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Research Article

Informing Snake Roadkill Mitigation Strategies in Taiwan Using Citizen Science

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ABSTRACT Despite their prevalence in roadkill in East Asia, there has been little research on snake mortality along roads, even though the region's fauna contains some of the highest proportions of threatened or data-deficient reptiles. We analyzed citizen-collected roadkill data from Taiwan, comprising >11,000 records of snake roadkill from 2006–2017. We used maximum entropy environmental niche modeling to predict roadkill sighting patterns across snake species differing in habitat use, foraging behavior, and taxonomic group. Roadkill sightings were highest in low to mid-elevation (i.e., 0–2,000 m) forests and strips of farmland or shrubland that cut through forests; these areas likely support high snake abundances or dispersal activity. Sightings were lowest in urban areas and at high elevations (i.e., >2,000 m), likely because of unfavorable habitat conditions. Road density had little influence on roadkill sightings; areas with dense roads may be of lower habitat quality and contain fewer snakes. Roadkill sighting patterns differed among snake species with different habitat use and behavior. Natural history and landscape factors should be considered in roadkill mitigation design to reduce snake roadkill effectively. We recommend the use of similar citizen-science projects elsewhere to supplement conservation planning. © 2018 The Wildlife Society.

KEY WORDS citizen science, East Asia, habitat use, maximum entropy models, reptile, road mortality.

Road development has proliferated globally since 2000, and is projected to continue expanding this century, with ≥25 million km of new roads planned by 2050 (Laurance et al. 2014). Most of this expansion is expected to occur in Asia, which is forecasted to have massive infrastructure development (especially hydropower, rail, and subway systems, and roads), and to contain nearly half of global urban expansion to meet the demands of an ever-growing population (Seto et al. 2012, Schmitz et al. 2013, Zarfl et al. 2015). China currently has the world's largest car market and ownership, and is projected to have a 3 million km highway network by 2020 (KPMG 2009). Road expansion is often interconnected with other infrastructure projects that will further fragment the region's natural landscapes.

Roads are considered a significant contributor to the global biodiversity crisis (Eigenbrod et al. 2009, van der Ree et al. 2011, Laurance et al. 2014), causing direct mortality from vehicle collision (Grilo et al. 2009), impeded dispersal and gene flow (Balkenhol and Waits 2009), habitat loss or degradation (Coffin 2007), and spread of invasive species (Gelbard and Belnap 2003). Roads are also catalysts for future roads, and promote human access, hunting, poaching, fires, and deforestation (Adeney et al. 2009, Laurance et al. 2009). Roads can even cause more wildlife mortality than hunting (Forman and Alexander 1998), illegal wildlife trade (Andrews et al. 2008), or predation (Bujoczek et al. 2011). Among the animals most susceptible to roadkill are snakes (Andrews et al. 2008), predominantly because of their attraction to warm road surfaces for thermoregulation (Mccardle and Fontenot 2016), the availability of certain prey along roads (Andrews et al. 2008), the immobilizing behavior of some species in response to oncoming traffic (Andrews and Gibbons 2005), and intentional killing by humans when snakes are seen on roads (Secco et al. 2014). To understand and formulate recommendations to reduce road mortality, several studies have investigated factors thought to influence snake roadkill, including proximity to water or wetlands (Langen et al. 2009, D'Amico et al. 2015, Seo et al. 2015), proximity to agriculture (Gonçalves et al. 2018), elevation (Pragatheesh and Rajvanshi 2013), roadside vegetation (Jochimsen 2005), temperature (D'Amico et al. 2015), season (Seo et al. 2015), and species size and taxonomic affiliation (Andrews and Gibbons 2005).

Most studies on the road ecology of snakes are from the Americas, and research on snake roadkill in East Asia is lacking. East Asia contains a considerable proportion of threatened or data-deficient reptiles as listed by the

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International Union for Conservation of Nature (IUCN; Böhm et al. 2013); therefore, road development plans could be especially disastrous for the region's snake species. To date, only 1 paper has investigated the underlying factors of roadkill for a single snake species in East Asia (Seo et al. 2015). There is an urgent need for more comprehensive research on snake road ecology in East Asia to reduce mortality caused by the region's ambitious road expansion plans in the coming century.

