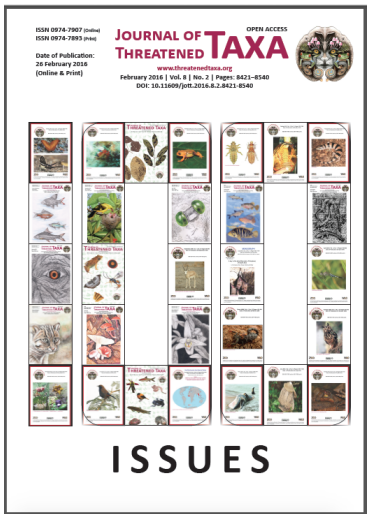

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SHORT COMMUNICATION

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Tangled skeins: a first report of non-captive mating behavior in the Southeast Asian Paradise Flying Snake (Reptilia: Squamata: Colubridae: *Chrysopelea paradisi*)

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Abstract: We describe the courtship behavior of the Paradise Flying Snake, *Chrysopelea paradisi*, from a series of images taken near Sandakan, eastern Sabah, Borneo, Malaysia. During the episode observed, four males moved together with a female in various states of entanglement, traveling at ground level and into a series of bushes. The observations took place over the course of a 30-min period until the snakes were lost to view. Our report is the first direct observation of mating behavior in *C. paradisi* in the wild and provides another rare glimpse of the multi-male courtship in Southeast Asian colubrids.

Keywords: Borneo, *Chrysopelea paradisi*, Colubridae, Malaysia, mating behavior, multi-male courtship, Sabah.

The Paradise Flying Snake, *Chrysopelea paradisi* H. Boie in F. Boie, 1827, is a colorful diurnal inhabitant of tropical forests, whose ability to flatten its ribcage and create an air cushion beneath its body enables it to glide for considerable distances, from tree to tree, or from perch to ground (e.g., Wall 1908, 1921; Mertens 1968). It is a medium-sized species (1.2m maximum length; Mertens 1968) with a distribution ranging throughout the Malay Peninsula (including Penang, Singapore, and the Seribuat Archipelago), north into Thailand and Myanmar, west to the Andaman Islands and Narcondam Island, Indian territories in the Andaman Sea, south into the Indonesian archipelago (Bali, Bangka, Belitung, Bintan, Galang, Java, Nias, Sipora, Sulawesi, Sumatra, Rakata, Weh), and across the South China Sea into the Natunas Archipelago, Borneo (Brunei, Kalimantan, Sabah, Sarawak,) and the Philippines (Balabac,

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Bantayan, Banton, Basilan, Bongao, Bubuan, Camiguin, Cebu, Dinagat, Jolo, Kalotkot, Leyte, Luzon, Marongas, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Romblon, Samar, Sibutu, Sibuyan, Siquijor, Tawitawi) (de Haas 1950; Haile 1958; Mertens 1968; Alcala 1986; David & Vogel 1996; Manthey & Grossmann 1997; Stuebing & Inger 1999; de Lang & Vogel 2005; McKay 2006; Das 2007, 2010; Grismer 2011; Cox et al. 2012; Koch 2012; Wallach et al. 2014). Three subspecies are recognized: *C. p. celebensis* Mertens, 1968, from Sulawesi, and *C. p. variablis* Mertens, 1968, from the Philippines, with the nominate form occupying Borneo and the remainder of the range. Even though *C. paradisi* was described in 1827, it was listed in the synonymy of *C. ornata* (Shaw, 1802) by Schlegel (1837) without further comment, and remained there until Smith (1943) revalidated it at the species level. It is generally not commonly seen where it occurs, and it has only been reported sporadically from Borneo (e.g., Stuebing 1991, 1994; van Rooijen & van Rooijen 2007). As a consequence, outside of observations and experiments related to its gliding ability (e.g., Mertens 1968; Sajdak 2010; Jafari et al. 2014) relatively little is known about the natural history of these flying snakes, particularly with regards to their reproductive behavior.

