## Research

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**Author for correspondence:**
Wen-San Huang
e-mail: wshuang.380@gmail.com

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# Sum of fears among intraguild predators drives the survival of green sea turtle (*Chelonia mydas*) eggs

Chen-Pan Liao[1,†], Jung-Ya Hsu[1,2,†], Shi-Ping Huang[3], Rulon W. Clark[4], Jhan-Wei Lin[1], Hui-Yun Tseng[1,5] and Wen-San Huang[1,2,3]

[1]Department of Biology, National Museum of Natural Science, Taichung, Taiwan
[2]Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan
[3]Department of Life Sciences, Tunghai University, Taichung, Taiwan
[4]Department of Biology, San Diego State University, San Diego, CA, USA
[5]Department of Entomology, National Taiwan University, Taipei, Taiwan

(iD) C-PL, 0000-0001-9703-1994; J-WL, 0000-0003-4211-2302; H-YT, 0000-0002-1166-4756; W-SH, 0000-0003-0073-3557

Ecologists have long theorized that apex predators stabilize trophic systems by exerting a net protective effect on the basal resource of a food web. Although experimental and observational studies have borne this out, it is not always clear what behavioural mechanisms among the trophically connected species are responsible for this stability. Fear of intraguild predation is commonly identified as one such mechanism in models and mesocosm studies, but empirical evidence in natural systems remains limited, as the complexity of many trophic systems renders detailed behavioural studies of species interactions challenging. Here, we combine long-term field observations of a trophic system in nature with experimental behavioural studies of how all the species in this system interact, in both pairs and groups. The results demonstrate how an abundant, sessile and palatable prey item (sea turtle eggs, *Chelonia mydas*) survives when faced by three potential predators that all readily eat eggs: an apex predator (the stink ratsnake, *Elaphe carinata*) and two mesopredators (the brown rat, *Rattus norvegicus*, and kukri snake, *Oligodon formosanus*). Our results detail how fear of intraguild predation, conspecific cannibalism, habitat structure and territorial behaviour among these species interact in a complex fashion that results in high egg survival.

## 1. Introduction

Apex predators have profound effects on lower trophic levels, and often limit the size of prey populations through density-mediated direct and indirect interactions [1–3]. They can also impact mesopredator populations through both competition and intraguild predation [4,5]. In response, the behaviour, natural history and morphology of prey evolve in ways that allow them to avoid predation—a process that also engenders changes at other trophic levels [6]. Consequently, predators structure communities along multiple paths and alter processes inherent to the functioning of ecosystems via trait-mediated interactions [7,8]. According to current theoretical and empirical studies on trophic cascades, the indirect effects of the 'landscape of fear' created by predators may be as, if not more, important than direct killing [9–11].

However, evaluating trophic cascades in a natural ecosystem requires data that are difficult to collect and inferences about causality that are difficult to make reliably [12]. For example, in our field observations of three potential predators of sea turtle eggs on a tropical island, we only ever observed one of them (reptile-egg-eating snakes, *Oligodon formosanus*) consuming turtle eggs. There was no clear reason we could detect for why the abundant brown rats (*Rattus norvegicus*) and stink ratsnakes (*Elaphe carinata*) did not consume the nutritious and undefended eggs. Classic optimal foraging theory predicts that foragers will minimize search and handling time to maximize net energy intake, which

should result in high consumption of sessile and energy-rich food sources that lack strong defences [13,14]. Sea turtle eggs should thus be an optimal energy source for a number of consumers, but they survive the sessile, defenceless period during the incubation stage at a remarkably high rate.

One possibility is that the eggs, as the basal resource of a food web, are protected by interactions among the consumers at higher trophic levels, such as competition or intraguild predation. Theoretical models suggest that a variety of alternative stable states are likely in systems with intraguild predation [15]. The net effect of multiple consumers on the basal resource in a food web could be either negative or positive, depending on the relative effects of increased consumption, competition, intraguild predation and indirect predator effects [16,17]. Both models and controlled experiments in mesocosms indicate that the number of species within a trophic level (horizontal diversity) and the number of trophic levels (vertical diversity) interact to affect food web stability and basal resource consumption [18,19]. In addition, habitat structure can influence susceptibility to predation by modifying predator foraging behaviour [20] and providing species-specific refuges from predation or consumption [21]. Sea turtle eggs are buried in the sand, and although they can be readily excavated by all the potential egg predators present, even this modest level of shelter could have important effects on the interactions between consumers. The ultimate effect of shelter is contingent on how it influences encounter probabilities and outcomes among the interacting species [22,23].

Although numerous studies show that fear of predators can greatly influence community function and that fear itself is a powerful enough factor to affect wildlife population dynamics (e.g. [6]), there remain important gaps in our understanding that studying this egg-based food web could address. Most empirical work in on food webs uses either highly controlled mesocosms with small organisms [9,24] or field-based observational studies with megafaunal species [10,25,26]. Experimental studies combining natural observations with behavioural quantification of species interactions are relatively rare, and are needed to more broadly evaluate whether the potential effects from a landscape of fear actually result in the predicted population-level patterns in natural systems.

