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Human-snake Conflict Patterns in a Dense Urban-Forest Mosaic Landscape

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Abstract.—**Human expansion and urbanization have caused an escalation in human-wildlife conflicts worldwide. Of particular concern are human-snake conflicts (HSC), which result in over five million reported cases of snakebite annually and significant medical costs. There is an urgent need to understand HSC to mitigate such incidents, especially in Asia, which holds the highest HSC frequency in the world and the highest projected urbanization rate, though knowledge of HSC patterns is currently lacking. Here, we examined the relationships between season, weather, and habitat type on HSC incidents since 2002 in Hong Kong, China, which contains a mixed landscape of forest, dense urban areas, and habitats across a range of human disturbance and forest succession. HSC frequency peaked in the autumn and spring, likely due to increased activity before and after winter brumation. There were no considerable differences between incidents involving venomous and non-venomous species. Dense urban areas had low HSC, likely due to its inhospitable environment for snakes, while forest cover had no discernible influence on HSC. We found that disturbed or lower quality habitats such as shrubland or areas with minimal vegetation had the highest HSC, likely because such areas contain intermediate densities of snakes and humans, and intermediate levels of disturbance. Hence, we warn that developing into forests could potentially increase HSC, and we advise placing preventative measures around human areas located in shrubland, farmland, and urban edges.**

Key Words.—Asia; human-wildlife conflict; snake rescue; translocation; wildlife management

Introduction

Continued growth of the human population and urbanization have led to an increase in human-wildlife conflicts, especially in locations where human expansion, habitat fragmentation, or biodiversity are highest (Soulsbury and White 2016; Archarya et al. 2017; de Souza et al. 2018). Of particular concern for human safety and wildlife conservation are conflicts between humans and snakes, which can include encounters with snakes in or near human property, gardens, villages, roads, farmland, infrastructure, or anywhere human and snake distributions overlap. We hereby define human-snake conflict (HSC) incidents as encounters between humans and snakes which negatively impacts (e.g., results in stress, injury, relocation, or death) one or both sides. HSC incidents can result in 1.2 to 5.5 million snakebites annually, and considerable amounts of mortality, morbidity, and strain on local health care systems (Kasturiratne et al. 2008; Williams et al. 2010). Snakebites are now considered a neglected disease in the tropics, and Asia is the most heavily affected region. In particular, India has around 35,000 to 50,000 fatal snakebites annually, while Pakistan, Nepal, Bangladesh, and Sri Lanka each experiences tens of thousands of reported snakebite incidents each year (Alirol et al. 2010; Gutiérrez et al. 2015). Because Asia is the region of the world projected to contain most of the global urban and infrastructure expansion this century (Seto et al. 2012; Schmitz et al. 2014), HSC incidents will likely intensify unless we gain a thorough understanding of the causes and implement effective mitigation measures (Anand and Radhakrishna 2017).

Snake activity and movement patterns are interconnected with weather, season, and landscape variables. Snake activity can be influenced by temperature, relative humidity, precipitation, and cloud cover, though different species have varying responses to weather variables (Marques et al. 2001; Brown and Shine 2002; Butler et al. 2005). Season also plays a critical role in snake activity. Most species from temperate to subtropical regions undergo brumation in the winter, when activity is minimal, and exhibit particularly high activity before and after brumation in search for food and refugia (Fuying 1989; Zhao and Adler 1993). There is also an increase in activity before and during the breeding season (Marques et al. 2001; Meshaka 2010); species in subtropical to tropical regions might have different breeding times, though subtropical snakes generally breed in the late spring to early summer, at the start of the wet season (Whitaker and Captain 2004; Das 2015). Finally, landscape variables, such as land cover or habitat type, can also influence snake activity according to their niche preferences, though these patterns vary for different species (Hartmann et al. 2009; Weatherhead et al. 2010).

HSC incidents are widespread across Asia, occurring frequently even in dense urban environments such as Bangkok, Hong Kong, and Singapore (Chippaux 1998). To mitigate HSC incidents, many snake capture-relocation programs have been initiated (e.g., ACRES in Singapore, Bomba Fire Department in Malaysia, Red Cross Snake Farm in Thailand, India Snake Rescue Network in India), and community snake catchers can be called into more rural parts of South Asia. The effectiveness of these efforts, however, remain unknown and HSC incidents continue to persist (Sinu and Nagarajan 2015; Anand and Radhakrishna 2017). Although potentially a serious global health issue, there is a disproportionately low number of ecological studies on HSC. A handful of studies have only quantified HSC incidents, mostly from India (Shankar et al. 2013; Vyas 2013; Roshnath 2017) or sub-Saharan Africa (Maregesi et al. 2013; Nonga and Haruna 2015). No study to our knowledge has looked at HSC incidents in highly urban environments, and only one study has investigated the ecological factors behind encounter probability for one snake species (Waldron et al. 2013).