Because of the synonymy between *C. paradisi* and *C. ornata,* reports in the time from 1837–1943 that actually pertain to *C. paradisi* may have been presented under the name *C. ornata*. This is important to note, given that there appears to be a significant geographic overlap in the ranges of these species. The most extensive treatments of *Chrysopelea* ecology were by Wall (1908, 1921 - under the name *C. ornata*) and Mertens (1968 - for the genus as a whole). *Chrysopelea* are described as elongate snakes, whose keeled body scales provide them with an excellent climbing ability. Prey includes lizards (particularly geckos and skinks) as well as a variety of mammals (rodents, bats) and smaller birds. Even though species of *Chrysopelea* are rear-fanged, their venom appears to be quite mild (Mertens 1968). The only limited reports of reproductive output in the wild in these snakes are those of Wall (1908, 1921), Wall & Evans (1901), and Evans (1904), and our knowledge can be summarized by stating that they are known to produce clutches of 6–11 eggs. Wall (1921) explicitly stated that the method of reproduction was unknown. It is noteworthy that for a group of snakes as diverse as colubroids in Borneo, with recorded species numbering nearly 100 as of this writing (Uetz 2015), our earlier report on *Dryophiops rubescens* (Gray, 1835) remains the only one in the primary literature on their reproductive behavior in nature (Kaiser et al. 2012). We here report the first observations of courtship behavior in *C. paradisi* outside of captivity.

Materials and Methods

During the morning of an unrecorded day in October/November 2012 (ca. 0900–1000 hr) [1], four individuals of *C. paradisi* were seen traveling slowly along the edge of a wooden walkway near the kitchen area of the Sepilok Jungle Resort, a popular tourist destination on the outskirts of Sandakan, Sabah, Malaysia (5.8659^{0}S & 117.9517^{0}E). Their movements were documented photographically over a period of 30 minutes, allowing the snakes to continue undisturbed along a path of their choosing. Observations ceased when the snakes entered the adjacent vegetation and became difficult to observe.

To simplify the presentation of our results (Image 1), we selected four frames from among the photographs to represent the interaction, and present each instance using both a photograph and a line drawing. In the line drawing we color-coded individuals in an attempt to show their respective positions, and to allow easy distinction between them. In our detailed description we refer to individuals by their colors to make the text easier to read; for example the blue-colored individual is simply referred to as “Blue.” In all frames, the largest, leading individual is colored dark gray and referred to as “Gray.” We attempted to maintain continuity during our observations by using the same color for each individual to allow identification throughout the encounter. This was possible by looking at enlargements of the images to observe color pattern differences along the snakes’ bodies. The complexity of the habitat combined with the movement made following them in detail difficult, but while we had to make judgment calls in cases where only small portions of an individual were visible, the constraints of snake morphology and sinuous locomotion provided valuable clues to identification. Regardless of whether each color-coded body part matches the same individual in each frame, our approach is optimal to illustrate the behavior involved. Measurements were made in units of head lengths of the largest snake, beginning at the tip of the snout of each snake. We made these measurements directly on photographic images using PixelStick software (version

[1] During the transfer of images between the photographer’s camera and multiple computers, the original data from the image files became modified. We have estimated the date range and the timing of the encounter from witness accounts.