Additionally, our understanding of how predator–prey behavioural interactions affect food web structure is limited in several other important ways: (i) the taxonomic diversity of studies is relatively narrow; (ii) predators are often treated as static risk factors rather than active participants in a behavioural interaction [1]; and (iii) predator and prey behaviour is often explored in dyads, even though their interactions are embedded in a more complex ecosystem where multiple species are interacting simultaneously (i.e. multi-predator effects [27]). For example, predation risk and feeding efficiency are the main components in the behavioural trade-off made by foraging animals [9,28,29]. Feeding and vigilance are often mutually exclusive because individuals have to lower their heads to feed and/or need to pursue prey, thereby impeding predator detection (e.g. [6,28]). Foragers may also have to expose themselves to collect, handle or digest food, thereby experiencing greater predation risk than individuals that remain hidden in more protected areas (e.g. [29]). However, most of these studies have been focused on highly visual species (i.e. birds and insects) in response to isolated presentations of artificial predator cues (i.e. predator models, chemical cues, human surrogates). Animals that rely on other sensory mechanisms (e.g. olfactory) to detect food or predators, or studies that incorporate the dynamic behavioural interactions of multiple species of predators and prey, are less common [30,31].

In an attempt to address some of these gaps in our understanding of food web dynamics and predator–prey interactions, we combine field observations with experimental behavioural assays in controlled conditions to evaluate the hypothesis that intraguild predation on Orchid Island ultimately results in relatively high survival of sea turtle eggs. Importantly, our study system consisted of multiple predators whose shared prey was a sessile food resource, and we had the ability to compare behavioural responses of these species to each other not only on Orchid Island, but also on mainland Taiwan, from which the island populations originated. To experimentally test whether the fear of larger predators could enhance sea turtle egg survival, first we used long-term field observations of multiple free-ranging predators foraging near their shared potential prey (sea turtle nests) to document the arrival times, abundances and behavioural interactions among the three predators. Second, because direct interactions in the field between different predators were rare, we set up manipulative experiments in a controlled setting to collect data on the interactions of both pairs and multi-species combinations. Third, we repeated the laboratory experiments using individuals of the same species from mainland Taiwan populations to see how their behaviour differed from the derived Orchid Island populations that co-occur with sea turtle nests (green sea turtles do not nest on mainland Taiwan). We used results from all these experiments to evaluate support for the hypothesis that different predators had asymmetric impacts on the foraging success and behaviour of their competitors, and to develop a model that would highlight the importance of intraguild predation in buffering lower trophic levels from high mortality.

# 2. Material and methods

## (a) Study site

The laboratory experimental data for both mainland Taiwan and Orchid island were collected from 1997 to 2019. The fieldwork was carried out on a beach on Little Paiday, Orchid Island, Taiwan (22° 03′ N, 121° 33′ E) a known nesting site for green sea turtles (*Chelonia mydas*). We surveyed a study plot of 30 m × 60 m on the beach every day from May to August, and less frequently in September and October, from 1997 to 2007, to estimate the population densities as well as their correlations of sea turtle nests, brown rats, kukri snakes and ratsnakes (see details in the following subsection). This area has a tropical climate, with the maximum mean air temperatures of approximately 26°C from June to August and approximately 19°C from December to February. The study beach was bordered by a sand dune that was vegetated by mixed stands of false pineapple (*Pandanus odoratissimus*) interspersed with silver-grass (*Miscanthus floridulus*) and saddle vine (*Ipomoea pescaprae*).

## (b) Focal species

Upon arrival at the beach, green sea turtles laid their eggs between the dune and the open beach at night. The main nesting season on Orchid Island lasted from June to September [32]. The average nest depth each year varied from 57.7 to 73.1 cm, and the average clutch size ranged from 73 to 110 eggs per clutch, with the mean egg mass being 43.3 g. The annual mean incubation

duration ranged from 50 to 56 days [32]. After laying their eggs, the females covered them with sand, and returned to the sea immediately.

These beaches are frequented by brown rats, *R. norvegicus*, a brown or grey rodent with a body up to 25 cm long, a similar tail length and an adult body mass of 200–400 g. The brown rat is a true omnivore and will consume almost anything, but the diet of this species is often population-specific, and varies by environment and food source [33]. Rats are known to burrow extensively in search of food, both in the wild and in captivity, if given access to a suitable substrate [34]. To collect specimens for this study, we put 20 rat cages (29.2 × 10.2 × 9.2 cm$^3$) under the mixed false pineapple (*P. odoratissimus*) stands near the turtle nests and smeared peanut butter on a piece of sweet potato or bread or sausage inside each cage to attract the rats. We collected two size classes of rats, large (body mass > 250 g) and small (less than 150 g) from Orchid Island ($n = 113$) and Taiwan ($n = 116$).

Kukri snakes (*O. formosanus*) are obligate egg eaters that primarily consume soft-shelled reptile eggs [35–38]. On Orchid Island, these snakes mainly eat the eggs of green sea turtles and long-tailed lizards (*Eutropis longicaudata*) [35,38]. Sea turtle eggs provide an unusually abundant and long-lasting food resource for snakes [38], but consuming turtle eggs also has important associated costs, due to strong intraspecific competition for this resource. Individual snakes will defend nests by biting the tail of competitors; these attacks are more costly for males than females because the hemipenes are housed in the tail, and male reproductive ability can be severely compromised by tail bites from conspecifics [36]. For the current experiment, we collected two size classes of *O. formosanus* adults, large (SVL > 60 cm and body mass > 100 g) and small (less than 50 cm and less than 70 g) from Orchid Island ($n = 151$) and Taiwan ($n = 148$).