Here, we analyze HSC incidents over the past decade in the Hong Kong Special Administrative Region (SAR), an area containing high frequencies of human-wildlife conflicts due to its mosaic landscape of natural and urban environments. Our objectives are to investigate how season, weather, and landscape affect these incidents, and see if there are differences in HSC trends between snakes of different functional trait groups. We expect that HSC will be lower during winter or lower temperatures, due to reduced snake activity. We also expect HSC to be high in habitats of intermediate or recent disturbance, as studies have found with other animals (Evans et al. 2014, Chen et al. 2016). As Asia continues to urbanize, while at the same time hosting one of the highest proportions of threatened or understudied snakes in the world (Böhm et al. 2013; Das and van Dijk 2013), understanding and mitigating HSC incidents would provide significant benefit to human welfare and snake conservation.

Materials and Methods

Study site.—Hong Kong SAR (22°N, 114°E) is situated along the southeastern coast of mainland China and has a subtropical climate with hot, humid summers with occasional thunderstorms and cyclones from May to September, and dry winters from November to February. The average daily temperature ranges from 25–31° C during the summer, while occasional cold fronts in the winter can bring the temperature below 10° C in lowlands or even < 0° C at higher elevations. Hong Kong was once predominantly forest, but due to human expansion and disturbance (notably a near complete clearance of forest during World War II), its total land area of 1,100 km^2 now consists of a mixture of dense urban areas, small villages, farmlands, wetlands, secondary forests, and successional habitats: shrublands and grasslands that are now 20–30 y post-clearance (Dudgeon and Corlett 2004). Thus, Hong Kong offers an interesting variety of habitat types to study, across a gradient of human disturbance and forest succession. Roughly 40% of its land area is designated as nature reserves or country parks, one of the largest proportions of protected areas in the Asia-Pacific region (Yip et al. 2004). In contrast, most of the 7.34 million population inhabit only a quarter of the land area, making Hong Kong one of the densest metropolises in the world (Census and Statistics Department 2017). Most of the natural areas remain undeveloped due to the steep, unsuitable terrain. Due to its mild subtropical climate, diversity of habitats, and relatively high proportion of protected areas, Hong Kong contains an impressive reptile diversity given its small area; at least 86 species of reptiles (representing 20% of the reptile species in China) including 53 snake species (Karsen et al. 1998). Geographically, Hong Kong is divided into 18 districts, with the largest being 175 km^2, and the smallest being 7 km^2.

Data collection.—Hong Kong's unique mosaic landscape of densely populated urban and natural environments gives rise to high frequencies of human-wildlife conflicts, involving wild pigs, macaques, barking deer, and especially high numbers of snakes (Dudgeon and Corlett 2004). Hong Kong has a territory-wide snake relocation program started by the Kadoorie Farm and Botanic Garden (KFBG) in 1999 in partnership with the Agriculture, Fisheries, and Conservation Department (AFCD) and the Hong Kong Police, to respond to HSC incidents. As HSC incidents are frequent and regularly published in the local media, people in Hong Kong generally know to call the police if they require a snake to be removed. Once a snake is encountered and is deemed a threat, the police can be called, who will subsequently inform a local snake-catcher to deliver the snake to KFBG. After inspection, identification, and confirmation of health condition by trained staff at KFBG, the snake is released in an appropriate location, usually inside country parks. Records of HSC incidents, including the location (usually the district name), date, and species involved, have been collected by KFBG since the start of the program, and we used this dataset for our study. Unfortunately, time of encounter was not recorded. We analyzed records starting from January 2002 to December 2016, as records prior to 2002 were relatively low and may not reflect snake composition accurately since the program was still at its infancy. We only used records of native snake species with date and

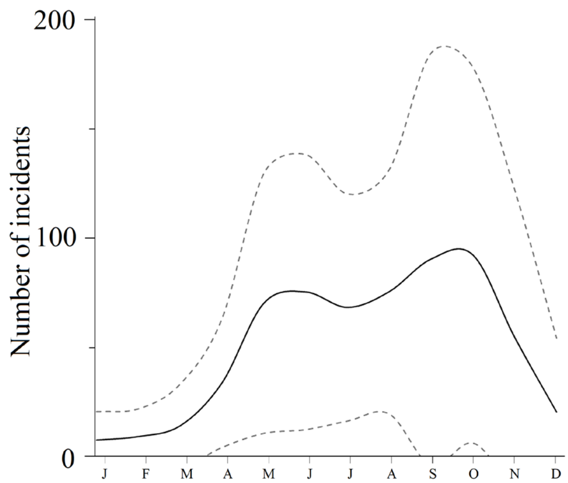

Figure 1. Monthly average number of human-snake conflict incidents reported to the police in Hong Kong from 2002 to 2016. Dashed lines represent 95% confidence intervals.

location recorded; non-native species records were rare and generally involved escaped pets.