Because of the variety of climate and ecological zones, Taiwan supports a diversity of snakes, with >50 species from 7 families, though ecological information on many snake species is still lacking (Lee 2005, Hsiang et al. 2009). We analyze roadkill data since 2006 from a citizen-science project in Taiwan. Our goal was to identify areas of high snake roadkill sightings in Taiwan; investigate how landscape and land cover type correlate with roadkill sightings in relation to snake behavior, habitat use, and taxonomic group; and provide recommendations for snake roadkill mitigation strategies. We hypothesized that roadkill sightings would vary depending on land cover type (Clevenger et al. 2003, Pragatheesh and Rajvanshi 2013, Seo et al. 2015), and may be higher in forests at low to mid elevations (i.e., 0–2,000 m) because more snakes occur in this environment relative to other areas in Taiwan (Hsiang et al. 2009). We predicted that sightings would increase with road density because of higher traffic (Fahrig and Rytwinski 2009). We also hypothesized that roadkill sightings would be higher for active foraging species compared with ambush species, which are less mobile, and higher for semi-arboreal and terrestrial species compared with aquatic and fossorial species, which have more restricted habitat requirements (Hartmann et al. 2011, Quintero-Ángel et al. 2012).

STUDY AREA

Taiwan (21°55′–25°20′N, 119°30′–122°00′E) is a seismically active island on the Tropic of Cancer. Around 58% of the island (36,200 km^2) is forest, half of which is broadleaf forest, and the other half coniferous or mixed forest. Vast areas of low elevation forests, representing around 30% of Taiwan's area, have been converted to agriculture, and remaining forests are limited to remote and steep mountainous regions or protected areas. Around 75% of Taiwan's land mass is mountainous, and the core of these mountains, known as the Central Ridge, run north to south along the central interior, and includes peaks >3,000 m above sea level (Lee 2007).

Taiwan's climate is strongly governed by altitude and latitude. The north is subtropical, with a mean annual temperature of 22°C and occasional frost events in the winter, whereas the south is tropical, with a mean temperature of 24°C and no frost (Li et al. 2013). Summer (Jun–Aug) is hot and humid and winter (Dec–Feb) in northern Taiwan is cool and dry. The central interior offers a cool, temperate climate because of the increased altitude. Taiwan generally experiences a noticeable dry and wet season, except for the northeast, which is regularly exposed to monsoons, and the central mountains, especially areas >1,500 m, where there is constant mist and precipitation (Li et al. 2015). The wide range in climate, altitude, and vegetation types gives Taiwan a notable amount of biodiversity. Taiwan has around 48,000 species of plants and animals (Shao 2011), including 110 species of reptiles (53 snake species), a quarter of which are endemic.

METHODS

Data Collection

We used data collected from the Taiwan Roadkill Observation Network (roadkill.tw, accessed 01 Sep 2017), a citizen science project that has recorded >40,000 roadkill sightings and other animal mortality incidents throughout Taiwan since 2004. It is run by the Taiwan Endemic Species Research Institute and Institute of Information Science, and its main goals are to mitigate roadkill, and promote citizen science, environmental education, and appreciation of biodiversity. Once a roadkilled animal is spotted, the contributor can record the time and global positioning system (GPS) location, take a photo, and submit the information online or via a mobile app (roadkill.tw/download/app, accessed 01 Sep 2017). For all incidents, species identification is verified by project staff through the submitted photos; we are therefore confident in the accuracy of species reports. Records are then published on the network's website as open-source data. For our analysis, we used only records of roadkilled snakes that had GPS and date recorded, and identification to at least the family level. Although the program started in 2004, the number of records were fewer in the early years because the program was less known, and may not accurately reflect snake roadkill composition; hence, we used only records from 2006 to 2017 when the program was more widely used, annual sample sizes were high, and inter-annual variation in observation number and composition was minimal. We excluded data from Taiwan's outlying islands, which may have considerably different traffic patterns and snake assemblages compared to the mainland.

Predictor Variables

To investigate spatial patterns of snake roadkill, we selected variables that we believed encompassed the environmental variation in Taiwan with the most explanatory power. We included latitude, elevation, and slope (Environmental Systems Research institute [ESRI], Redlands, CA, USA; Terrain image service, 30-m resolution) because these determine the climate of Taiwan. Latitude determines whether the lowlands in Taiwan experience a subtropical or tropical climate, whereas areas of high elevation, such as the central mountains, provide a temperate climate. Steep areas generally remain undeveloped and are colder and wetter compared to flatter areas, most of which have a drier, hotter climate and have been anthropogenically disturbed.