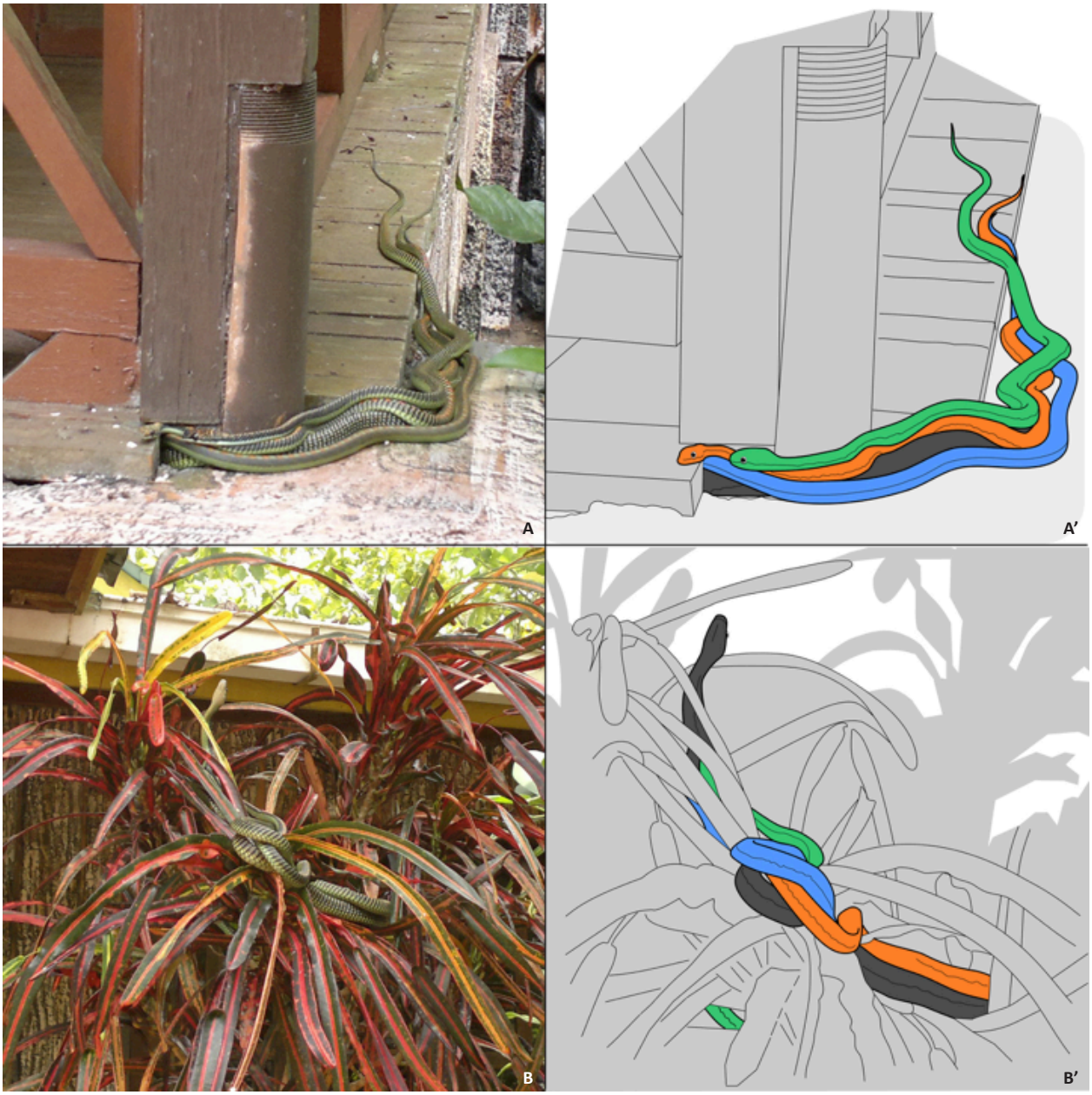

Image 1. Photographs and corresponding illustrations showing the courtship behavior of four Paradise Flying Snakes, *Chrysopelea paradisi*, recorded at the Sepilok Jungle Resort in Sandakan, Sabah, Malaysia. (A, A') The four snakes are moving together into a small opening at the edge of the boardwalk. The female (dark grey) is almost entirely covered by the three smaller males, whose bodies overlap to varying degrees. The blue male is followed by the orange and green males. (B, B') The four snakes moved into a small bush, with the female (dark grey) in the lead. The males' position relative to the female has shifted, with the green male now leading the blue and orange males.