We selected several weather and landscape variables for our analyses. For weather variables, we chose the monthly maximum, minimum, and mean temperatures, mean relative humidity, mean cloud cover, and total rainfall, obtained from the Hong Kong Observatory. We did not use daily weather data because weather can be highly variable between and within districts, and weather information for each HSC site was not available. As most records only provide the district name for the capture location, we used the percentage of habitat type per district as landscape variables, derived from the global MDA BaseVue 2013 Land Cover Map at 30 m resolution (http://www.mdaus.com/products/land-cover-products). Habitat type included forest, defined as trees of > 3 m tall, and canopy closure of > 35%; shrubland, defined as vegetation < 3 m tall; barren land or minimal vegetation, defined as land with < 10% vegetative cover; water, which included wetlands and paddy fields that are inundated for most of the year; agriculture, defined as croplands that are not usually inundated; and urban, defined as areas of > 30% constructed material, including asphalt, concrete, buildings, and infrastructure.

Data analysis.—To analyze trends in seasonality, we looked at the mean monthly total of HSC incidents from 2002 to 2016. To compare the relationships of weather and habitat variables on HSC incidents, we first checked for multicollinearity between variables by calculating the Pearson Correlation Coefficient (r) and variance inflation factor (VIF) for each variable (Appendix Table 1 and 2). We removed correlated variables that we deemed were least relevant until all remaining variables had low cross-correlation values ($|r| < 0.8$) and a VIF of < 10. Next, we ran a Generalized Linear Mixed Model (GLMM) on the HSC dataset with the remaining variables using a zero-inflated poisson family, with an alpha of 0.05. All variables were standardized with a mean of 0 and standard deviation of 1. To correct for temporal and spatial autocorrelation, we included year and district as random effects. To compare differences in responses between functional groups, we divided the dataset based on several functional traits and ran the GLMM on each one. We compared species based on being venomous or not; foraging mode (active or ambush hunting); reproduction (oviparous or live bearing: viviparous or ovoviviparous); habitat use (aquatic, arboreal or semi-arboreal, fossorial, or terrestrial); primary diet; and activity period (diurnal or nocturnal). To compare differences in responses among species, we also ran the GLMM on HSC records of each species. For species-specific models, we excluded species with fewer than 80 records due to insufficient power.

Results

There were 9,121 reported incidents of 33 species of snakes entering human areas in Hong Kong from January 2002 to December 2016 (Table 1). The top five most frequent species, in descending order, were the Common Rat Snake, *Ptyas mucosa* (2,415 incidents), Chinese Cobra, *Naja atra* (1,641 incidents), Bamboo Pit Viper, *Trimeresurus albolabris* (1,164 incidents), Red-necked Keelback, *Rhabdophis subminiatus* (701 incidents), and Copperhead Racer, *Coelognathus radiatus* (607 incidents). The mean monthly HSC frequency was high in late spring to summer, peaked in autumn, and was lowest in the winter (Fig. 1). HSC incidents were lowest in districts with the most urban cover, and high in districts with mostly shrubland cover (Fig. 2).

Mean, maximum, and minimum monthly temperatures were correlated, humidity was correlated with cloud cover ($r = 0.81$), and percentage of urban cover was negatively correlated with shrubland cover ($r = -0.93$). Hence, we omitted maximum and minimum temperatures, cloud cover, and shrubland cover from the GLMM analyses (Appendix Table 2). We found that mean temperature had a strong positive correlation with HSC incidents overall ($\beta = 0.69 + 0.32$ SD), while percentage urban cover per district had a strong negative correlation ($\beta = -0.71 + 0.48$), and humidity and rainfall had weak negative correlations (Table 2). Percentage of forest, water, barren, or agricultural cover had no significant correlation with HSC records overall.

In terms of functional traits, temperature had a positive relationship with HSC incidents involving all functional groups except fossorial snakes (Table 2).

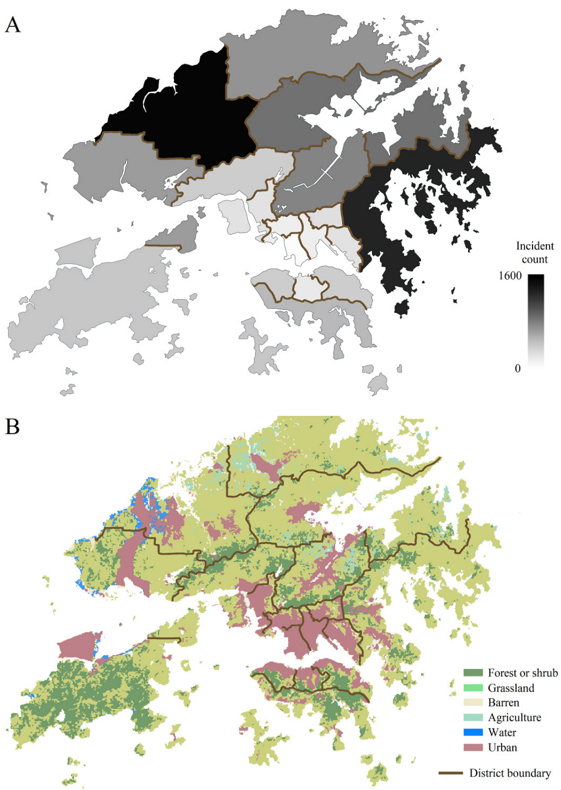

Figure 2. (A) Number of human-snake conflict reports in each district of Hong Kong, China, from 2002 to 2016. (B) Habitat cover of Hong Kong. (Derived from MacDonald, Dettwiler, and Associates [MDA] BaseVue 2013 Land Cover at 30 m resolution).

