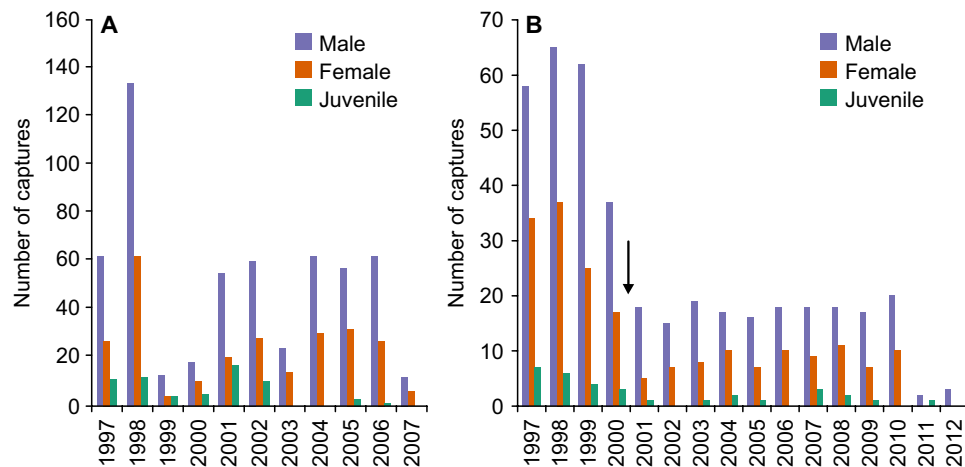*Corresponding author. Email: wshuang.380@gmail.com

Fig. 1. Number of individual kukri snakes (*O. formosanus*) captured annually at our study sites. Snakes captured in (**A**) Little Paiday Bay (where sea turtles nested throughout our study) and (**B**) Tungching (where sea turtles nested from 1997 to 2000, and nests were absent from 2001 to 2012), shown separately for adults and juveniles. Arrow indicates that a severe storm eroded the beach.

study site, Little Paiday, which, while being close to Tungching, did not suffer beach erosion [adult: estimated decline ratio = 0.847, $z = -0.461$, $P = 0.967$ (table S1); juvenile: estimated decline ratio = 0.431, $z = -1.703$, $P = 0.303$ (Fig. 1A and table S2)]. Accordingly, while the two sites did not differ in snake abundance before the storm [adult: population size ratio = 1.015 $z = 0.037$, $P = 1.000$ (table S1); juvenile: population size ratio = 0.625, $z = -1.649$, $P = 0.332$ (Fig. 1 and table S2)], Tungching had fewer snakes after the storm. This suggests that turtle eggs are a key resource driving the population density for kukri snakes, at least at our study sites. When recategorizing year as a three-level (1997–2000, 2001–2007, and 2008–2012) explanatory variable, both models attained higher Akaike information criterion (AIC) values (adult, 0.96; juvenile, 1.90), and there were no significant differences in abundance between 2001–2007 and 2008–2012 at Tungching [adult: estimated decline ratio = 0.696, $z = -1.037$, $P = 0.428$ (table S3); juvenile: estimated decline ratio = 0.784, $z = -0.331$, $P = 0.741$ (table S4)].

Body size differences between the sexes
Despite being the territorial sex, females were actually smaller than males at both sites: At Little Paiday, mean snout-vent length (SVL) of males was 51.78 mm (SD = 0.84, $n = 476$), while that of females only measured 48.86 mm (SD = 1.27, $n = 139$; $t_{411} = 3.88$, $P < 0.001$); at Tunching, SVL of males measured 50.94 mm (SD = 1.05, $n = 302$) compared with 48.04 mm for females (SD = 1.02, $n = 172$, $t_{472} = 4.22$, $P < 0.001$).