The stink ratsnake *E. carinata* (hereafter 'ratsnake') is the top predator on Orchid Island and can almost always be found in the vicinity of its major prey species, kukri snake [39]. The ratsnake is a large snake with a total length of up to 240 cm. The common name 'stink ratsnake' refers to this species's highly developed post-anal glands which, when the snake is disturbed, release a very strong, foul-smelling odour. The ratsnake is an active, predatory snake that eats everything from beetles and birds to small mammals and snakes, with a particular preference for the latter [40]. We collected large (SVL > 150 cm and body mass > 250 g) and small (less than 100 cm and less than 150 g) individuals from Orchid Island ($n = 127$) and Taiwan ($n = 125$) for our study.

## (c) Collection and maintenance

We collected the three focal species (brown rats, kukri snakes and ratsnakes) from both the beach at Little Paiday, Orchid Island, and also from mainland Taiwan populations (Yilan County, Pintung County and Taichung City). We used adults whose sexes were not determined, and individuals were randomly assigned to treatments, so no sex bias is expected. All animals were temporarily housed in small containers (30 × 20 × 20 cm$^3$) before experiments. All containers had an approximately 4 cm depth of sand as a substrate, shelter for hiding and water available ad libitum. In order to ensure hunger, all snakes were housed individually for two weeks, and rats were housed for 3 days, prior to conducting experiments. We built three larger glass testing arenas (30 × 60 × 90 cm$^3$) lidded with plastic sheeting and filled to a depth of 63 cm with sand collected from the beach because this depth corresponded to the mean depth of nests dug by green sea turtles [32]. Testing arenas were arranged on metal shelving units and visually isolated from each other with opaque barriers. In between trials, we removed the sand, emptied and cleaned the containers with ethanol, and allowed them to dry before refilling with fresh sea sand in order to prevent chemotactic cues left by organisms from influencing future trials. Temperatures in captivity ranged from 25 to 33°C.

We did not use the same individuals in more than one trial—all trials involved unique individual organisms. After the experiment was completed, all organisms were released in the field at the site of capture. A passive integrated transponder tag was inserted between the skin and muscle in the belly region of each released snake to prevent a recaptured snake being used again. The fourth toe on the left hind foot of each surviving rat was cut after experiment to prevent a recaptured rat being used again. All animals collected for the laboratory study were weighed using an electronic scale (±0.01 g) (Model: FA-200; A&D Company Limited, Japan) and SVLs were measured using electronic vernier calipers (±0.01 cm) (Model: CD-8″BS; Mitutoyo Corporation, Japan).

## (d) Pre-experimental tests

Because green turtle is a protected species in Taiwan (classified as 'endangered' internationally by the International Union for Conservation of Nature and Natural Resource), its eggs must not be collected directly from the field; therefore, we only opportunistically collected eggs that were disturbed and dug out from nests built earlier on the same site by other, later-arriving green sea turtles from 1997 to 1998 ($n = 18$). We used these eggs for pre-experiment tests designed to find whether snakes and rats from Orchid Island and Taiwan consumed those eggs ($n = 3$ for each predator in both populations). All predators consumed these unburried eggs regardless of population of origin. We purchased eggs of the Chinese stripe-necked turtle (*Mauremys sinensis*) from a turtle farm in Pintung, Taiwan. These eggs also have flexible egg shells similar to green sea turtles, and although much smaller (approx. 14 g versus approx. 43 g), we found that all three focal predators would readily consume both egg types. Thus, we were able to substitute farmed turtle eggs for the endangered green sea turtle eggs in subsequent predation trials.

## (e) Paired predator–prey tests

To determine predator–prey relationships among the four species (ratsnakes, kukri snakes, brown rats and turtle eggs), we first conducted paired tests. We created predator–prey pairs by randomly coupling individuals of each species in all possible combinations, including conspecifics (nine treatments total). In conspecific treatments, we randomly assigned one larger and one smaller individual to be housed together to test for the occurrence of cannibalism. We monitored predation outcomes in trials with snakes and rats by checking testing arenas once per hour for 12 h, after which surviving individuals were returned to their home cages. For trials with turtle eggs, we allowed predators to stay in the container overnight before a check was made to determine whether the eggs had been consumed.

In addition to these nine treatments, we evaluated the effect of burial in sand on egg predation by including treatments where turtle eggs paired with egg predators were either exposed, or buried to a depth of 66 cm (three additional treatments, one per predator).

To evaluate the protective effect of sand for kukri snakes hiding from ratsnakes, we also included an additional kukri–ratsnake treatment with no sand substrate present. In total, we conducted 10 replicates for all 12 of these treatments, and repeated all replicates and treatments with individuals collected from mainland Taiwan, for a total of 260 trials across 24 treatments (figure 1).

## (f) Multiple-predator tests

Sea turtle conservation measures at Little Paiday involved the removal and translocation of most sea turtle nests laid there after 2008. Thus, during the period of our study, sea turtle eggs were

only widely available for consumption from 1997 to 2007. However, because the conservation team left a small number of eggs buried in nests Little Paiday, rats and snakes could still be found around the beach, allowing us to collect additional experimental animals and conduct multiple-predator tests in captivity.