Forest cover had a negative relationship with incidents involving ambush, live bearing, aquatic, or nocturnal snakes. Agricultural cover was negatively associated with incidents involving ambush, live bearing, arboreal or semi-arboreal snakes, or snakes that feed mainly on invertebrates or lizards. Urban cover was negatively associated with all functional groups except fossorial snakes and snakes that feed on lizards. For the species-specific models, temperature had significant positive correlations on HSC incidents for each species while humidity had significant, but mixed correlations on most species (Appendix Table 3). Percentage of forest cover per district had a significant negative correlation for four species: *C. major*, *R. subminiatus*, *T. albolabris*, and the Large-spotted Cat Snake, *B. multomaculata*. Percentage of urban cover per district had a significantly negative correlation for most species, except for *C. major* and *T. albolabris*, which were positively correlated.

Discussion

Asia is one of the fastest developing regions in the world and is forecast to have the highest rates of urban and infrastructure expansion this century (Klynveld Peat Marwick Goerdeler 2009; Seto et al. 2012). Asia also contains the highest amount of human-snake conflicts and snakebite incidents in the world, causing serious medical and economic strain (Kasturiratne et al. 2008; Williams et al. 2010), though there is a dearth of knowledge on the factors behind these incidents. Here, we examined HSC patterns in relation to season, weather, and habitat type in Hong Kong, and found that HSC was likely influenced by the thermal biology and ecological preferences of snakes, and also the degree of human disturbance in a habitat, though patterns varied among species. As human expansion continues, such conflicts will only escalate, and this study is an important start to improving our ecological understanding of HSC to devise effective mitigation measures.

From 2002 to 2016, Hong Kong received an annual average of 608 HSC incidents reported to the police and delivered to KFBG. Of the top three most frequently encountered snakes, two are highly venomous (*N. atra*, *T. albolabris*), together representing 31% of all HSC incidents. This is in accordance with records for hospitals in Hong Kong of medically significant snakebites, which largely comprises these two species (Hon et al. 2004; Shek et al. 2009). Further, three of the 33 species recorded (*N. atra*, Burmese Python, *P. bivittatus*, King Cobra, *O. hannah*), covering 24% of all the incidents, are threatened species in the International Union for Conservation of Nature (IUCN) Red List (IUCN 2018); one of which, *P. bivittatus*, is a protected species in Hong Kong. Evidently, HSC in Hong Kong can pose a serious risk to human safety and is also a concern for the conservation of threatened species. Compared with the handful of studies done in India and neighboring countries, our HSC species composition was very similar. The most frequent HSC species in Hong Kong were also frequent, or had frequent congeners, in South Asia; for example, *P. mucosa*, Common Wolf Snake (*L. aulicus*), Buff-striped Keelback (*A. stolatum*), Checkered Keelback (*X. piscator*), *Bungarus* sp., *Colelognathus* sp., *Naja* sp., and *Python* sp. also commonly occur in HSC in India (Purkayastha et al. 2011; Vyas 2013; Deshmukh et al. 2015). This suggests that commonly encountered snakes share ecological or biological traits that increase likelihood of HSC, and these traits can be targeted when devising prevention measures. For example, a majority of the aforementioned genera seem to be terrestrial, active-hunting, and prey on rodents or small vertebrates, though a more rigorous comparison of HSC species composition across Asia is warranted.

HSC incidents exhibited seasonal variation; frequency increased in late spring, was highest in autumn, and was minimal during winter months. Accordingly, temperature had a strong positive correlation with HSC frequency of all species. This result is expected as the

Table 1. Number of human-snake conflict reports per species from January 2002 to December 2016 in Hong Kong, China. The conservation status of each species is derived from the International Union for Conservation of Nature (IUCN) Red List, and includes not assessed (NA), least concern (LC), vulnerable (VU), and data deficient (DD).

Species		Number of incidents	IUCN status
Ptyas mucosa	Oriental Rat Snake	2415	NA
Naja atra	Chinese Cobra	1641	VU
Trimeresurus albolabris	Bamboo Pit Viper	1164	LC
Rhabdophis subminiatus	Red-necked Keelback	701	LC
Coelognathus radiatus	Copperhead Racer	607	LC
Python bivittatus	Burmese Python	490	VU
Xenochrophis piscator	Checkered Keelback	405	NA
Bungarus multicinctus	Many-banded Krait	326	LC
Lycodon aulicus	Common Wolf Snake	260	NA
Cyclophiops major	Greater Green Snake	192	LC
Oligodon formosanus	Taiwan Kukri Snake	189	LC
Ptyas korros	Indo-Chinese Rat Snake	134	NA
Boiga multomaculata	Spotted Cat Snake	132	NA
Bungarus fasciatus	Banded Krait	112	LC
Amphiesma stolatum	Buff-striped Keelback	99	NA
Orthriophis taeniurus	Beauty Rat Snake	87	NA
Ophiophagus hannah	King Cobra	66	VU
Psammodynastes pulverulentus	Mock Viper	38	NA
Enhydris chinensis	Chinese Water Snake	18	LC
Pareas margaritophorus	Spotted Slug Snake	9	LC
Enhydris plumbea	Plumbeous Water Snake	5	LC
Opisthotropis balteata	Banded Stream Snake	4	NA
Lycodon subcinctus	Banded Wolf Snake	4	LC
Oligodon cinereus	Golden Kukri Snake	4	LC
Sinonatrix percarinata	Mountain Water Snake	4	LC
Sinomicrurus macclellandi	MacClelland's Coral Snake	3	NA
Lycodon futsingensis	Futsing Wolf Snake	3	LC
Oreocryptophis porphyracea	Red Bamboo Rat Snake	3	NA
Achalinus rufescens	Rufous Burrowing Snake	2	LC
Sibynophis chinensis	Chinese Mountain Snake	1	LC
Ramphotyphlops braminus	Brahminy Blind Snake	1	NA
Sinonatrix aequifasciata	Asiatic Water Snake	1	LC
Amphiesma atemporale	Mountain Keelback	1	DD
Total		9121	

