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Short Note

Social Behavior Displayed by the Green Pit Viper *Trimeresurus* (*Cryptelytrops*) *macrops*

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Study of behavior and sociality has historically been well-represented in non-squamate amniotic organisms[1-3]. Such study with squamates (lizards, snakes, and amphisbaenians) is still in the infancy stage however, especially regarding snakes[4,5]. While more complex and visible social systems may be observed for mammals and birds, understanding of seemingly simpler behavior and sociality displayed by snakes may provide valuable insight from which complexity may be derived[5].

Reliable and comprehensive knowledge is essential if behavioral ecology is to serve as an effective conservation tool[6]. Contesting the traditional perception that the snake clade completely lacks complex and noteworthy social behavior has been a considerable challenge[7,8]. Viper home ranges in temperate regions frequently overlap with conspecifics and limited interactions between species were infrequently reported until fairly recently[9]. To date, most behavioral and social study of wild snakes has been conducted with temperate climate vipers, particularly rattlesnakes. Camera technology has recently been utilized with considerable success on red diamond (*Crotalus ruber*), northern pacific (*C. oreganus*), timber (*C. horridus*), Arizona black (*C. cerberus*), and sidewinder (*C. cerastes*) rattlesnakes to evaluate social behavior (summarized[5,10]). Investigation of viper behavior in the tropics has progressed little past spatial ecology. Arboreal vipers are among the least studied snakes because of limiting factors such as body size and challenging habitats[11]. Recent study of green pit vipers (*Trimeresurus* spp.) suggests moderate home range overlap between conspecific females, as well as interspecies overlap in males[12].

Behaviors related to sexual activity, such as male combat, courtship, and mating, are considered as evidence of social systems[13]. Snakes also interact and aggregate with conspecifics for reasons other than procreation-even before they are born-aggregations of gravid females in several rattlesnake species, a form of parental care (> 50 species of > 30 genera), and cooperative hunting in sea snakes, all evidence snakes are an overlooked source of social behavior[8].

We present observations of social interactions of wild adult big-eyed pit vipers (*Trimeresurus* (*Cryptelytrops*) *macrops*[14]) at ambush sites within the Sakaerat Biosphere Reserve (SBR) in northeast Thailand. Like most other green pit vipers, *T. macrops* exhibits profound sexual dimorphism both in size and coloration[15]. Male *T. macrops* display a vibrant white "racing stripe" (postocular stripe) above each eye, which females lack, and could play a role in signaling of body condition. Females are significantly larger morphologically, not only in body mass and snout-vent length but also in head width and length.

Study site and animals: Our observations were part of a larger project looking at green pit viper behavior, spatial ecology, and habitat selection within the Sakaerat Biosphere Reserve in northeast Thailand. At our sites, we opportunistically captured vipers during visual searches after dark and then recorded morphometrics (snout-vent length [SVL] and body mass) the following day with an acrylic tube and isoflurane anesthesia described by Wilkinson (2014)[16]. We sexed each individual under anesthesia. We gently palpated for the presence of vitellogenic follicles and embryos under anesthesia, if present we considered them to be "gravid" and if not then "not gravid." Radio transmitters (1.8 g, Holohil BD-2T and BD2-THX) were implanted in adult pit vipers deemed large enough and in good condition (transmitter < 5% of body mass) following [17,18].

We radiotracked one adult female *T. macrops* in the core zone of SBR and two adult females in the transitional zone. All three females were gravid during transmitter implantation (n = 3, median SVL = 580 mm, range = 514 - 612; mass = 91.3 g, range = 52.5 - 109, Table 1). Big- eyed pit vipers exhibit profound sexual dimorphism (females being larger than males), with adult males in our study area at mean mass precariously close to the 5% body mass cutoff for transmitter implantation (they are too small to ethically implant)[15]. To safely observe sex differences without unethically implanting adult male vipers which were too small, we included an adult non-tracked male (SVL = 424 mm, mass = 24.2 g, Table 1) at the transition zone study site in our investigation.

Field videography: We set Bushnell trail cameras Model X-8 (model #119327, f/3, exposure time 1/20 sec, ISO 100, 35mm focal length, infrared night capability) and Trophy Cam (model #119636C, f/2.8, exposure time 1/20 sec, ISO 100, 35mm focal length, infrared night capability) approximately 1-3 m from focal adult green pit vipers after a minimum 2 week recovery period from latest capture (Fig. 1). The camera interval was one minute with one or three consecutive photographs taken each minute. Care was taken when placing cameras not to disturb vipers or considerably alter natural behavior and habitat, and we did not use recordings in which vipers abandoned ambush or resting sites within an hour of setting cameras for analyses.