We also included land cover variables as derived from BaseVue 2013 (MDA Information Systems, Gaithersburg, MD, USA; 30-m resolution), currently the highest resolution land cover map for the whole of Taiwan. Our land cover categories included evergreen forest (stands of trees >3 m high, 35% canopy closure, composed of species that do not seasonally shed leaves), shrub (woody vegetation <3 m high), grassland (>10% cover in herbaceous grasses), barren land or minimal vegetation (<10% vegetative cover), paddy agriculture (croplands inundated for most of the growing season), general agriculture (other croplands), water (all bodies of water >0.08 ha, including ponds, rivers, and streams), high-density urban areas (areas where constructed materials including asphalt, concrete, buildings, and infrastructure formed >70% of land cover), and low-density urban areas (areas with 30–70% land cover of constructed materials). Traffic data were not available so we included road density (km of road/km^2 area) as a variable to correct for any sampling bias because more roads should be correlated with more traffic and a higher sampling effort by a citizen science project (Fahrig and Rytwinski 2009, Mair and Ruete 2016).

We tested for multicollinearity between all predictor variables using the Pearson correlation coefficient (r) and excluded variables with high cross-correlation values ($|r| > 0.8$). Because the effects of land cover may vary at different spatial scales, we tested buffers of 3 different radiuses (100 m, 500 m, and 1,000 m) to quantify the proportion of each land cover type surrounding each cell (Langen et al. 2009). To determine the best spatial scale to use, we initially ran 3 models on all snake roadkill records using the proportion of land cover within either a 100-m, 500-m, or 1,000-m radius as variables. We then compared the models using the area under the receiver operating characteristic curve (AUC) and the sample size corrected Akaike's Information Criterion (AIC_c; Warren and Seifert 2011).

Data Analysis

Analysis of citizen science datasets usually requires modeling algorithms for presence-only data because absences are not recorded. Though a variety of options are available (e.g., boosted regression trees, environmental niche factor analysis, random forest; García-Callejas and Araújo 2016, Shabani et al. 2017), we used one of the most robust and widely used methods, maximum entropy (MaxEnt) models, to correlate spatial variables with roadkill reports (Phillips et al. 2006, Elith et al. 2011, Duque-Lazo et al. 2016). MaxEnt is a machine-learning approach that optimizes species-environment associations using multiple function types including quadratic and product functions (Merow et al. 2013) and is thus especially useful in mapping ecological phenomena that may have complex, non-linear correlations, such as roadkill patterns. It has been shown to outperform alternative methods especially when there is a sufficient sample size and wide species distribution (Kasampalis et al. 2013, Duque-Lazo et al. 2016), and has been used in analyzing citizen science data (Crall et al. 2015, Fournier et al. 2017) and mapping roadkill hotspots (Ha and Shilling 2017, Garrote et al. 2018). Because absence data are unavailable, MaxEnt compares presence points with a sample of points, known as background or pseudo-absence points, from the study area of interest. It assumes that the unknown probability distribution has maximum entropy while subject to the constraints of predictor variables (Jaynes 1982) and its optimization is mathematically equivalent to generalized linear models (Renner and Warton 2013). To analyze which and how spatial factors influence snake roadkill sightings in Taiwan, we ran models using MaxEnt 3.4.1 (Phillips et al. 2006) with a convergent threshold of 0.00001, maximum iteration of 500, regularization of 1, and 10,000 maximum background points. To reduce overfitting, we cross-validated each model 10-fold. We estimated the percentage contribution of each variable to the regularized gain of the model and verified it with jackknife analysis. An important consideration in analyzing citizen-science, presence-only data is the potential of sampling bias and spatial autocorrelation (Yackulic et al. 2013). To account for these potential biases, in addition to including road density as a variable, we restricted the sampling area of MaxEnt to the road network of Taiwan so pseudo-absence points were selected on roads only (Merow et al. 2013). Further, we checked for spatial autocorrelation by running a Moran's I test (Moran 1950) on the model residuals.