majority of snakes in Hong Kong are generally active in the summer and brumate during winter (Karsen et al. 1998). HSC frequency peaked in autumn, likely due to preparation for brumation; snakes generally increase food intake and search for brumation dens before winter (Fuying 1989; Zhao and Adler 1993). We also noticed a second, less pronounced, peak in HSC frequency in mid to late spring. This may reflect the period when snakes emerge from brumation, when feeding activity is also considerably high (Gregory 1982). Incident frequency was slightly lower in the summer, perhaps because temperatures in the summer are too hot during the day but suitable at night to encourage nocturnal activity (Moore 1978; Sperry et al. 2013); humans are mostly inactive at night, so the chance of encounter is lower. Conversely, the peaks in HSC frequency in spring and autumn might be because night temperatures may drop below the thermal tolerance of snakes during these times, restricting their activity to daytime hours, which overlaps with human activity. The relationship

Table 2. Coefficients (± 95% confidence intervals) of weather variables and habitat cover on human-snake conflict (HSC) frequency in Hong Kong from 2002–2016. Weather variables (i.e., temperature, humidity, rainfall) were monthly averages, and habitat cover was the percentage of a particular habitat per district in Hong Kong. We used a zero-inflated poisson Generalized Linear Mixed Model (GLMM) for all HSC records, and significant coefficients ($P < 0.05$) are listed in bold. We ran additional GLMMs after dividing the HSC records based on different trait groups of the snakes involved. An asterisk (*) indicates aquatic snakes and fish- or frog-eating snakes consisted of the same species.

	Temperature	Humidity	Rainfall	%Forest	%Water	%Barren	%Agriculture	%Urban
All species	**0.69±0.32**	**-0.10±0.03**	**-0.03±0.02**	-0.33±0.39	0.28±0.35	0.17±0.25	-0.30±0.34	**-0.71±0.48**
Venomous	**0.85±0.05**	**-0.17±0.05**	-0.02±0.03	-0.40±0.45	0.30±0.39	0.21±0.29	-0.31±0.38	**-0.82±0.55**
Non venomous	**0.63±0.04**	**-0.06±0.03**	**-0.03±0.02**	-0.28±0.38	0.27±0.33	0.15±0.24	-0.28±0.32	**-0.66±0.46**
Foraging mode								
Active	**0.71±0.03**	**-0.05±0.03**	**-0.03±0.02**	-0.28±0.40	0.31±0.35	0.16±0.26	-0.26±0.34	**-0.71±0.49**
Ambush	**0.67±0.07**	**-0.33±0.06**	-0.02±0.05	**-0.52±0.39**	0.17±0.34	0.17±0.24	**-0.45±0.34**	**-0.80±0.47**
Reproduction								
Oviparous	**0.71±0.03**	**-0.07±0.03**	**-0.03±0.02**	-0.26±0.40	0.30±0.35	0.17±0.26	-0.27±0.34	**-0.69±0.49**
Live birth	**0.63±0.08**	**-0.29±0.07**	-0.03±0.05	**-0.73±0.40**	0.14±0.35	0.15±0.25	**-0.45±0.35**	**-0.89±0.49**
Habitat use								
Aquatic*	**0.33±0.07**	**-0.16±0.07**	-0.09±0.08	**-1.04±0.66**	0.04±0.57	0.27±0.41	-0.27±0.56	**-1.27±0.80**
Arboreal or semi-arboreal	**0.70±0.04**	**-0.10±0.04**	-0.03±0.03	-0.34±0.37	0.26±0.33	0.14±0.24	**-0.32±0.31**	**-0.71±0.45**
Fossorial	0.74±1.25	1.44±1.53	-0.27±3.68	2.48±3.18	-0.90±2.07	0.20±3.74	-55.17±255.17	2.05±3.96
Terrestrial	**0.92±0.06**	**-0.07±0.05**	-0.01±0.03	-0.14±0.41	0.37±0.36	**0.22±0.26**	-0.22±0.35	**-0.56±0.49**
Primary diet								
Eggs	**1.69±0.35**	**0.43±0.27**	-0.01±0.09	-0.51±0.51	0.28±0.41	**0.31±0.28**	-0.23±0.41	**-0.88±0.64**
Fish or frogs*	**0.33±0.07**	**-0.16±0.07**	**-0.09±0.08**	**-1.04±0.66**	0.04±0.57	0.27±0.41	-0.27±0.56	**-1.27±0.80**
Generalist	**0.81±0.05**	**-0.19±0.05**	-0.01±0.03	-0.31±0.44	0.29±0.39	0.22±0.28	-0.34±0.38	**-0.76±0.54**
Invertebrates	**1.43±0.31**	**0.85±0.29**	-0.22±0.42	**-0.82±0.54**	-0.08±0.52	**-0.55±0.45**	**-0.75±0.49**	**-0.88±0.68**
Lizards	**0.59±0.13**	**0.21±0.13**	0.04±0.06	-0.01±0.29	**0.34±0.26**	0.18±0.14	**-0.42±0.26**	-0.14±0.36
Rodents	**0.71±0.05**	**-0.06±0.05**	-0.03±0.03	-0.17±0.38	0.32±0.34	0.14±0.25	-0.23±0.33	**-0.61±0.47**
Snakes	**0.99±0.13**	**-0.22±0.12**	-0.07±0.10	**-0.63±0.45**	0.26±0.38	0.11±0.28	-0.05±0.38	**-0.71±0.54**
Activity period								
Diurnal	**0.70±0.04**	**-0.04±0.03**	**-0.03±0.02**	-0.29±0.42	0.28±0.37	0.15±0.27	-0.30±0.36	**-0.78±0.51**
Nocturnal	**0.70±0.05**	**-0.21±0.05**	-0.02±0.03	**-0.42±0.37**	0.27±0.32	0.20±0.23	-0.29±0.32	**-0.64±0.45**