For these trials, we followed the same general procedures described above for the paired experiment, except we housed eggs with combinations of multiple predators, including trials with eggs and mesopredators (kukri snakes, rats and turtle eggs) and trials with all four species (ratsnakes, kukri snakes, rats and turtle eggs). These trials were designed to determine the hierarchy of prey preference for the top predator (ratsnakes) and compare behaviours of mesopredators with and without the presence of ratsnakes. We used direct observation to score outcomes of predatory events. Once ratsnakes began to constrict a prey item, we separated them and recorded the outcome as 'consumed'. We conducted trials only during the daytime (9.00–18.00). If there had been no consumption events during the daytime, we stopped the trial, collected the eggs, separated the predators (moved the predators back to their individual housing) and then resumed the experiment the next day during the daylight hours. If there was no interaction between the ratsnakes and the prey within 7 days, we stopped the experiment.

As with the paired experiments, we also included treatments with buried eggs for each predator combination, and a treatment with no eggs, resulting in seven treatments. We repeated these seven treatments with individuals from mainland Taiwan (14 total treatments). We conducted 10–13 replicates per treatment, resulting in a total of 158 multiple-predator trials.

## (g) Statistical analyses

We calculated the Spearman's rank correlation coefficients between annual numbers of observed sea turtle nests, and individuals of rats, ratsnakes and kukri snakes. We compared the proportion of prey consumed in paired and multiple-predator treatments using Fisher's exact tests. All of the $p$-values of pairwise comparisons were adjusted according to the Benjamini–Hochberg procedure in order to control the type I error rate by using the R function 'p.adjust' included in the built-in package 'stats'. Raw data and analytic R scripts are available in electronic supplementary material.

## 3. Results

### (a) Field observations

Overall, we observed 203 green sea turtle nests, 107 brown rats, 78 ratsnakes and 842 kukri snakes during the period from 1997 to 2007 in Little Paiday, Orchid Island (electronic supplementary material, figure S1). The abundance of turtle nests, brown rats and ratsnakes all positively correlated with each other (turtle nests versus brown rats, Spearman's correlation $r = 0.897$, $p_{adj} = 0.001$; turtle nests versus ratsnakes, Spearman's correlation $r = 0.837$, $p_{adj} = 0.005$; brown rats versus ratsnakes, Spearman's correlation $r = 0.905$, $p_{adj} = 0.001$), but there was no significant correlations between any of those and kukri snake abundance (turtle nests versus kukri snake, Spearman's correlation $r = 0.369$, $p_{adj} = 0.521$; brown rats versus kukri snake, Spearman's correlation $r = 0.338$, $p_{adj} = 0.527$; ratsnakes versus kukri snake, Spearman's correlation $r = 0.506$, $p_{adj} = 0.337$). We found that brown rats were the first egg predators to appear at the nests (usually within 1 h after the sea turtles had left), but when kukri snakes arrived (within 0.5–2 h), the rats retreated immediately; thus, rats were never observed digging up sea turtle eggs. Kukri snakes, on the other hand,

immediately tried to enter nests upon arrival at the beach. The apex predators, ratsnakes, typically appeared soon after the arrival of kukri snakes but never entered turtle nests; instead, ratsnakes searched around the nests, occasionally capturing and consuming kukri snakes. The arrival hierarchy of focal species on Orchid Island is shown in electronic supplementary material, figure S2 [39].

### (b) Paired predator–prey tests
#### (i) Predator–egg pairs
In the paired experiments using buried turtle eggs, we found that brown rats and ratsnakes from the Orchid Island population never dug into the sand to consume turtle eggs (0% consumption), but kukri snakes always did (100% consumption; figure 1a). By contrast, all predators consumed the eggs when the eggs were exposed (100% consumption; figure 1b). In experiments with the same species from mainland populations, all three readily dug up eggs: all predators almost always consumed turtle eggs (90–100% consumption) regardless of whether eggs were buried or exposed (figure 1a,b).

#### (ii) Predator–predator pairs
In paired trials with different predators, ratsnakes always consumed rats (100% consumption; figure 1c), but kukri snakes never did, regardless of population of origin (0% consumption; figure 1c). Ratsnakes also always consumed kukri snakes when kukri snakes exposed themselves above the sand (100% consumption; figure 1c). In trials with two conspecifics, rats and kukri snakes never exhibited cannibalism, regardless of population of origin (0% consumption; figure 1c). By contrast, larger ratsnakes from both locations readily consumed smaller ones (90% consumption; figure 1c).

### (c) Multiple-predator tests
When paired with kukri snakes, brown rats from Orchid Island did not dig up buried eggs (0% consumption; figure 2a) but always consumed exposed eggs (100% consumption; figure 2b), while brown rats from Taiwan readily consumed both buried and exposed eggs (buried eggs, 91% consumption; exposed eggs, 100%; figure 2a,b).

By contrast, kukri snakes never consumed eggs in any of the multiple-predator scenarios (0% consumption; figure 2c–f), which was very different from the results in the paired predator–egg tests, indicating that the presence of either rats or ratsnakes prevented kukri snakes from consuming eggs.

In trials with all three predators present, ratsnakes consumed brown rats at a high rate (85–100% consumption; figure 2e–g), but rarely consumed kukri snakes (0–9% consumption; figure 2e–g). If eggs were present (either buried or exposed) in these trials, they were left unconsumed by any of the three predators (0% consumption; figure 2e–f). These patterns were similar across both mainland and island populations.