2.3; plumamazing.com).

Results and Discussion

Initial movement of the snakes extended for a length of ca. 4m along the outer edge of a wooden walkway. This is not an area frequented by humans, who would move and remain inside the railing and not near the edge (Image 1A). The movement was coordinated, such that all four individuals were traveling at approximately the same slow speed, with some slight differences due to what we have called "jockeying for position" (Kaiser et al. 2012). When the throng encountered a corner of the walkway, the leading snake (Gray) moved underneath a wooden ledge, which formed an opening next to a pillar (Image 1A). While Gray and its closest follower, Blue, were moving into the opening and disappearing from view (Image 1A'), Orange and Green remained outside of the hole. Orange appeared to investigate the

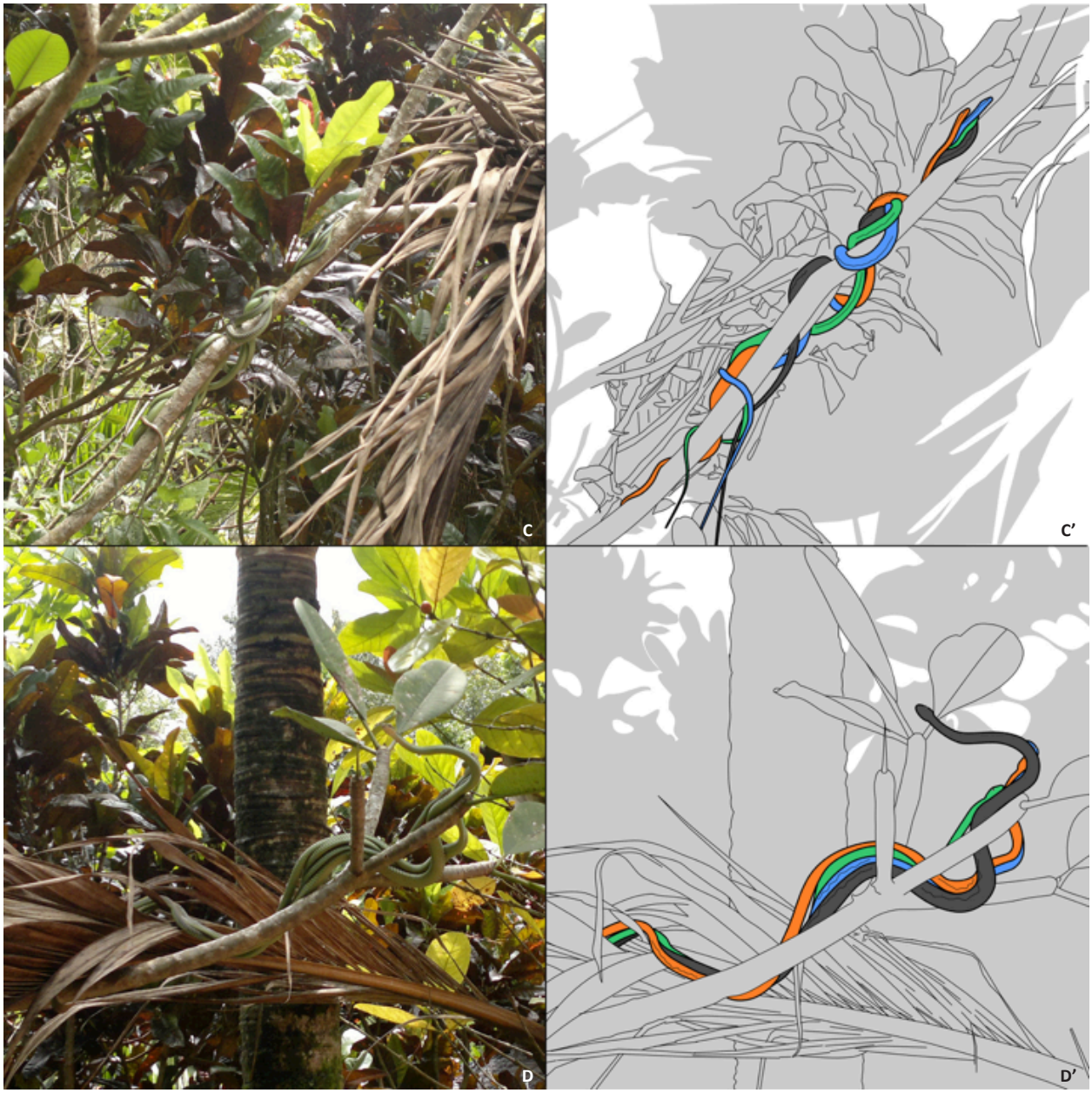

Image 1 (cont.). (C, C') The snakes have moved into a second tree, with the female (dark grey, head hidden) still in the lead, followed by the green, blue, and orange males, respectively. As seen by the position of bodies and tails along the branch, the courtship continues with significant overlap of all participants. (D, D') The female (dark grey) has moved several head lengths ahead of the males, which now appear to be aligned in a different sequence as before, blue male followed by orange, then green. It is noteworthy that at this stage, the bodies of the snakes are lined up nearly in parallel. Photos by Jason Lim.

environment above the hole, while Green was facing forwards towards the hole (Image 1A'). Ultimately, Orange and Green also moved their heads into the opening, and all four individuals squeezed through the hole in a writhing, side-by-side tangle of snake bodies. Gray subsequently led her pursuers beneath the walkway for a short distance, to emerge into the adjacent garden area. Even though the snakes were temporarily lost from view beneath the walkway (for a period of less than 5 min), they could easily be followed when they re-emerged from underneath the walkway to be followed once again. At the time when the photograph in Image 1A was taken, it is uncertain how much of a lead Grey might have had, yet several seconds before entering the hole, Gray led Blue by ca. 2.0 head lengths. The position of the heads of Orange and Green