between intraday activity and season, however, remains to be verified for Asian snakes.

In terms of habitat type, forest cover had an insignificant influence on HSC incidents overall, even though forests in Hong Kong are presumed to contain relatively high numbers of snakes (Karsen et al. 1998). This may be because fewer humans frequent forests, and/or because forests contain sufficient resources and refugia for snakes, so encounter rates are not particularly high. Additionally, forest cover was negatively associated with incidents involving several trait groups, notably ambush, nocturnal, or aquatic snakes. Snakes with such characteristics likely have lower overlap with human activity in forests. Predominantly urban areas had low HSC incidents, likely because fewer snakes are found near dense urban environments due to lack of suitable habitat or food. Interestingly, rodent-eating snakes also had low incidents in urban environments, perhaps suggesting that foraging does not outweigh the cost of entering highly disturbed environments, as shown in other animals (Blecha et al. 2018). Discrepancies in variable correlations among different trait groups or species likely reflect differences in ecological preferences. Notably, percentage of water or agricultural cover was positively correlated with HSC incidents involving *A. stolatum*, *B. fasciatus*, and *P. korros*, and these species do frequently occur in or near water and farmlands (Li et al. 2009). Arboreal and ambush species, which are presumed to be more forest dependent, had a negative relationship with agricultural cover. Incidents of *C. major* and *T. albolabris* were positively correlated with urban cover; these two species rank among the most common snakes in Hong Kong and are generalists, capable of occurring in anthropogenically disturbed habitats (Karsen et al. 1998; Das 2015).

It is important to note that percentage of urban areas was negatively correlated with percentage of shrubland, so we omitted shrubland cover from the GLMM. The strong negative coefficients of urban cover in the GLMM, however, would conversely imply that shrublands may yield high frequencies of HSC incidents. Farmland and minimal vegetative cover also had positive correlations with HSC incidents for several species. It seems, therefore, that HSC incidents are less likely in forests and urban areas, where densities of either humans or snakes are low, but highest in successional or secondary habitats like shrublands or areas with low vegetation, which may contain intermediate levels of both snakes and humans. This is in accord with other spatial studies that have shown higher human-wildlife conflicts or encounter rates in habitat edges, areas of intermediate or recent disturbance, or the wildland-urban interface (WUI; Kretser et al. 2008; Evans et al. 2014; Acharya et al. 2016; Chen et al. 2016; Pitts et al. 2017). Hence, adding prevention or mitigation in such areas would be most effective at reducing HSC.