Growth rates
We next tested whether females benefitted from access to turtle eggs by growing faster. We compared the growth rate (daily increase in body mass) among sexes and study sites by using a bootstrapping heteroscedastic one-way analysis of variance (ANOVA) and its corresponding multiple comparisons. Females grew more than males at both Little Paiday [0.894 g/day (female, $n = 23$) versus 0.446 g/day (male, $n = 76$); $P < 0.001$] and Tunching [1.069 g/day (female, $n = 10$) versus 0.518 g/day (male, $n = 24$); $P = 0.011$] (Fig. 2 and table S5). When snakes of the same sex were compared between study sites, the growth of either males or females was statistically similar [$P = 0.175$
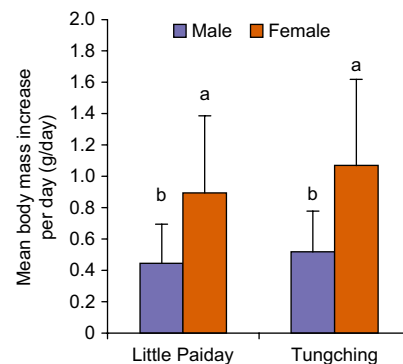

Fig. 2. Means ± SD of kukri snakes (*O. formosanus*) body mass increase per day at our Little Paiday Bay (1997–2007) and Tungching (1997–2000) study sites in Orchid Island, Taiwan. Lowercase letters summarize the results of pairwise multiple comparisons.

(male) and $P = 0.469$ (female); Fig. 2 and table S5]. Thus, at both sites, female grew faster than males, a pattern consistent with their increased access to turtle eggs.

Sex-specific injury ratios
Next, we tested whether females incurred more injuries when turtle eggs were available, thus incurring a cost of territoriality while defending this high-value resource. A distinct pattern of sex-specific injury rates was observed at both study sites, when sea turtle eggs were available (Fig. 3). Overall, females had significantly more injuries on their body than males (odds ratio = 1.848, $P < 0.001$; table S6). Before 2001, injury odds between two locations for both sexes were statistically similar (odds ratio = 1.237, $P = 0.689$; Fig. 3 and table S6). However, this pattern changed after sea turtle eggs became unavailable at Tungching after 2001, as revealed by a significant interaction between location and year ($P = 0.001$; table S6). The injury odd at Tungching declined and became statistically different to that at Little Paiday (odds ratio = 0.331, $P = 0.003$; Fig. 3 and table S4), although female injury rates remained higher than male injury rates. Consequently, although females might fight more than males even in the
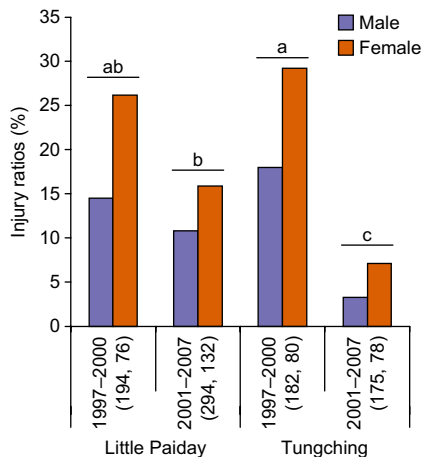
Fig. 3. Ratios of injuries incurred by male and female kukri snakes (*O. formosanus*) at Little Paiday Bay (where sea turtles nested throughout our study) and Tungching (where sea turtles nested from 1997 to 2000, and nests were absent from 2001 to 2012), shown separately by sex. Lowercase alphabets summarize the results of pairwise multiple comparisons among location-year groups. Numbers inside the parentheses present the denominators (total number of observed sea turtles).

absence of turtle eggs, the level of fighting was significantly higher when this valuable resource was present. The refitted models after recategorizing year as a three-level (1997–2000, 2001–2007, and 2008–2012) explanatory variable resulted in a greater AIC value (5.33) and no significant injury ratio difference between 2001–2007 and 2008–2012 in Tungching (odds ratio = 0.172, $P = 0.190$).

Sex-specific annual apparent survival rates of snakes

When turtle eggs were available, male snakes had higher survival rates than females at both sites [survival probability (males versus females): 0.661 versus 0.357, paired $t_2 = 7.352$, $P = 0.018$ (at Little Paiday); 0.877 versus 0.30, paired $t_2 = 5.284$, $P = 0.034$ (at Tungching); Fig. 4A]. However, when eggs were no longer available at Tungching between 2001 and 2012, there was no significant difference between the sexes in terms of survival rates (0.409 versus 0.201, paired $t_{11} = 1.696$, $P = 0.118$; Fig. 4A); on the other hand, the intersexual difference in survival persisted at Little Paiday, where eggs were present simultaneously (0.645 versus 0.33, paired $t_6 = 2.525$, $P = 0.045$; Fig. 4A).