Ethology: We specifically looked at interactions between focal *T. macrops* and conspecifics which occurred on the cameras while pit vipers were ambushing. We defined ambush behavior as stationary foraging, coiled with the head set in a ready-to- strike position[19]. We defined interactions as direct if a viper came within half of a body length (or closer) to another viper, and indirect if further but still visible on camera. Outcome of interactions were defined as neutral, distracting, or agonistic. We classed interactions as neutral when the focal viper did not appear to be aware of or did not acknowledge a conspecific. The interaction was distracting when the focal viper appeared aware of or acknowledged a conspecific, but no subsequent responses were evident. Agonistic outcomes included active responses, requiring subsequent movement, of a focal viper to a conspecific.

FIGURE 1. Bushnell trail camera set to observe an ambushing big-eyed pit viper (*Trimeresurus* (*Cryptelytrops*) *macrops*).

We report median values for duration and occurrence of interactions.

This research found that, in total, we opportunistically set cameras (mean 8556.5 minutes per individual, n = 4, Table 1) on and observed nine interactions between focal *T. macrops* and conspecifics for a total of 272 minutes from May 2015- January 2017 (see at Movie Archives of Animal Behavior (http://movspec.mus-nh.city.osaka.jp/ethol/title-e.php) and https://www.youtube.com/channel/UCdRlzXz9YbUR2eWyEAEGU4g). Median duration of each bout was 14 minutes, for a median number of 2 bouts per individual (Table 1). All interactions occurred between early evening and early morning time (19:20 - 05:21) from late November to early May.

Females (n = 3) were observed interacting with other vipers for a total of 248 min for a median of 74 min per viper. All female interactions were at the low ground height level (>0 - 0.5 m) except for one which was at groundstory height (0.5 - 1 m). Two of the three female *T. macrops*, one in the transition (TRMA220) and one in the core

TABLE 1. Summary of focal big- eyed pit viper (*Trimeresurus* (*Cryptelytrops*) *macrops*) biometrics (snout-vent length [SVL] in mm and mass in g), time observed on camera (in min), and number and duration (in min) of interactions observed. Locations are the same as Strine et al. (2018, "upper dam pond, shortened to "pond") and Barnes et al. (2017, "canal").

		Biometrics				**Interactions**	
Viper ID	**Location**	**Sex**	**SVL**	**Mass**	**Time observed**	**Number**	**Duration**
TRMA220	Canal	Female	580	91.3	16307	4	28
TRMA226	Canal	Male	424	24.2	7735	1	24
TRMA232	Canal	Female	612	109.0	2254	1	74
TRMA271	Pond	Female	514	52.5	7930	3	146

area (TRMA271), in this study interacted with conspecifics on multiple occasions (median 3.5 interactions, median 7 min per interaction) within a short time frame for a median of 70 min between interactions. The single male (TRMA226) had a single observable interaction, for a total of 24 min, at low ground level height (>0 - 0.5 m).

Interactions of focal female vipers were primarily indirect (6 bouts) rather than direct (2 bouts). The most frequently observed outcome of interactions with focal female vipers was neutral (4 bouts), with distracting (2 bouts) and agonistic (2 bouts) outcomes infrequent. One female bout was direct and agonistic in the transition area of SBR (TRMA220), and one was direct and agonistic in the core area of the reserve (TRMA271). The single focal male (TRMA226) interaction was direct and agonistic.

Agonistic interactions (Fig. 2) varied in behavior following the encounters. One female in the transition area (TRMA220) and the male (TRMA226) continued to ambush at the same sites following agonistic interactions for at least one night afterwards. The viper which disturbed the male (TRMA226) appeared to shelter within close proximity (<0.5 m, observed entering and exiting on camera) of it during the day following the interaction. The male returned to the same ambush site on the night immediately following the agonistic interaction after the conspecific (presumably the same which disturbed him) had left its shelter and moved elsewhere (not visible on camera). A conspecific appeared to chase a focal female off an ambush site in the core area (TRMA271) during an agonistic interaction. The focal viper completely abandoned the site (did not return, moved >5 m lateral distance to a new foraging site), while the conspecific immediately proceeded to forage at the ambush site previously occupied after the focal female was out of sight on camera.