We acknowledge some limitations to our study. First, our dataset does not encompass all HSC encounters, only those reported to the police and the snake was caught. Numerous factors can influence the likelihood of a person reporting an encounter, including the age of a person, their education, their previous experience with and attitude towards snakes, their risk and nuisance perception, and the surrounding environment (Prokop et al. 2009; Hayman et al. 2014). Because HSC is regularly publicized and the option of calling the police to remove snakes is well known throughout Hong Kong, we are confident that the dataset has encompassed the majority of incidents where the person felt threatened enough by the snake to report it. Detectability was likely a confounding factor in our dataset, as we found that smaller species had fewer HSC reports, even if they are relatively common. For example, the Brahminy Blind Snake (*R. braminus*) and Spotted Slug Snake (*P. margaritophorus*) are among the most common snakes in Hong Kong (Karsen et al. 1998), but they only had one and nine reports, respectively, since 2002, implying that smaller snakes were less likely detected, or that they may be deemed less dangerous and fewer calls to the police were made. Another limitation is that our dataset did not have information on individual size or sex. We posit that another underlying factor of HSC could be reproductive biology of the snake (e.g., increased activity during juvenile dispersal or mating), though this could not be determined with our data. Finally, the spatial data of these incident records were at the district level, so we could only use percentage of land cover at each district as landscape variables, which is a very low resolution, though this might not be an issue for our study given the small size of Hong Kong (the mean district area is 59.96 + 26.90 km^2). To further understand HSC incidents, we encourage future efforts to record finer resolution spatial data, such as GPS location, and record more information such as how the snake was encountered, what the snake or human was doing, and where specifically the snake was found.

In conclusion, HSC incidents in Hong Kong were correlated with season, weather, and habitat type, suggesting that thermal biology and ecological preferences are involved. We found that successional or disturbed habitats (i.e., shrublands and areas of low vegetative cover) contained the highest numbers of HSC; the implication of which is that forests, although likely serving as source populations for snakes, do not generate high HSC incidents, but once destroyed or degraded into lower quality habitats, HSC could increase in these areas. Though urban areas had low HSC overall, incidents involving the most common venomous snake in Hong Kong, *T. albolabris* (also responsible for the majority of medically significant snakebites in Hong Kong), were highest here. We suggest relevant government departments (e.g., AFCD) to offer regular public workshops or seminars to those living near shrublands, grasslands, or urban edges, with emphasis on identifying commonly encountered species and how to handle HSC. We also suggest the Education Bureau to include a short HSC workshop annually in the primary or secondary school syllabus; younger people tend to be less fearful of, and more open to learning about snakes (Ballouard et al. 2012, 2013), so educating students about HSC would be particularly effective. Additionally, preventative measures such as removal of clutter, sealing holes and gaps in external walls, or placing snake proof fencing or snake deterrent plants should be implemented in high conflict areas. These measures, however, have not yet been scientifically evaluated and an important next step would be to test these approaches. We believe that prevention would be much more practical in the long run than relying on snake relocation programs, especially since snakes may return to the capture location or die from relocation (Devan-Song et al. 2016), and HSC incidents do not seem to have declined in recent years (Sinu and Nagarajan 2015; Anand and Radhakrishna 2017). Finally, while there are numerous snake relocation programs across Asia and other parts of the world, including Wildlife Alliance (Cambodia), Wildlife at Risk (Vietnam), Wildlife in Need (Philippines), Creative Conservation Alliance (Bangladesh), fire departments of Singapore and Malaysia, Krabi Snake Rescue (Thailand), Madras Crocodile Bank (India), and many people in communities who help catch snakes in India and neighboring countries, but most of them have not kept records of incidents (Jose Louies of Indiansnakes.org, Yamini Bhaskar of Madras Crocodile Bank, Kartik Shanker, and Anslem de Silva, pers. comm.). We recommend starting a region-wide, open source, citizen science database on HSC incidents (e.g., India Snake Rescue Network; http://isrn.org.in), where contributors can report incidents online, verified and regulated by qualified staff (in case of any sensitive data involving rare, poached species; Lindenmayer and Scheele 2017). With these data, we can gain a better understanding of HSC patterns, so that relocation and mitigation can be improved effectively.

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Appendices

Appendix Table 1. Pearson correlation table of weather and landscape variables in Hong Kong from 2002-2016. Weather variables included monthly temperature, mean relative humidity, mean cloud cover, and total rainfall, derived from the Hong Kong Observatory. Landscape variables included the % cover of various land uses in Hong Kong. Highly correlated variables ($|r| > 0.80$) are in bold. Abbreviations are MaxT = Maximum Temperature (°C), MeanT = Mean Temperature (°C), MinT = Minimum Temperature (°C), CC = Cloud Cover.

	MaxT	MeanT	MinT	Humidity	CC	Rainfall	%Forest	%Shrubland	%Urban	%Barren	%Agriculture	%Water
MaxT	1.00											
MeanT	**0.97**	1.00										
MinT	**0.92**	**0.97**	1.00									
Humidity	0.40	0.36	0.32	1.00								
CC	0.20	0.17	0.14	**0.81**	1.00							
Rainfall	0.11	0.12	0.12	0.06	0.04	1.00						
%Forest	0.00	0.00	0.00	0.00	0.00	0.00	1.00					
%Shrubland	0.00	0.00	0.00	0.00	0.00	0.00	0.25	1.00				
%Urban	0.00	0.00	0.00	0.00	0.00	0.00	-0.56	**-0.93**	1.00			
%Barren	0.00	0.00	0.00	0.00	0.00	0.00	-0.15	0.12	-0.08	1.00		
%Agriculture	0.00	0.00	0.00	0.00	0.00	0.00	-0.13	0.53	-0.48	0.16	1.00	
%Water	0.00	0.00	0.00	0.00	0.00	0.00	-0.07	0.57	-0.54	0.16	0.55	1.00

Appendix Table 2. Variance inflation factors (VIF) for (A) all initial variables which we selected to analyze human-snake conflict patterns in Hong Kong. After removing highly correlated variables (VIF > 10), we used the remaining variables (B) as predictor variables for our Generalized Linear Mixed Model (GLMM) analysis.