To compare the relationships of environmental variables on snakes differing in biological traits or taxonomic group, we ran the MaxEnt models on subsets of the roadkill data. We categorized the data based on species' habitat use, foraging behavior, and family (Hsiang et al. 2009, Das 2015). Habitat use refers to a snake's adaption to a specific microhabitat and has been widely used to categorize snakes (Sheehy et al. 2016). For habitat use, we included arboreal (i.e., species that spend most of their time in vegetation and usually have prehensile tails, such as the square-headed cat snake [*Boiga kraepelini*], bamboo viper [*Trimeresurus stejnegeri*], and slug snakes [*Pareas* spp.]), semi-arboreal (i.e., species that spend similar times in vegetation and on ground, such as the greater green snake [*Cyclophiops major*], beauty snake [*Orthriophis taeniurus*], and rat snakes [*Ptyas* spp.]), terrestrial (i.e., species that often occur on the ground, including the many-banded krait [*Bungarus multicinctus*], red-banded snake [*Lycodon rufozonatus*], and habu viper [*Protobothrops mucrosquamatus*]), fossorial (i.e., species that often occur underground, under leaf litter, or in crevices, such as the collared reed snake [*Calamaria pavimentata*], odd-scaled snakes [*Achalinus* spp.], and coral snakes [*Sinomicrurus* spp.]), and aquatic snakes (i.e., species that live in or near water and feed mostly on aquatic prey, such as the eastern water snake [*Sinonatrix percarinata*] and checkered keelback [*Xenochrophis piscator*]; Table S1). We divided foraging behavior into ambush species, which are often sedentary for days and tend to remain still in response to oncoming traffic, and active-hunting species, which have higher movement rates but are likely to move rapidly in response to oncoming traffic; these differences might have implications for roadkill (Hartmann et al. 2011).

RESULTS

The screened data from the Taiwan Roadkill Observation Network contained 11,287 records from 2006 to 2017 and consisted of observations of 36 snake species from 6 families. The 5 most frequently sighted species in roadkill, in descending order, were the greater green snake, an active, semi-arboreal species (14.89%); the habu viper, an ambush, terrestrial species (10.54%); the square-headed cat snake, an active, arboreal species (9.30%); the red-banded snake, an active, terrestrial species (7.92%); the many-banded krait, an active, terrestrial species (7.91%); and the bamboo viper, an ambush, arboreal species (6.33%; Table S1).

We found that the 1,000-m scale had the best fit (i.e., it had the highest AUC and lowest AIC_c), so we used the predominance of each land cover type within a 1,000-m radius buffer of the road network as variables for subsequent analyses. None of the environmental variables were highly correlated ($|r|<0.8$) so we included all variables in subsequent analyses. Spatial autocorrelation across the whole dataset was minimal (Moran's $I = 0.11$) but significant ($P < 0.05$), though significance is not unexpected because of our large sample size. Elevation and predominance of evergreen forest and agriculture within a 1,000-m road buffer made the largest contributions to explaining the pattern in snake roadkill sightings, contributing 34.1%, 29.5%, and 16.6% to the data, respectively; slope and predominance of urban landscapes, grasslands, barren lands, and water made almost no contribution (<1%; Table 1). We calculated percentage contribution as the change in regularized gain of the model with inclusion of a particular variable to indicate the predictive power of the variable. The overall model had an AUC value of 0.642, whereas the subset models based on habitat use, foraging behavior, and family generally had higher AUC values (~0.7–0.9; Table 1). The AUC value indicates model performance; an AUC value of >0.5 indicates better performance than random, and a value of 0.8 would be considered fair performance. For all roadkill sightings combined, the mean predominance of land cover within 1,000 m was around 50% forest cover, 10–20% agriculture or shrublands, and 0.6–2% grasslands or urban areas (Table S2).

Roadkill sightings generally occurred on roads located in low- to mid-elevation (i.e., 0–2,000 m) forests or forest edges (Fig. 1). Of the 13 variables included in models, elevation and predominance of evergreen forest cover were repeatedly in the top 3 contributing variables explaining patterns in roadkill sightings, whether records were grouped by snake habitat use, foraging behavior, or family (Table 1). Either predominance of general agriculture or paddy agriculture was also in the top 3 for most groupings. Notably, predominance of general agriculture contributed substantially to models of roadkill patterns of semi-arboreal, terrestrial, and active snakes, whereas paddy agriculture played a greater role for arboreal, fossorial, and ambush snakes. The marginal response curves, in which each environmental variable was varied while keeping other variables at the average value, showed that predominance of evergreen forest generally had a positive correlation, elevation had a negative correlation, and predominance of agriculture had varying non-linear associations with roadkill sightings, depending on a species' habitat use, foraging behavior, or family (Fig. 2).