Sex-specific life spans in wild and captive snakes

On the basis of our mark-release-recapture data, the expected life span (*Ax*) of males at Little Paiday was estimated to be more than twice as long than for females, both before and after the storm [$t_2 = 5.29$, $P = 0.034$ (1997–2000) and $t_6 = 3.13$, $P = 0.02$ (2001–2007); Fig. 4B]. Similarly, male longevity was much greater than female longevity at Tungching before the storm ($t_2 = 7.33$, $P = 0.018$; Fig. 4B). On the other hand, once turtle nests disappeared after the storm, there was no intersexual difference in longevity ($t_{11} = 1.14$, $P = 0.276$; Fig. 4B). Thus, we can conclude that the presence of a high-value resource, and the associated territorial behavior, was the likely driver of the difference in longevity between males and females. Conversely, when eggs were no longer available at Tungching (after 2000), the between-sex differences in survival rates and expected life span disappeared, although longevity decreased significantly for males, probably as a result of a decrease in overall food availability in the broader area.
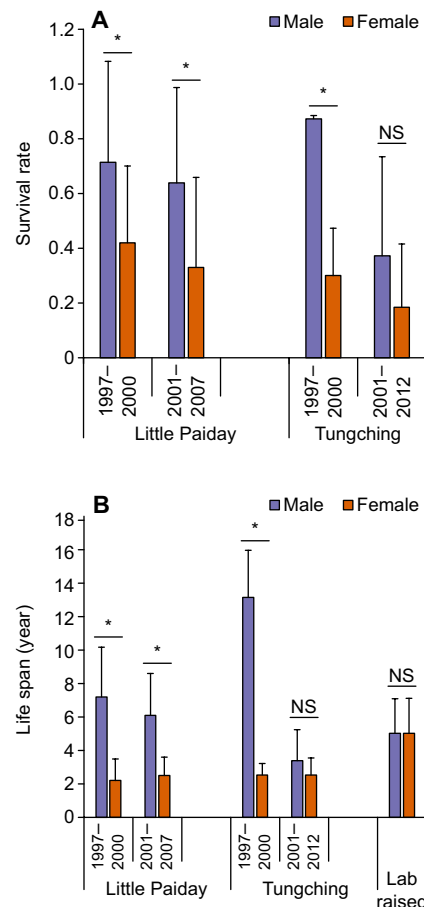

Fig. 4. Survival rates and estimated life span of male and female kukri snakes (*O. formosanus*) at Little Paiday and Tungching. Annual apparent survival rates (**A**) were calculated using mark-recapture analysis, and life-span estimates (**B**) are based on these survival rates. Data are shown for Little Paiday (sea turtles nested throughout our study), Tungching (sea turtles nested in 1997–2000 but were absent in 2001–2012), and laboratory-raised snakes from 1997 to 2015. NS, not significant. *$P < 0.05$.

The lack of sea turtle eggs as a food resource presumably led to lower levels of aggression, as the numbers of injuries decreased in both sexes and the differences in injury frequency were no longer significant between males and females following the loss of sea turtle eggs [see also (*17*)].

We tested whether we could detect any intrinsic sex difference in longevity by comparing males and females raised in the laboratory, where food availability was not a constraint. *Ax* was statistically similar ($t_{24} = 0.01$, $P = 0.991$) between males and females [5.02 years, range = 1.8 to 9, $n = 12$ (males) and 5.01 years, range = 3 to 10, $n = 14$ (females); Fig. 4B]. Captive-reared male snakes had a significantly longer *Ax* than their Tungching counterparts from 2001 to 2012 ($t_{22} = 2.92$, $P = 0.008$) but a shorter one than the Tungching male population from 1997 to 2000 ($t_{14} = 8.75$, $P < 0.001$). We found no significant difference in *Ax* between captive-reared and Little Paiday males ($t_{20} = 1.91$, $P = 0.07$; Fig. 4B). In contrast, laboratory-raised females had a significantly longer *Ax* than those at Little Paiday and those at Tungching during either time period [$t_{22} = 4.80$, $P = 0.004$ (Little Paiday); $t_{15} = 4.39$, $P = 0.003$ (Tungching) 1997–2000; $t_{24} = 5.13$, $P = 0.0012$ (Tungching) 2001–2012; Fig. 4B].