A		B	
	VIF		VIF
Max temperature	17.50	Mean temperature	1.16
Mean temperature	38.59	Mean humidity	1.15
Min temperature	16.29	Rainfall	1.02
Mean humidity	3.59	%Forest	2.61
Cloud cover	3.14	%Urban	3.79
Rainfall	1.02	%Barren	1.07
%Forest	∞	%Agriculture	1.89
%Shrubland	∞	%Water	2.01
%Urban	∞		
%Barren	$2.64E^{14}$		
%Agriculture	$3.00E^{15}$		
%Water	$3.00E^{15}$		

Appendix Table 3. Coefficients and 95% confidence intervals of weather and habitat cover on human-snake conflict frequency involving each species in Hong Kong from 2002-2016. Weather variables (i.e., temperature, humidity, rainfall) were monthly averages, and habitat cover was the percentage of a particular habitat per district in Hong Kong. We excluded species with < 80 records due to insufficient power. We used a zero-inflated poisson generalized linear mixed model for each species, and significant coefficients ($p < 0.05$) are listed in bold.

	Temperature	Humidity	Rainfall	%Forest	%Water	%Barren	%Agriculture	%Urban
Amphiesma stolatum Buff-striped Keelback	**0.50±0.31**	**0.89±0.36**	-2.23±4.31	-0.27±0.66	**0.43±0.23**	**0.76±0.18**	**0.91±0.39**	-0.27±0.66
Bungarus fasciatus Banded Krait	**0.85±0.27**	**-0.28±0.23**	-0.01±0.15	-0.38±0.41	**0.57±0.21**	**0.21±0.17**	**0.26±0.24**	**-0.51±0.41**
Bungarus multicinctus Many-banded Krait	**1.09±0.20**	**-0.32±0.19**	1.54±2.53	-0.74±0.57	0.14±0.47	0.11±0.34	-0.01±0.46	**-0.77±0.68**
Boiga multomaculata Spotted Cat Snake	**0.74±0.25**	0.21±0.24	0.05±0.09	**-0.80±0.35**	**0.42±0.24**	**0.25±0.15**	**-0.58±0.23**	**-0.78±0.35**
Cyclophiops major Greater Green Snake	**1.72±0.38**	**0.86±0.31**	-0.22±0.41	**-0.86±0.57**	-0.14±0.54	**-0.53±0.46**	**-0.78±0.52**	**1.01±0.73**
Coelognathus radiatus Copperhead Racer	**0.56±0.10**	**0.20±0.10**	-0.03±0.08	-0.29±0.45	0.32±0.39	0.04±0.28	-0.06±0.39	**-0.68±0.56**
Lycodon aulicus Common Wolf Snake	**0.49±0.15**	**0.23±0.16**	0.05±0.08	0.36±0.39	0.34±0.35	0.16±0.25	**-0.44±0.36**	0.13±0.49
Naja atra Chinese Cobra	**1.02±0.08**	-0.02±0.06	-0.01±0.04	0.02±0.59	0.45±0.52	0.29±0.37	-0.13±0.51	-0.71±0.73
Oligodon formosanus Taiwan Kukri Snake	**1.83±0.39**	**0.47±0.28**	-0.01±0.10	-0.50±0.51	0.26±0.41	**0.31±0.28**	-0.20±0.41	**-0.88±0.64**
Python bivittatus Burmese Python	**0.80±0.13**	**-0.43±0.14**	0.01±0.09	0.01±0.43	0.28±0.37	0.23±0.26	-0.29±0.37	-0.21±0.53
Ptyas korros Indo Chinese Rat Snake	**0.86±0.26**	-0.07±0.23	0.02±0.12	0.21±0.31	**0.60±0.26**	0.15±0.19	-0.15±0.26	0.26±0.35
Ptyas mucosa Oriental Rat Snake	**0.75±0.05**	**-0.12±0.05**	-0.03±0.04	-0.24±0.43	0.28±0.38	0.18±0.28	-0.32±0.37	**-0.75±0.53**
Rhabdophis subminiatus Red-necked Keelback	**0.25±0.09**	**-0.17±0.09**	-0.10±0.11	**-1.28±0.75**	-0.41±0.65	0.01±0.46	-0.56±0.62	**-1.71±0.91**
Trimeresurus albolabris Bamboo Pit Viper	**0.63±0.08**	**-0.30±0.07**	-0.04±0.06	**-0.76±0.42**	0.15±0.37	0.15±0.26	-0.51±0.37	**0.98±0.52**
Xenochrophis piscator Checkered Keelback	**0.52±0.12**	**-0.32±0.11**	-0.10±0.15	-0.82±0.83	0.44±0.68	0.38±0.48	0.17±0.69	**-1.02±0.99**