DISCUSSION

East Asia is one of the most rapidly developing regions in the world and is projected to undergo some of the highest rates of urban, infrastructure, and road expansion this century (KPMG 2009, Seto et al. 2012, Zarfl et al. 2015). Because snakes are one of the most susceptible animals to roadkill, high amounts of snake mortality may occur in East Asia in concert with road expansion unless adequate mitigation measures are in place. We examined snake roadkill observation patterns in Taiwan and found that roadkill sightings were largely associated with elevation, land cover type, and ecological preferences of snake species. An understanding of snake roadkill in East Asia is urgently needed to develop effective mitigation strategies amid the proliferation of roads, and our study is an important start to filling this knowledge gap.

Snake roadkill sightings were highest in areas between low to mid elevation forests, and to a lesser extent, some agricultural areas adjacent to forests (Fig. 1, Table S2). Thus, elevation and predominance of evergreen forest made large contributions toward explaining roadkill sightings (Table 1). The high roadkill sightings in these locations likely reflect high snake abundance and traffic density. Forests in Taiwan contain high snake diversity and abundance (Hsiang et al. 2009) and traffic density at low to mid elevations is relatively high, together producing a higher chance of roadkill. Roadkill sightings were low along the tall mountain ranges of Taiwan's central interior, likely because of the low road and traffic density and the colder, more extreme climate, which is unfavorable for many snakes; only a few montane species can be found regularly in Taiwan's highest mountains (Huang et al. 2007). Urban areas also had low snake roadkill sightings, even though they contain the highest road and traffic density. This is likely because there are very few snakes in or near urban areas because of high human disturbance and inhospitable conditions (Clevenger et al. 2003). The only exception was Typhlopids (notably, the brahminy blind snake [*Ramphotyphlops braminus*]), where the number of roadkill sightings was strongly and positively correlated with predominance of urban areas (Table 1). The brahminy blind snake is the world's only parthenogenetic snake, so the species is an efficient colonizer (often via human introduction) and can be common in urban environments (Nussbaum 1980). Perhaps the abundance of blind snakes is comparable or even higher near urban centers versus more natural areas, which explains the increased probability of observing roadkills there. Road density itself had minimal influence on roadkill sightings, relative to other variables (Table 1). This may be because areas of high road density are associated with greater anthropogenic disturbance and contain fewer snakes. Alternatively, snake populations could be previously depressed near old, high traffic roads, even in favorable land cover types (Teixeira et al. 2017).

Environmental variables had differing relationships with snake roadkill sightings depending on species' habitat use, foraging behavior, and family. This variation was related to the different niche requirements of the different snake categories. For example, predominance of paddy agriculture had a particularly strong negative correlation with roadkill sightings of arboreal and fossorial snakes (Table 1); such

Table 1. The percent contributions of environmental variables to the outcome of maximum entropy (MaxEnt) models describing patterns of snake roadkill sightings for species groups based on habitat use, foraging behavior, and family in Taiwan, 2006–2017. We calculated percent contribution as the change in regularized gain of the MaxEnt model; it represents the relative predictive power of the variable. Land cover variables were based on percent cover within a 1,000-m buffer of the road network, and road density was in km of road/km^2. The 3 highest contributing variables for each model are noted with an asterisk. The area under the curve (AUC) statistic of MaxEnt indicates the ability of a model to discriminate between presence points and pseudo-absence points by comparing the model's results to a random selection of background points. An AUC value above 0.5 means a model performs better than random, and a value of 0.8 is considered a fair performance.