In conclusion, novel findings of our investigation include clear agonistic behavior between conspecifics which has not yet been recorded outside of a sexual context (male combat) for green pit vipers and insight into more frequently observed apathetic interactions.

Direct social interaction of green pit vipers may be reduced due to largely sedentary lifestyle. Green pit vipers are extremely sedentary and only the smallest viper in the world, the Namaqua dwarf adder (*Bitis schneideri*), displays smaller known home range sizes among all snakes[12,19,20]. How limited movement

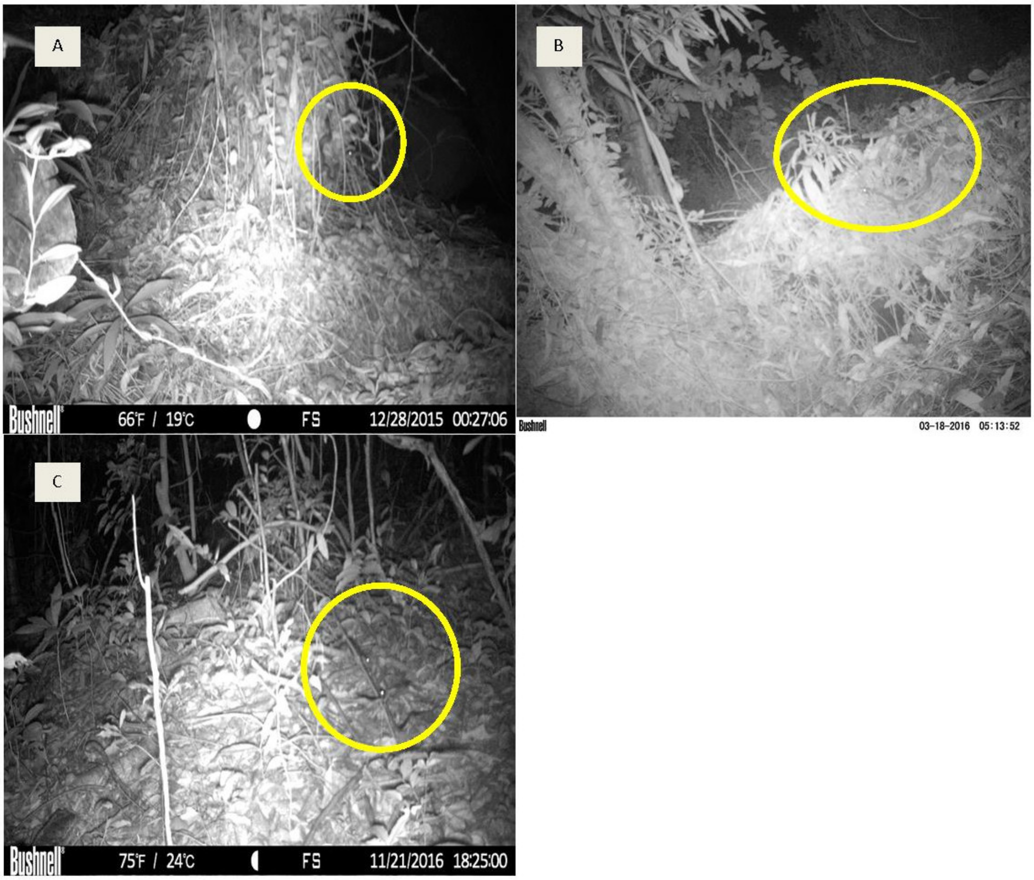

FIGURE 2. Agonistic interactions of three focal big-eyed pit vipers (*Trimeresurus* (*Cryptelytrops*) *macrops*) including female TRMA220 (A), male TRMA226 (B), and female TRMA271 (C) recorded on Bushnell trail cameras. Interacting vipers are circled in yellow for reference.

translates into social behavior remains largely unknown. Understanding of behavior and communication within subpopulations is worth investigating with green pit vipers due to their small home ranges. Subpopulations which are naturally or anthropogenically isolated from others may show different behaviors or degrees of sociality.

Previous observations of big-eyed pit viper morphology and natural history have suggested unique adaptations for social behavior and reducing direct competition. Sexual dimorphism, both in coloration and in size, likely reduces competition and agonistic interactions[15,21]. Additionally, several studies suggest niche partitioning and vertical stratification among green pit vipers, including *T. macrops*[15,21,22]. These factors may explain the higher number of neutral interaction outcomes compared to agonistic, and perhaps why we observed so few interactions overall.