DISCUSSION

Our study of the Taiwanese kukri snake provides a clear example of how sex-specific survival and longevity can be highly plastic and heavily shaped by environmental factors, specifically resource availability and associated territorial defense. The natural experiment we report provides evidence for the role of aggressive interactions as the major mechanism driving differences in sex-specific mortality in this species. The captive data further support this conclusion, with no detectable differences in expected life spans under conditions where animals were housed individually and therefore were not involved in physical combat, experienced costly movements, or spent energy reproducing.

Sex-specific differences in life span have been attributed to reproduction-related behaviors in species across wide phylogenetic lineages, including invertebrates and vertebrates (1, 4, 6, 13). Studies of mortality in primates showed that, in species with relatively more intense male-male competition over access to mates, males had higher rates of aging and shorter life spans (compared with their conspecific females), whereas species with less intense intraspecific conflict over females did not exhibit between-sex difference in aging patterns and life spans (16). This pattern is suggesting that male-male competition may be a key factor driving faster aging in males in polyandrous species (16). Our study supports the conclusion by taking advantage of a natural experiment that allowed us to investigate these differences among populations of the same species. Furthermore, our study also provides an independent test of this explanation in a species where the sex roles are reversed: Females exhibited territorially aggressive behavior, suggesting that aggressive behavior (or the environment conducive to aggressive behaviors), not the sex per se, is a critical driving factor that shapes sex-specific life-span patterns.

Our results do not support some of the proposed hypotheses that attribute shorter life spans to factors intrinsic to the male sex. For example, the "mother's curse hypothesis" predicts the higher mutational load in the mitochondrial genome, which is passed down the female line, that is detrimental to male-specific traits (18). It has also been suggested that males bear the damaging effects of having higher levels of testosterone and stress hormones (15). Rather, we suggest that territorially aggressive behaviors, traits that tend to be environmentally shaped or context-conditioned, are major factors determining life span. Plasticity of territorially aggressive behavior was readily demonstrable in female snakes, which ceased to display territorial aggression when eggs were no longer available. Mortality rates have been shown to be phenotypically plastic for several primate species (including humans): Mortality rates were significantly different among populations of a given species, with those occurring in more demanding habitats exhibiting higher mortality rates (16).

What are the benefits for female snakes adopting turtle nesting site-defensive behavior? Although this territorial behavior obviously allowed females' greater capacity to obtain calories, their life span was not greater than that observed after the storm, when eggs were not available (when resources were actually scarcer). It seems likely that the key advantage of territorial defense and egg consumption was a higher reproductive output: Both population density and number of offspring were higher when sea turtle eggs were present (1997–2007 in Little Paiday) than when they were not (2001–2012 in Tungching). Obviously, reproductive investment on the part of female snakes demands ample supply of energy and nutrients, which could be provided by a high-value food resource such as sea turtle eggs. When reproductive output is concerned, the benefits derived from egg con-sumption could outweigh the costs of territorial aggression (i.e., a shorter life span); female snakes might thus be able to maximize their own reproductive output at the expense of their life span.

MATERIALS AND METHODS

Study system

We studied snakes (*O. formosanus*) from 1997 to 2012 at two independent sites in Orchid Island, Taiwan (46 km^2; 22°02′N, 121°34′E); Little Paiday (22°01′35.5′′N, 121°32′43.2′′E) is a 110-m long sea turtle (*Chelonia mydas*) nesting beach and Tungching (22°03′09.7′′N, 121°33′48.7′′E) is a 220-m long sea turtle nesting beach. At the start of our study, both sites were composed of rock covered by a deep sand layer (>1 m) in which sea turtles buried their eggs. These sites were located across the island from one another (an overland distance of 4 km) and separated by a hill 400 m in elevation; there was virtually no migration between sites (17). Snakes typically migrated from inland areas to sea turtle nesting beaches during summer, when sea turtles were laying eggs (fig. S1) (17, 19). However, the availability of sea turtle eggs as a food resource changed markedly for snakes during our study. The sandy beach at Tungching unexpectedly eroded during a large storm, and the underlying rocky substrate rendered this site unsuitable for the construction of turtle nests after 2000. Conservation measures at Little Paiday removed the sea turtle nests laid there after 2008. Thus, during the study period, sea turtle eggs were available for consumption by snakes at Tungching from 1997 to 2000 and at Little Paiday from 1997 to 2007 (19). The loss of turtle eggs as a food resource altered kukri snake ecology; snakes ceased migrating from inland areas to these two beaches, and consequently, females halted territorial behaviors (19). The sex-specific behavioral response by females provided us with an opportunity to understand whether territoriality shaped sex-specific life history traits; if so, the loss of female territorial behavior should result in an increase in female life span and survivorship. By studying both the sea turtle nesting beaches and the inland concrete walls, we were able to collect snakes at both study sites in every year, regardless of whether sea turtles were able to nest.

