Social Snakes? The role of kin selection in rattlesnake aggregations

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Studies of animal sociality have long challenged our understanding of evolution and provoked some of the greatest debates in the field. Although sociality takes a variety of forms, researchers have historically selected the most extreme forms of eusociality and cooperative taxa for intensive study (Ebensperger 2001, Cahan et al. 2002, Davis et al. 2011, Clark et al. 2012). However, simpler, often overlooked forms of sociality may better inform us about the evolutionary causes and consequences of social behavior (Cahan et al. 2002, Chapple 2003, Davis et al. 2011).

Aggregations (groups) of animals represent some of the simplest forms of sociality and may lead to the evolution of complex sociality (Graves and Duvall 1995). Animals may aggregate for active (e.g., alloparenting, group defense, kin selection; Vonhof et al. 2004) or passive benefits (e.g., thermoregulation; Graves and Duvall 1995). According to Hamilton's rule, an individual can increase its fitness by helping relatives (Hamilton 1964); thus, active and passive benefits of grouping may be enhanced by associating with kin (Vonhof et al. 2004, Davis et al. 2011). Kin-based groups are widespread, but have only recently been described in lizards and snakes (Chapple 2003, Davis et al. 2011, Clark et al. 2012).

Although typically regarded as asocial, some rattlesnakes form aggregations (Graves and Duvall 1995, Clark et al. 2012), recognize and preferentially associate with kin (Clark 2004, Clark et al. 2012), and possess traits linked to complex sociality: long lifespan, late maturation, and viviparity (Ebensperger 2001, Chapple 2003). Rattlesnake aggregations are assumed to be resource-based because they usually occur in cool climates where habitat providing opportunities to thermoregulate may be limited (Graves and Duvall 1995). However, in the relatively warm climate of Arizona, Arizona Black Rattlesnakes (*Crotalus cerberus*) aggregate at winter hibernacula and nesting sites.

We hypothesize that *C. cerberus* preferentially aggregate with kin to increase their indirect fitness through kin selection (Hamilton 1964). We will test the kin selection hypothesis by calculating relatedness and an association index (percent time seen together) for each pair of rattlesnakes. We predict that, if kin selection



Figure 1. Yellow Man (center, adult male *Crotalus cerberus*) with several juveniles and females basking at a den entrance. Photo by Melissa Amarello, April 2011.

plays a role in rattlesnake aggregations, pairs with higher association indices will be more related than pairs that do not spend much (or any) time together.

Since April 2011, we have used remote timelapse cameras (Timelapse PlantCam and TimelapseCam 8.0, Wingscapes, Inc., Alabaster, AL, USA) to record behavior of *C. cerberus* in aggregations at a site near Prescott, Arizona. Some pregnant females, their offspring, and the occasional male aggregate at these sites during the summer active season (Amarello et al. 2011), but most aggregation behavior happens during the spring, so we focused our efforts during this period (ca. mid-April through mid-May). We identified 78 individual rattlesnakes (42 adults and 36 juveniles), collected DNA samples from over 50, and observed them a total of 531 times.

To date, we have documented nonrandom patterns of association in *C. cerberus*, suggesting that they aggregate for active rather than passive benefits. Some rattlesnakes are more gregarious than others, and they are choosy about whom they associate with (Amarello 2012). Our collaborator at the University of Arizona, Dr. Hans-Werner Herrmann, identified 38 informative microsatellite DNA markers for genotyping *C. cerberus*, so we can examine how relatedness affects the strength of these associations.

We are only beginning to understand the complex social lives of rattlesnakes (Clark et al. 2012, Amarello 2012) and comparing the ecology of *C. cerberus* to asocial and social squamates will provide further information on the evolution of sociality (Chapple 2003). But perhaps most important, our data are used to facilitate snake conservation through education. Pernicious

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myths and popular media that have long portrayed snakes as malicious villains instill and nurture fear of snakes, which has led to widespread persecution and obstruction to conservation efforts (Seigel and Mullin 2009). In contrast to how snakes are usually seen in the media, recent research on rattlesnakes reveals behavior that appeals to the general public: parental care (Greene et al. 2002, Amarello et al. 2011), cooperation (Amarello et al. 2011), and social interactions (Clark et al. 2012, Amarello 2012). By revealing the social nature of rattlesnakes through live and virtual outlets (Amarello and Smith 2012), we are helping to change the public's perception of snakes from "cold-blooded killer" to social creatures with complex family lives.

Thanks to those who inspired, supported, and assisted us: M. Cardwell, R. Clark, D. DeNardo, M. Feldner, H. Greene, K. McGraw, J. Porter, R. Repp, B. Rogers, G. Schuett, M. Seward, J. Slone, B. Sullivan, Arizona Game and Fish Department (SP796730 and SP729143), and ASU IACUC. The Tucson Herpetological Society, National Science Foundation, Chicago Herpetological Society, Herpetologists' League, Wingscapes, and Rocket Hub supporters provided funding for this project.

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Figure 2. Barb (left, juvenile *Crotalus cerberus*) basking with Flash (right, adult male) near a den. Photo by Melissa Amarello, April 2012.

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Vonhof, M.J., H. Whitehead, and M.B. Fenton. 2004. Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Animal Behaviour 68:507-521. By revealing the social nature of rattlesnakes through live and virtual outlets (Amarello and Smith 2012), we are helping to change the public's perception of snakes from "cold-blooded killer" to social creatures with complex family lives.