	Environmental variable													
	Elevation	Evergreen forest	General agriculture	Latitude	Paddy agriculture	Low-density urban	Shrub	Road density	High-density urban	Grassland	Slope	Barren land	Water	AUC
All snakes	34.1*	29.5*	10.1*	6.6	6.5	4.6	4.5	2.2	0.6	0.6	0.4	0.3	0.0	0.642
Habitat use														
Aquatic	9.1	8.1	14.5*	20.2*	20.0*	4.8	4.0	4.0	7.3	0.1	2.6	4.0	1.2	0.728
Arboreal	17.8*	40.3*	7.4	5.4	12.6*	2.8	6.3	0.6	0.8	2.0	3.6	0.2	0.1	0.806
Fossorial	26.6*	24.8*	3.4	4.9	27.4*	0.4	2.3	6.5	0.9	0.1	1.5	0.2	1.0	0.849
Semi-arboreal	46.0*	32.3*	6.9*	3.0	5.5	6.2	4.0	1.6	1.5	1.3	0.3	0.4	0.1	0.760
Terrestrial	27.6*	21.7*	16.4*	8.7	8.5	3.0	7.6	3.4	1.3	0.8	0.2	0.6	0.2	0.685
Foraging														
Active	34.1*	25.0*	10.8*	5.6	8.0	5.1	5.1	2.9	1.6	0.8	0.5	0.4	0.1	0.653
Ambush	15.4*	49.5*	6.3	5.7	10.4*	2.9	4.5	1.8	0.5	2.1	0.1	0.6	0.1	0.798
Family														
Colubridae	39.6*	19.4*	10.6*	5.4	7.8	5.1	6.4	2.4	1.5	0.7	0.5	0.4	0.0	0.674
Elapidae	7.0	32.4*	25.3*	5.9	11.8*	2.7	4.2	6.0	3.8	0.2	0.3	0.2	0.1	0.727
Pareidae	39.0*	23.7*	4.4	5.8	15.5*	1.3	1.8	3.3	0.6	0.3	3.9	0.2	0.3	0.908
Typhlopidae	28.2*	6.1	12.1*	2.4	7.3	0.5	4.5	6.3	19.2*	4.9	0.2	7.4	0.9	0.594
Viperidae	14.8*	49.7*	6.5	4.9	11.3*	2.8	4.8	1.9	0.5	2.1	0.1	0.6	0.1	0.788
Xenodermatidae	78.8*	0.8	0.9	2.0	6.7*	0.8	0.1	8.3*	0.1	0.0	0.9	0.6	0.1	0.940

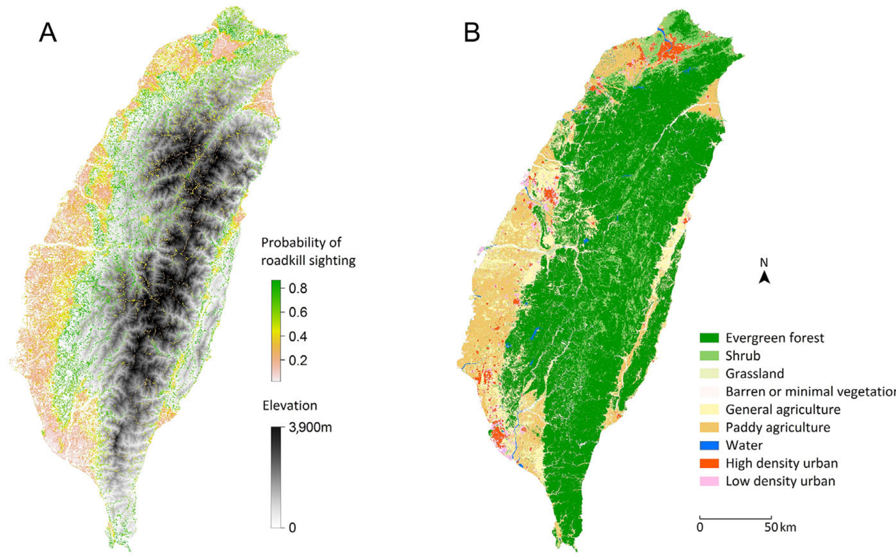

Figure 1. A) Probability of snake roadkill sightings from 2006–2017 across the road network of Taiwan overlaid on the elevation map of Taiwan. We calculated probability using all environmental predictors and 10-fold cross validation in MaxEnt. B) BaseVue 2013 30-m resolution land cover map of Taiwan.

snakes are likely in low abundance in paddy fields because of unsuitable habitat conditions. Arboreal snakes require woody vegetation, whereas fossorial snakes require dry burrowing substrate, but paddy fields are too open and often inundated. Elevation had a negative relationship with roadkill sightings of active snakes but a positive one for ambush snakes (Fig. 2). This is likely because most of the cold-tolerant snakes of Taiwan are ambush species (Hsiang et al. 2009), and are physiologically capable of inhabiting cooler, high-elevation forests (Huang et al. 2007).