Finally, in the absence of brown rats, ratsnakes almost always consumed kukri snakes (90–100% consumption; figure 2c,d), but ignored buried or exposed eggs (0% consumption; figure 2c,d), regardless of population of origin. Thus, ratsnakes exhibited strong preferences for brown rats, followed by kukri snakes, and then turtle eggs.
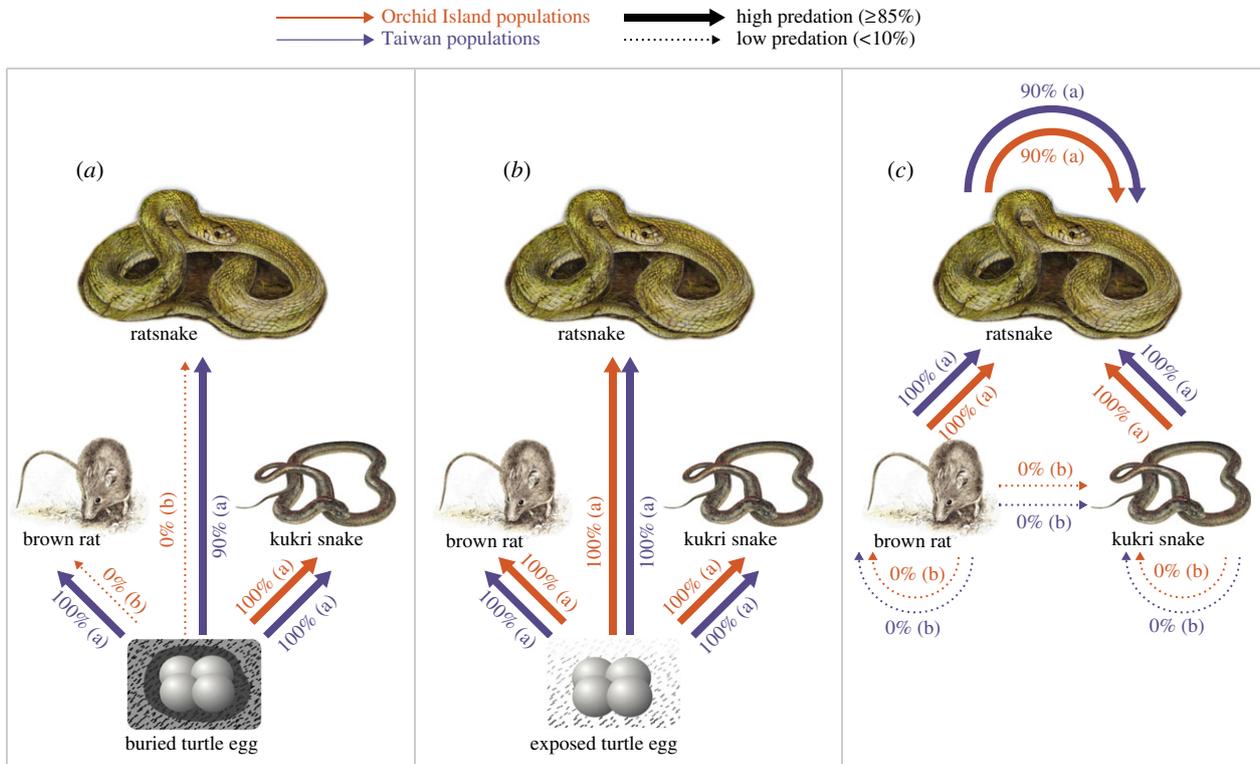
**Figure 1.** Percentage of prey consumed in paired trials using Orchid Island and Taiwan populations. Experiments included buried turtle eggs paired with either a brown rat, a kukri snake or a ratsnake (*a*); exposed turtle eggs paired with either a brown rat, a kukri snake or a ratsnake (*b*); all intraspecific and interspecific pairings of brown rats, kukri snakes and ratsnakes (*c*). Trials in each of these 24 experiments were replicated 10 times. Each arrow corresponds to one experiment (a pairing in either Orchid Island or Taiwan). Lower-case letters in parentheses indicate the results of Fisher's exact tests comparing all trials to each other; different letters indicate significantly different consumptions after correction for multiple comparisons using the Benjamini–Hochberg procedure. All pictures drawn by Peng, Shuan-Yu. (Online version in colour.)

## 4. Discussion

On Orchid Island, sea turtle eggs are numerous, sessile, defenceless and highly nutritious, and co-occur with three abundant predators that readily consume them under experimental conditions, even when the eggs were buried under sand. We found surprisingly high rates of survival of sea turtle eggs in nature under these conditions. How do they survive? Our results demonstrate that the behaviours of the three predators (brown rats, kukri snakes and ratsnakes) towards each other and towards turtle eggs vary depending on the population of origin, presence of other predators and exposure of the eggs. The net effect of this combination of factors, along with the female-biased territoriality of kukri snakes [38], is protective for sea turtle eggs.