Number of adults and offspring

We surveyed both sea turtle nesting beaches six times every night from May to October (1997–2007 in Little Paiday and 1997–2012 in Tungching), recorded all sea turtle nests laid, and individually marked all snakes using microchips (20). On each 30-min visit along turtle nesting area (about 10 m in width between sand dune and vegetation) in each site, we captured snakes and recorded their sex by hemipenal eversion and tail shape [to accommodate the paired hemipenes, males had longer and stouter tails than females at the same body length (17)]. We measured snake body size SVL to 1 mm by extending snakes along a tape measure (electronic vernier calipers; code no. 500-138, model: CD-8"BS, Mitutoyo Corporation, Japan) and mass to 0. 01 g by electronic scale (model: FA-200, A&D Company Limited, Japan) and quantified the locations of all injuries. We attributed the higher incidence of injuries (including fresh injury and scar; fig. S2) on Orchid Island snakes to intraspecific agonistic encounters rather than to injuries inflicted by other kinds of predators because there were no nocturnal snake predators in our study area, so that the presence of snakes emerging from turtle nests with fresh injuries to their tails or body provided strong evidence that those injuries were obtained from territory defenders (17). We classified juvenile snakes as those with SVLs smaller than 36 cm (21).

Annual apparent survival rates

To investigate the costs and benefits of territorial resource defense of sea turtle eggs by male and female snakes, we compiled capture-mark-recapture (CMR) data and used program MARK to estimate sex-specific annual apparent survival rates (*22*), as described in Huang and Pike (*23*). We pooled recapture data for each year to estimate survival using a Cormack-Jolly-Seber model implemented in program MARK (*22*). Our main interest was in comparing survival between male and female snakes in natural habitats rather than in estimating recapture rates. We developed a set of candidate models that held recapture rates constant or differed between nest types and that tested for constant survival, time-dependent survival, differences in survival between sexes, or interactions between these variables. We derived an estimate for the lack of fit for the global (i.e., most parameterized) model in our candidate set using program RELEASE implemented in MARK. The global model did not fit the data well ($\chi^2 = 17.72$, df = 12, $P = 0.18$), so we adjusted our models for overdispersion (on the basis of the variance inflation factor, $\hat{c} = 1.54$) using quasi-likelihood AIC (QAIC$_c$) values before model selection (*1*, *24*, *25*). QAIC$_c$ values were used to select the best-approximating (hereafter, best) model for the data based on the principles of parsimony and trade-offs between under- and overfitting models (*24*). The best-supported models were those that make up the top 90% of Akaike weights and had relative deviations from the best model of less than two (i.e., ΔQAIC$_c$ < 2) (*24*). We used the highest-ranking candidate model to estimate survival and compared annual survival between male and female snakes over time using a paired *t* test. Survival estimates incorporated the probabilities of dying and emigrating (termed apparent survival), which in our study, equated to local persistence in the study area (*22*). We then used these survival rates to estimate expected life span.

Expected life span in the field

Expected life span (*Ax*) was estimated by the age-specific survivorship equation (l_x): $l_x = l_{x-1} \times S_i$ (1), where S_i represents survival rate (*26*, *27*). Starting from $l_0 = 1$, the value of l_x was repeatedly calculated until $l_x \leq 0.05$. For each iteration, the value of S_i was resampled from the apparent survival rates calculated from previous CMR exercises to factor in the parameter uncertainty (*19*). The number of age *x*, which had $l_x \leq 0.05$, was then defined as *Ax*. We ran 5000 simulations of *Ax* and calculated the average, SD, and confidence interval of *Ax* for both sexes at each of our two study sites.