did not permit a statement about who was ahead, given that even though Orange is advanced in position, the snake is not facing into the direction of Gray and Blue.

About 5 min after the photograph along the walkway (Image 1A) was taken, and ca. 10 min into the encounter, the four snakes were observed in a small tree they had ascended together after emergence from beneath the walkway. The photographs (Image 1B, B') show that Gray remains in the lead, with the three pursuers positioned in an overlapping arrangement beneath and behind. Based on the specific alignment of snake bodies, all three pursuers are resting parts of their bodies on Gray's, with Orange paralleling much of Gray's body (Image 1B'). While the vegetation hides significant portions of the snakes, it looks as if the lead among the colored pursuers has changed, and that Green is positioned more closely to the front of the group. The posterior portion of Green's body also appears to have slipped from a position paralleling Gray's, and a small portion of Green is visible well below the level of main activity.

Ten minutes later, the snakes had moved off the first tree and onto a second, demonstrating the ability of entwined snakes to move as a unit. The four snakes are clearly visible as they move along a thick branch (Image 1C, C'). Due to their visibility, it is possible to observe once again the order, in which the snakes are moving: Gray in the lead, followed by Green, then Blue, and finally Orange. Orange is ca. 1.8 head lengths behind Blue (Image 1C'). Close observation of the first set of body coils below the heads shows that all four individuals remain in touch with each other, and that there exists some degree of irregular intertwining. In this image, positioning at head level appears to have no correlation with positioning at body level.