When no other predators are present, all three species from mainland Taiwan (from which the Orchid Island populations are derived) consumed turtle eggs placed in the enclosure with them, even if the eggs are buried under 66 cm of sand (the typical depth of a sea turtle nest), indicating that all of these predators will readily eat turtle eggs and are capable of locating them when they are buried (figure 3*a*). However, ratsnakes and rats from Orchid Island never attempted to dig up buried turtle eggs, either in the wild or during captive experiments (figure 3*b*). These results indicated a strong interaction between predator species, population of origin and egg exposure, with rats and ratsnakes from the island population being wary of digging up turtle eggs, even though individuals from the parental mainland populations readily did so. Our experiments combining

multiple predators provide an explanation for this derived wariness: buried turtle eggs on Orchid Island attract large numbers of kukri snakes and rats, which in turn attract large numbers of ratsnakes, which readily consume rats, kukri snakes and other ratsnakes (figures 1 and 2). Thus, digging up turtle eggs on Orchid Island comes at the cost of increased exposure to ratsnake predation. Even ratsnakes themselves would be vulnerable to larger conspecifics, as this species is cannibalistic and individuals would presumably be strongly disadvantaged if a conspecific attacked while their head was buried in the sand.

Our field observations support the hypothesis that the fear of ratsnakes exerts a net protective effect on sea turtle eggs. Rats are continually present at the nesting beach, and are the first predator observed around sea turtle nests after the eggs are laid and the sea turtles depart. However, although Orchid Island rats will scavenge eggs present on the surface, they are wary of digging into turtle nests. This is probably because, within 0.5 h of eggs being laid, kukri snakes are attracted to the beach and nests in large numbers, followed by ratsnakes. Rats are the favoured prey of ratsnakes (figure 2), and heightened vigilance of rats is probably responsible for the low rates of ratsnake predation on rats; we never witnessed free-ranging ratsnakes successfully capturing rats. By contrast, ratsnakes were very successful at capturing and consuming kukri snakes, which they prefer to turtle eggs (figure 2). The availability of kukri snake prey combined with the risk of conspecific predation is a plausible explanation for why ratsnakes were also unwilling to dig into turtle nests. Only kukri snakes were willing to dig into sea turtle nests.
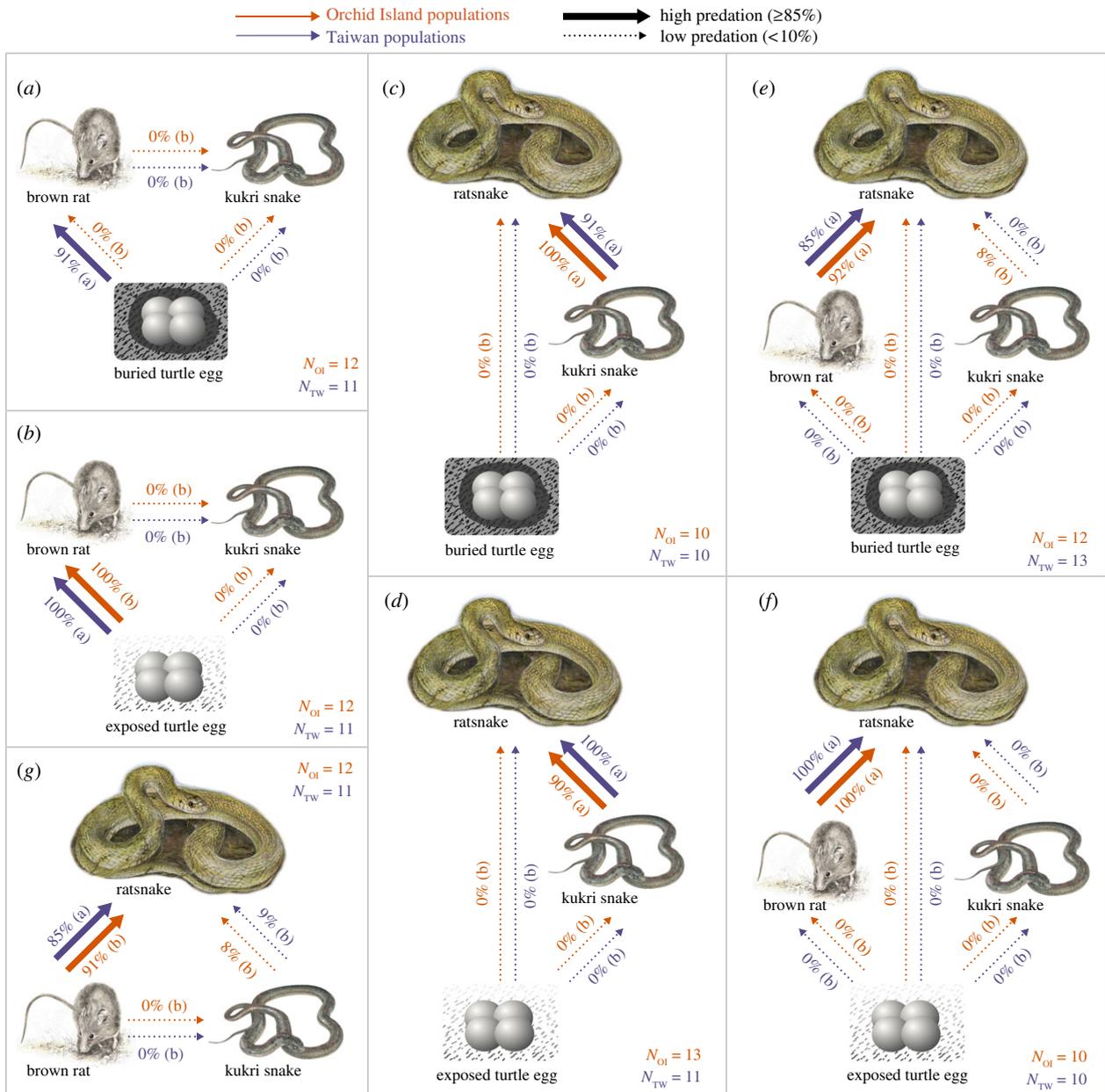
**Figure 2.** Percentage of different prey items consumed in multiple-predator trials using Orchid Island and Taiwan populations. Experiments include buried (*a*) and exposed (*b*) turtle eggs placed in enclosures with both a brown rat and a kukri snake; buried (*c*) and exposed (*d*) turtle eggs with both a kukri snake and a ratsnake; buried (*e*) and exposed (*f*) turtle eggs with all three predators; and a brown rat, kukri snake and ratsnake with no turtle eggs (*g*). Each arrow represents one experiment (a multi-species group in either Orchid Island or Taiwan). $N_{OI}$ and $N_{TW}$ represent numbers of replicates within experiments conducted on Orchid Island and Taiwan, respectively. Lowercase letters in parentheses indicate the results of Fisher's exact tests comparing all trials to each other; different letters indicate significantly different consumptions after correction for multiple comparisons using the Benjamini–Hochberg procedure. All pictures drawn by Peng, Shuan-Yu. (Online version in colour.)