Annual body mass increase

Because sea turtle eggs were the only food resource for snakes from the study sites, any snake body mass was likely directly due to egg consumption. Therefore, we used the body mass increase from recaptured snakes as a direct estimate of turtle-egg consumption in snakes.

Life span in the laboratory

To determine the intrinsic sex differences in longevity that influenced life span (*8*, *28–31*), we collected 13 males (SVL, 32 to 35 cm) and 14 females (SVL, 31 to 35 cm) juvenile snakes [less than 1 year old (*21*)] by hand from Orchid Island and raised them in the laboratory (1997–2015). Snakes were housed individually in glass containers [80 cm by 30 cm by 40 cm (length by width by height)] with a substrate of beach sand 5 cm in depth, a wooden shelter, and water available ad libitum. Temperatures ranged from 25° to 28°C. Snakes were fed a fresh chicken yolk every 3 days. Sex was determined by manual eversion of the hemipenes when animals grew into adults. Life span for each snake was determined as the period between initial capture and natural death in captivity. All work was performed in accordance with animal ethics protocols approved by the Wildlife Conservation Act by the Forestry Bureau, Council of Agriculture, Taiwan.

Statistical analysis

We used independent two-sample *t* test to compare kukri snake SVL among study sites and sexes. Residual normality and homoscedasticity were detected by using Shapiro-Wilk test and Bartlett's test, respectively. The kukri snake adult and juvenile capture numbers were fitted in a mixed-effect negative binomial regression model and a mixed-effect Poisson regression model, respectively. Year (before or after the storm in 2001), site (Little Paiday or Tungching), and their interaction were used as binary fixed factors, and the survey year (1997–2012) was considered as a random factor. We also merged these fixed factors (i.e., year and site) to achieve multiple comparisons, where the family-wise type I error rates were controlled. Whether or not these models fitting count data encounter overdispersion was checked by using χ^2 test of goodness. To fit the injury ratio, we used a logistic regression model, where snake sexes, study sites, year (before or after the storm in 2001), and their interaction were considered as binary independent variables. A backward model selection process to eliminate nonsignificant interaction was performed, and the reduced model reached a minimal AIC value. If there was any interaction remaining, then we merged the factors involved in the interaction to achieve multiple comparisons. A Hosmer-Lemeshow test was performed to check the lack of fit for logistic regression model. Because of the lack of data of kukri snake adult/juvenile capture numbers and injury ratios in Little Paiday during 2008–2012, we also fitted kukri snake adult/juvenile capture numbers and injury ratios against year, recategorized into three levels (1997–2000, 2001–2007, and 2008–2012). With this refitted model, if the AIC value increased and no significant difference between data collected in 2001–2007 and in 2008–2012 from Tungching was found, then we only reported the original model in which year was categorized as a two-level factor (before or after the storm in 2001). Data of snake body mass increase per day among sexes and sites were analyzed by using a bootstrapping heteroscedastic one-way ANOVA and its corresponding multiple comparisons. All body mass data were collected only when sea turtle eggs existed in the field. We used paired *t* test to compare the survival rates and life spans of snakes among sites and sexes, where years (1997–2012) were considered as statistical blocks, and used Shapiro-Wilk tests to confirm the normality of difference value. Recaptured snakes were used to calculate snake body mass increase per day (Fig. 2). For example, we captured a snake (no. 0001; body mass, 33 g) on 28 September 1997 and recaptured it in 8 October 1997 (body mass, 43 g). Then, the calculated body mass increase would be 43 − 33 = 10 g in 10 days (1 g/day). Regarding survival rates, if we captured a snake two times in 1997 and six times in 1998, then we used only one data point each year for survival analysis in MARK program.

SUPPLEMENTARY MATERIALS

Fig. S1. Territorial behavior of female snakes in Orchid Island, Taiwan.
Fig. S2. Photos of injury in snakes.
Table S1. Fitting numbers of adult kukri snakes against years and sites.
Table S2. Fitting numbers of juvenile kukri snakes against years and sites.
Table S3. Refitting numbers of adult kukri snakes against three-level years and sites.
Table S4. Refitting numbers of juvenile kukri snakes against three-level years and sites.

Table S5. Multiple comparisons of snake body mass increase among sites and sexes.
Table S6. Fitting injury ratios among sites, years, and sexes.

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