The last set of illustrations (Image 1D, D') shows the four snakes ca. 10 min after the previous images, still advancing through the same tree, but higher up. This is the only image, in which the heads of all four individuals are visible. Gray remains in the lead, having moved her body upwards off the branch and swaying left and right while searching for the next perch. The other individuals' heads are all in contact with Gray's body. Blue is following at a distance of ca. 4.8 head lengths, with his head just visible. He is followed by Orange and Green, whose heads are 1.0 and 2.1 head lengths behind Blue, respectively (Image 1D'). This figure shows a close parallel arrangement of all four snakes' bodies, as they wind themselves around a branching point in the tree. The arrangement of bodies from top to bottom is not indicative of the sequence of heads, and it therefore appears to be a serendipitous arrangement. It is noteworthy that this elongate species moving in three-dimensional "tree space" manages to keep bodies so closely aligned. Observations ended because the snakes moved further into the cluster of trees, quite high off the ground, and became difficult to follow, let alone photograph. The total distance these snakes were observed to travel in an intertwined group was over 15m.

As with our earlier report of the courtship behavior in *Dryophiops rubescens* (Gray, 1835) at the same locality (Kaiser et al. 2012), the only activity that can explain our observations of the four individuals of *Chrysopelea paradisi* is courtship behavior. In our series of photographs (Image 1 A–D), Gray appears to be a female pursued by three male suitors (Blue, Green, Orange). Lured by Gray's pheromone trail, the males clustered around her body while matching her speed as she moved through the habitat. From our observations it is not clear whether the female attracted first one male, then another and then a third, or whether an initial emission of pheromones rapidly attracted all three. It also appeared to us that all three males were similarly-sized and healthy-looking, so it is doubtful that any mate choice on the part of the female had taken place before our observations began. The four individuals displayed movement akin to the "chase-mount behavior" described for captive *Boiga irregularis* (Merrem in Bechstein, 1802) and *D. rubescens* (Greene & Mason 2000; Kaiser et al. 2012), in which males jockey for position around the body of the leading female (the "chase") and use the body of the female itself as a substrate (the "mount") in order to achieve copulation. The behavior in *B. irregularis* was described for interactions between one female and one male, whereas in *D. rubescens* two males and one female were involved. It therefore appears that this type of behavior is not limited to interactions of two individuals. In addition, the three-dimensional surfaces presented by the habitat resulted in various levels of body intertwinement, which did not produce the ordered appearance of the "mating braid" as in *D. rubescens* (Kaiser et al. 2012) and did not appear to be the result of specifically coordinated movements. Head position of males reflected advances by one male or another, but our limited data do not allow us to analyze the performance (or putative success) of either of the males. Even though some of the movement of the males could be considered competitive, the thin, elongated body form of *Chrysopelea* allowed continuous, unimpeded group movement from the walkway into the trees.

Multi-male courtship behavior precedes communal

mating in a variety of snakes, and it includes the phenomena called "mating balls" (e.g., garter snakes: Gregory, 1975; Mason & Crews 1985; anacondas: Rivas & Burghardt 2001) and "mating braids" (Kaiser et al. 2012). Mating achieved in this way has been classified as "scramble polygyny" (Shine et al. 2003), in which males attempt to mate with several females in competition with other males. However, since the terms polygyny (one male mating with multiple females), polyandry (multiple males mating with one female), and polygynandry (multiple matings by multiple individuals) are all related to the mating outcome (i.e., related to the genetic contribution of partners) and not to the courtship process, their use leaves unclear the behaviors underlying the mating system. We therefore believe that the most appropriate term for our single observation, in the absence of data regarding the true mating outcome, is multi-male courtship.

The behavior we document here appears to be the first observation of courtship for the genus *Chrysopelea* in the wild. In these slender, elongate and arboreal snakes an elongate courtship configuration with bodies spread out along the anterior-posterior axis is advantageous over a mating ball on the ground (e.g., Rivas & Burghardt 2005) or even in a tree (e.g., Aleksiuk & Gregory 1974; Gregory 1975). This type of behavioral adaptation readily allows movement across all layers of a diverse habitat without disrupting the courtship process, and it likely reduces the potential for predatory attack on the moving target. While *Chrysopelea* is a genus best known for its spectacular coloration and its ability to glide, we are happy to report that the interesting feats of these snakes now includes multi-male courtship behavior.

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