Although kukri snakes are vulnerable to ratsnake predation, the risk of digging into nests is probably worth the substantial reward, especially for female snakes. Individual kukri snakes can defend nests from conspecifics, leaving them with a large food reward many times their own body mass. Furthermore, kukri snakes buried with eggs are relatively safe, as neither rats nor ratsnakes attempt to dig into nests. Although kukri snakes will consume as many eggs as they are able, the large number of eggs laid and the relatively small size of a single snake results in a protective effect for the clutch: the territorial behaviour of a single snake prevents other kukri snakes from entering the nest, and the fear of ratsnakes protects the nest from the other mesopredator. Together, the combination of the fears expressed by the various predators of sea turtle eggs drives the survival of the abundant, sessile and palatable turtle eggs, and eventually most of the eggs hatch (i.e. hatching rate 53–94% [32]).

Given the heterogeneous landscape of food and fear, it is not surprising that carnivores often balance the two behaviourally. These sublethal costs of predation can have as much influence on overall prey dynamics as direct mortality [11,42]. The Orchid Island ecosystem may be somewhat unique in that even the apex predator is subject to this trade-off. Ratsnakes from mainland Taiwan will dig into sand to consume eggs or kukri snakes, but Orchid Island ratsnakes will not, presumably because buried turtle eggs on Orchid Island are associated with both the risk of conspecific cannibalism and the presence of more appealing prey.
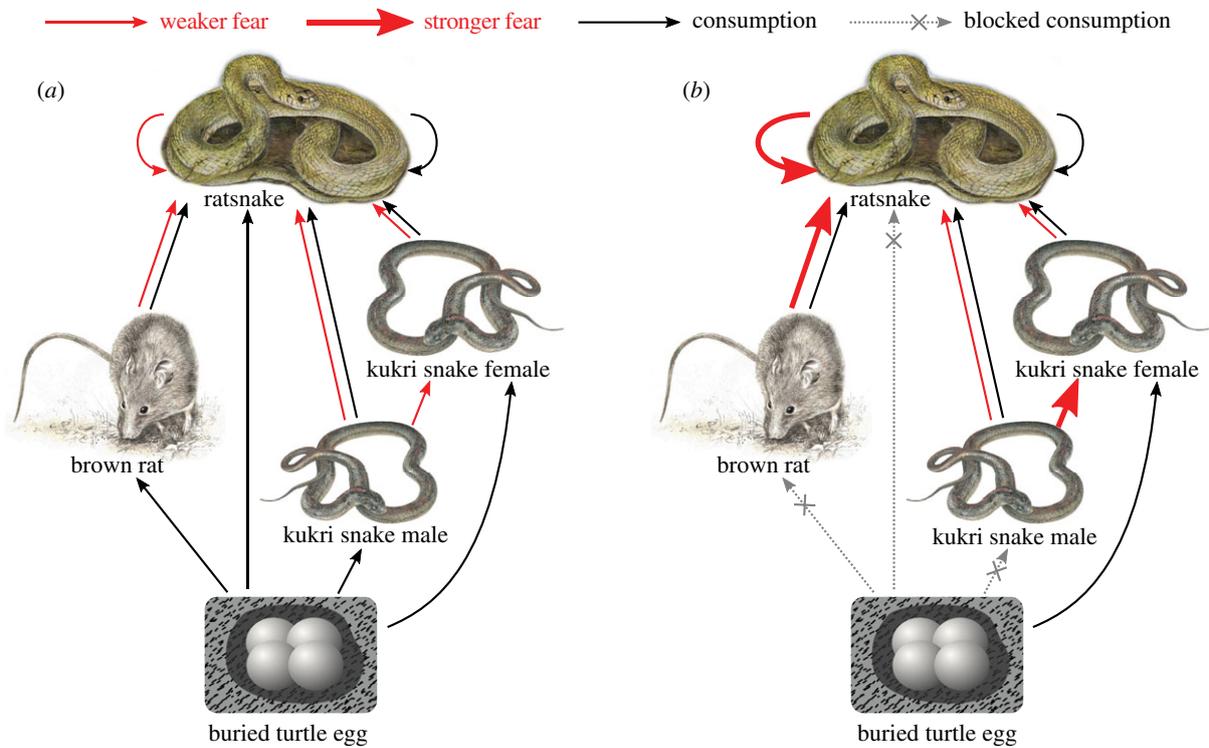
**Figure 3.** The altered trophic relationships between the organisms on both Taiwan (*a*) and Orchid Island (*b*). Red and black arrows indicate the direction of fear and consumption, respectively. Males expelled by female kukri snake reported by Lee *et al*. [41]. (Online version in colour.)