Though predominance of evergreen forest cover within a 1,000-m buffer from roads generally had a positive correlation with snake roadkill sightings, the relationship peaked at around 80–95% forest cover and dropped near 100% cover (Fig. 2), suggesting that roadkill may not be highest in forest interiors but near forest edges or transitional areas between forest and shrubland or farmland. This might be because there is less traffic and fewer roads in forest interiors or because of higher snake movement at transitional areas to travel between forested areas. We report high frequencies of roadkill sightings along valleys of grassland and shrubland that penetrate the central forests of Taiwan, and also along the large strip of farmland that fragments forests along the east coast (Fig. 1). This suggests that, although the presence of large areas of grassland, shrubland, or farmland *per se* do not contribute to roadkill sighting patterns (e.g., along the west coast), if they are surrounded by forests, these areas might act as dispersal corridors between forest patches, resulting in high amounts of roadkill. Previous studies reported that periods of frequent movement of snakes, such as during juvenile dispersal or the mating season, lead to increased road mortality (Bonnet et al. 1999, Seo et al. 2015). However, size, sex, and age were not recorded in our dataset, so this possibility remains untested. Our dataset does include dates, so the relationship between roadkill timing and breeding cycles could potentially be examined, though at present, there are no empirical data on the dispersal patterns of any snake in Taiwan, and only data on the reproductive biology of 1 species (Tsai and Tu 2001).

We acknowledge limitations to our study. First, roadkill sighting patterns could reflect habitat preference of the snakes, roadkill risk, or both. For example, high roadkill records of arboreal snakes in forest could be because there are more arboreal snakes in forests or because of high risk of roadkill in forests for arboreal snakes, though we could not differentiate among these factors given the available data. Our results do not reflect actual roadkill probability but rather the probability of roadkill sightings, which is affected by detectability factors. Juveniles or smaller species are more likely to be missed or are scavenged completely (Santos et al. 2011). Size was not recorded in our dataset, but we generally found fewer roadkill sightings for smaller species, though most of these snakes are also rare and fossorial (Table S1). Scavenging of roadkill carcasses will deflate roadkill estimates (DeGregorio et al. 2011, Santos et al. 2016), and may also explain the low number of roadkill sightings in interior forests of Taiwan, where we presume scavenger numbers are highest, though scavenger density in Taiwan has not been investigated. Potential scavengers in Taiwan include corvids, some raptors, and mustelids. Moreover, high traffic volume and road speed affect the sampling effort and can increase the decomposition rate and the chance of a missed carcass (Santos et al. 2016). Unfortunately, traffic information was also unavailable, so we included the best alternative, road density, as a variable. We found that spatial autocorrelation was negligible, but we acknowledge that we could not correct for sampling effort fully. This is a common problem for many opportunistic citizen science projects because sampling effort is not recorded or controlled (Isaac et al. 2014).

Our study is a first step in understanding snake roadkill in East Asia. New roads are already being built at unprecedented rates, and more roadkill studies in Asia are needed for other taxa, especially amphibians, which are very susceptible to