Big-eyed pit vipers have been previously documented and suggested to breed primarily between September and November, which corresponds to the end of the rainy season in Thailand[24,25]. This species is unique among vipers in that biting has been directly observed in the wild during male combat during the breeding season, which has been suggested to be a period of increased agonistic behavior[25]. Our observations (late November to early May) occurred outside of previously reported mating season for the species. We describe the first evidence of social interactions in conspecific green pit vipers. Interactions primarily resulted in what appeared to be neutral outcomes, however, several interactions were clearly agonistic which is novel for the green pit viper taxon outside of breeding activities.

Resource defense and territorial behavior likely evolved or occurs when the benefits gained by defending a particular area that contains required resources exceed the costs of defending it[26,27,28]. It is frequently observed in terrestrial vertebrate groups, including birds, mammals, lizards, frogs, and salamanders[29,30]; although evidence is scarce for snakes. Only two insular colubrids (*Oligodon formosanus* and *Dinodon semicarinatum*) defending sea turtle nests (food resource) against conspecifics have conclusively been suggested to display resource defense and territoriality among all known snake species[31,32]. Infrequent feeding and the unpredictability of exact time and place of available prey were factors suggested by[32] as to why snakes generally do not defend food resources. Not enough evidence was provided in our work to definitively characterize *T. macrops* as territorial by sex, season, or with increased human disturbance; however, our observations suggest they may display similar agonistic characteristics at least occasionally (3 out of 9 interactions in our study) outside of the breeding season.

We cautiously suggest limited resources and sub-optimal seasonal conditions may be driving factors behind the interactions we witnessed on camera. Pit vipers in our study interacted during the cold and hot dry seasons, which were not optimal foraging periods for anuran prey. Frogs likely comprise a significant portion of *T. macrops* diet[24,33]. Presence and utilization of quality foraging sites may also be a premium during these time periods (cold and hot dry seasons). Lateral distance between ambush and shelter sites is negligible[12,19], and the two are likely not independently related. Thus, site selection (and social behavior, subsequently) is likely influenced by the balance of thermoregulation and energy expenditure to obtain additional nutrients.

Shelter, resting, and ambush sites with adequate prey abundance may be scarce in rural communities and other highly disturbed areas, additionally increasing opportunities for interactions and competition. Decreased prey and increased habitat homogeneity were observed for timber rattlesnakes (*C. horridus*) in a rural landscape in North America, which subsequently altered foraging behavior[34]. Further investigation of ambush site selection, chemical cues, and prey availability would greatly augment behavioral inferences. Whether social interaction prevalence is related to ambush site availability or quality would be a beneficial testable hypothesis for future study.

From our camera observations, the conspecifics interacting with our focal vipers appeared to be female *T. macrops* on the basis of size and general morphology, however, recording quality of the cameras was not sufficient to positively confirm species, sex, or fecundity. Similarly, low recording rate (1-3 frames per minute) may indicate missed or misinterpreted behaviors. Thus, we were conservative with our characterizations of behaviors and outcomes of interactions, as we believe acknowledging the limitations of camera technology is essential for reducing potential misinterpretation and overstating our results. Similarly, we believe it is essential to not over-extrapolate our results due to our limited sample size and having a single study area in northeast Thailand.

While certainly a time intensive method, we encourage further study with fixed cameras to better understand the consequences of intra and interspecific interactions of animals employing ambush foraging strategies. Green pit vipers employ ambush strategies and sedentary lifestyles which make them ideal for investigating behavioral interactions with fixed cameras. As a result we propose the group as a model species for behavior and social interaction study of ambush foraging predators.

To conclude, even broadly trained scientists are frequently ignorant of basic information about snakes, including social behavior[30,35-36]. Lin et al. (2007)[37] provided personal observation that green pit vipers "tend not to interact in an antagonistic or repellent manner; in fact they generally ignore each other's presence even when they are in physical contact or in ambush positions on the same or adjacent sites in the field or laboratory," and fashioned their retreat site selection study design accordingly. While social interaction between green pit vipers may be rare (272 minutes of 34, 226 minutes for the *T. macrops* observed in our study), consequences of such contact and knowledge of subsequent communication and resulting behavior are crucial for ecological study and conservation.

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