We never observed rats digging up turtle eggs on Orchid Island, either in the field or in the laboratory, even though rats from mainland Taiwan dig up deeply buried eggs and brown rats are known to burrow extensively if given access to a suitable substrate [34]. It is probable that the first rats colonizing Orchid Island (presumably in concert with human colonists) retained this trait and dug into turtle nests, but high levels of predation by Orchid Island ratsnakes (attracted to the beach in search of kukri snakes) led to a swift alteration in their behaviour. Animals will forage in safe areas if they can [43], but, when they must forage in risky areas, they adopt many behaviours to manage this risk, including reduced time allocation to foraging, increased periods of vigilance or simply abandoning feeding in risky areas [6]. Predation risk has clear sublethal behavioural impacts on prey, modifying where they go and how long they stay at a feeding patch [44]. Therefore, natural selection may have favoured rats on Orchid Island that maintain high levels of vigilance, which, in the case of Little Paiday, would preclude burying one's head in the sand to burrow for eggs. Rats are still readily observed around the beach, however, due to the opportunity to find and consume eggs on the surface which are accidentally dug out from nests by later-arriving green sea turtles—a foraging activity that is more compatible with avoidance of ratsnake predation.

The differential behaviours of rats and ratsnakes towards buried eggs also underscores the role of habitat structure in mediating indirect effects of predators. Just as elk feed preferentially on lower-quality food closer to the safety of the forest when wolves are nearby [45,46], rats and ratsnakes seem unwilling to engage in risky excavation activities when their own predators are abundant. The sand provides not only a refuge for the eggs, but also for the kukri snakes that are willing to dig into them, as kukri snakes remain safe from ratsnake predation once they have entered a nest.

This finding is similar to effects commonly documented in mesocosm studies, where increased habitat complexity can either reduce consumption of basal resources or enhance it, depending on the specifics of how different consumers use the structure [19–21].

The foraging strategy of the reptile-egg-eating kukri snake (*O. formosanus*) is quite different from that of the other two predators. Regardless of the numbers of turtle nests or the presence of ratsnakes, kukri snakes still appeared on the beach (within 0.5–8 h of egg laying [36]) and immediately try to enter nests, regardless of the presence of ratsnakes. Why do they exhibit no apparent fear of the apex predator? We can infer three non-mutually exclusive explanations for this phenomenon: low behavioural plasticity, the dilution effect and the relative safety of turtle nests.

Kukri snakes are dietary specialists, eating mainly reptile eggs. This highly specialized diet could result in relatively low levels of foraging plasticity; the two best quality food resources for kukri snakes on Orchid Island are eggs of green sea turtles and long-tailed sun skinks (*E. longicaudata*) [38]. Not only are turtle eggs more abundant and predictable (see Material and methods), but skinks violently defend eggs, making the eggs even more costly to consume [35,47]. As a consequence, sea turtle eggs are a key food source for kukri snakes, which they are willing to pursue even in the face of substantial predation risk. Additionally, turtle nests are relatively safe areas for kukri snakes; as we infer above, Orchid Island ratsnakes do not attempt to enter turtle nests, so kukri snakes are safe from ratsnakes once buried.

Finally, kukri snakes are present in much larger numbers than ratsnakes (figure 1). For example, in 1998, we recorded 195 kukri snakes present on the beach, compared to only 9 ratsnakes. Ratsnakes can consume only one prey item at a time, and, if successful, will stop foraging for a prolonged period while digesting their meal. Thus, if kukri snakes

invade the beach in large numbers in a narrow window of time, they may be protected by the dilution of risk—a phenomenon known as the 'dilution effect' which has been reported by researchers studying several different animals. For example, 'puddling' butterflies can create tightly packed, conspicuous groups [48]. Although these aggregations are likely to be spotted by butterfly-eating birds, the conspicuousness of the groups is offset by the dilution effect reducing the *per capita* mortality rate [49,50].

The territorial behaviour of female kukri snakes is another key element in the protective effect these interacting predators have on sea turtle eggs (electronic supplementary material, figure S2 [36]). Without such female defence, a nest (with an average of 102 eggs) could be consumed completely in only 5 days by male kukri snakes [36] (electronic supplementary material, figure S2). But because of the fear of sterilizing tail bites from females, males retreat from the nests, resulting in turtle nests being subject to predation by only a single snake, with up to 80% of eggs hatching [32]. Under such circumstances, turtles reproduce successfully largely because 'the enemy of my enemy is my friend', with rats and male kukri snakes as enemies thwarted by ratsnakes and female kukri snakes.

Our findings are based on long-term observations focused on the only remaining sea turtle nesting beach on Orchid Island. Although there are clear limitations associated with studying this system at just one site, trophic dynamics in natural systems are often contingent on environmental and ecological conditions specific to particular locations [51]. Even so, such case studies in natural systems are necessary for evaluating the predictions derived from models and experimental studies conducted in artificial mesocosms.

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