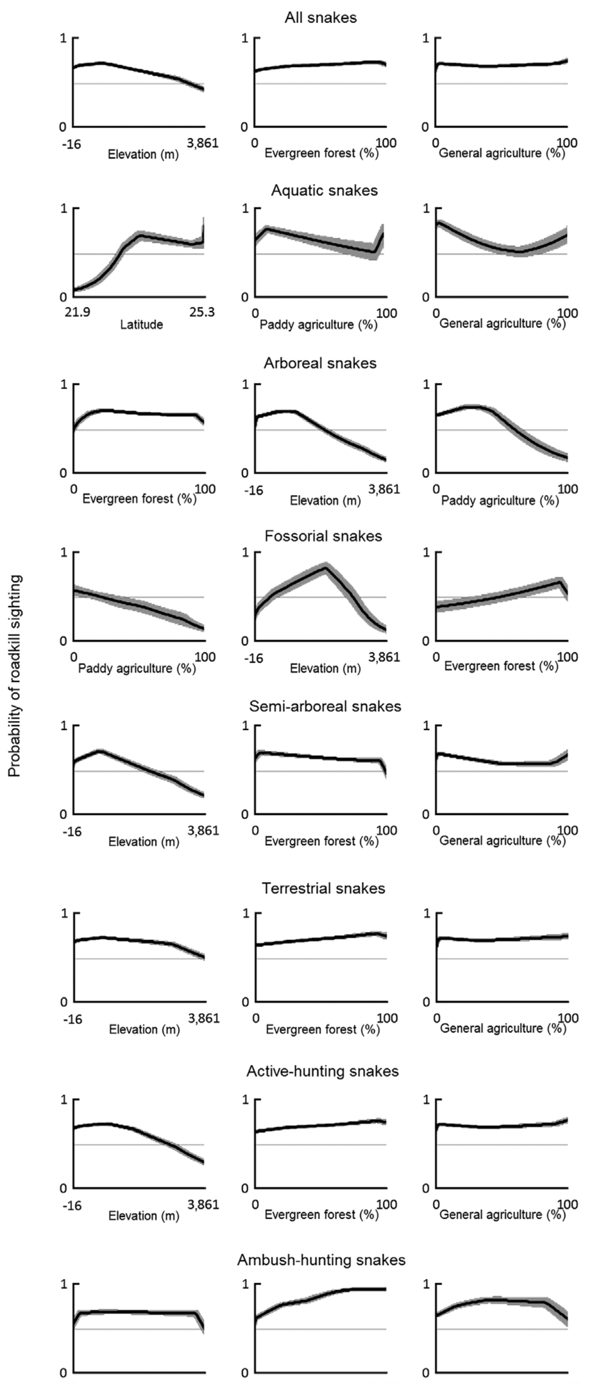

Figure 2. The relationship between the probability of snake roadkill sightings in Taiwan from 2006–2017 and the 3 highest contributing environmental variables. The black line is the mean response of the probability of roadkill sighting, while keeping all other variables at the average value, and grey areas represent ± 1 standard deviation. We ran models in MaxEnt with 10-fold cross validation.

roadkill and environmental change (Glista et al. 2008), and for other areas because roadkill patterns seem to be area-specific (Pragatheesh and Rajvanshi 2013, Seo et al. 2015). An important next step is to perform applied studies in Asia, testing the effectiveness of different mitigation methods such as drift fences, culverts, bridges, or other wildlife passages (Patrick et al. 2010, Ascensão et al. 2013, D'Amico et al. 2015). There are currently no such studies in Asia, but a meta-analysis of the success of mitigation measures in other regions reported that fences are more effective than passages, and the combination of both is the most effective (Rytwinski et al. 2016). Finally, citizen-reported roadkill databases have been reported to be accurate for information on location and identification (Ha and Shilling 2017, Waetjen and Shilling 2017, Périquet et al. 2018), and we recommend their further use in wildlife conservation and management. However, most citizen science roadkill projects are based in temperate areas, such as Belgium (http://waarnemingen.be), the Czech Republic (http://srazenazver.cz/en/), Ireland (http://biology.ie), and the United States (http://wildlfecrossing.net). As such, we encourage conservation groups in tropical regions to initiate and use similar projects because these regions contain high proportions of threatened and understudied taxa that could be especially vulnerable to ongoing human developments.

MANAGEMENT IMPLICATIONS

To reduce snake roadkill in Taiwan, we recommend adding mitigation (e.g., fences and passages) with priority given to roads in low to mid-elevation forests, followed by roads in forest edges and strips of farmland or shrubland that fragment forests. Our models that focused on snakes with a particular habitat use or behavior performed better (i.e., had a higher AUC value) compared with the overall model for all snakes, suggesting that one general mitigation strategy may not be effective for all species. Mitigation should be placed in multiple land cover types to reduce roadkill of various snake groups; for example, roadkill of aquatic and terrestrial snakes would be effectively reduced by also placing mitigation measures in farmlands, in addition to forests. We caution that our results from Taiwan should only be extrapolated to areas with similar climate and taxa, such as southern China and Japan, because roadkill patterns may vary for different snake species and geographical locations. Because we found that the spatial configuration of land cover types and the locations of potential dispersal corridors were important determinants of roadkill sightings, for future roadkill studies, we recommend against using just the land cover type at the roadkill location or the shortest distance to a particular land cover type as predictor variables because these variables do not incorporate the spatial configuration of land cover; instead, we suggest looking at the percentage of land cover within a wide buffer of the road network.

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