Allometry and sexual dimorphism in the lung morphology of prairie rattlesnakes, *Crotalus viridis viridis*

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Abstract. We quantified sexual dimorphism and allometric changes in the lung morphology of 160 juvenile and adult specimens of prairie rattlesnake, *Crotalus viridis viridis*, from a single population. In virtually all lung components, those of males are located more posteriorly than are those of females of the same body size. Males display a longer vascular component than females but there is no sexual dimorphism in size of the avascular component. Thus, males generally have longer lungs than do females at all body sizes. With increasing body size, the lung components are found more anteriorly, relative length of the vascular lung decreases, and relative length of the avascular lung increases in both sexes. However, total lung length increases isometrically with body size. These sexual and allometric differences suggest that intraspecific variation should be taken into account when lung size characters are used in snake systematic studies.

Introduction

Sexual dimorphism in snakes generally is not extreme; however, sexual differences in body size, shape and squamation, coloration, and ecology are evident in most snake lineages, and it is these subjects which have received virtually all of the research attention (Shine, 1993). Comparatively few studies have investigated sexual dimorphism in the position of internal organs (Wallach, 1991; Keogh, 1993; Wong, 1994). The most important early contributions are the many works of Bergman (e.g., 1949, 1962; reviewed in Wallach, 1998), who studied basic anatomy and addressed sexual dimorphism in organ position in various Asian snake species. Rossman et al. (1982) studied the non-pulmonary comparative visceral topography of a large series of the North American tribe Thamnophiini, and Benton (1980) addressed sexual dimorphism in organ position in *Thamnophis sirtalis*. Thorpe (1975, 1979, 1989) studied sexual dimorphism in visceral morphology of the European grass snake *Natrix natrix*. More recently, sexual dimorphism in visceral morphology has been examined in the

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African Aparallactinae and Atractaspidinae (Wallach, 1991) and the Typhlopidae (Wong, 1994). These studies outline a general trend that the visceral organs of male snakes are placed more caudally than those of females. Although each of these studies contributed important data on interspecific and intraspecific variation in the position of visceral organs, most had small sample sizes for individual species or populations and none has considered allometry in organ position within a single population. Only Thorpe considered how the position of visceral organs can vary geographically in snakes.

We were interested in two main questions, (1) to what extent is sexual dimorphism in organ position present in a single population where the confounding effects of geographic variation is not an issue, and (2) does the study population also display allometry in organ position, and if so are the patterns the same in males and females? We chose to examine lung morphology in the ecologically and behaviorally well known prairie rattlesnake, *Crotalus viridis viridis*. Lung morphology was targeted in particular because this is the best studied of the snake visceral systems, there may be functional morphological implications of dimorphism or allometry, and lung morphology also is used as a source of important systematic characters in snakes. While there have been studies of sexual dimorphism in several crotaline snakes (Klauber, 1956; Clark, 1967; Gibbons, 1972), there have been no studies of intraspecific variation in the internal anatomy of any crotaline species. This research represents the first large scale study of sexual dimorphism and allometry in the lung morphology of any species of snake.

Materials and methods

Lung morphology

All snakes possess a right lung; the left lung is smaller, vestigial, or absent (Cope, 1894). As the gross morphology and ultrastructure of the respiratory system of *C. viridis* has been described in detail (Kardong, 1972; Luchtel and Kardong, 1983), we provide only a general outline of the lung structures pertinent to our study (fig. 1). The respiratory system of viperid snakes is composed of the trachea, tracheal lung, right lung and occasionally a bronchus and vestigial left lung (*C. v. viridis* does not possess a left lung). The trachea typically extends into the right lung where it continues as an intrapulmonary bronchus. The tracheal lung is a weakly vascularized membrane supported between the incomplete semicircular cartilaginous rings of the trachea. The right lung typically has a distinct cranial vascular portion and a caudal avascular or saccular portion. The division between the vascular and avascular areas of the right lung is distinct. The vascular region possesses parenchyma described as faveolar, edicular or trabecular (Duncker, 1978; Perry, 1983), and is divided accordingly into the cranial dense vascular portion (DVP or faveolar) and the caudal sparse vascular portion (SVP or edicular/trabecular) regions (fig. 1). The change from faveoli to trabeculae or ediculae occurs over an area of less than 10 mm lung length.

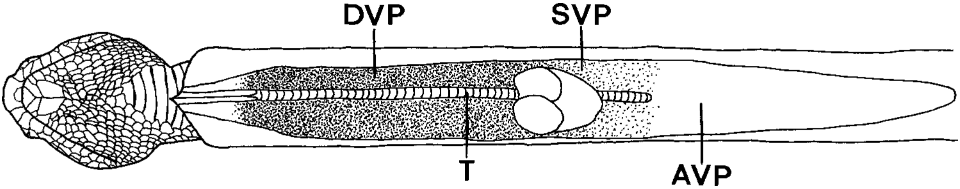

Figure 1. Diagram of gross lung morphology of the prairie rattlesnake *Crotalus viridis viridis*. The trachea (T) leads into the single, elongated right lung, which can be as long as 67% of snout-vent length in this species. The right lung can be divided easily into three sections: the anterior dense vascular portion (DVP), the more posterior sparse vascular portion (SVP), and the avascular (AVP) or saccular portion.

Specimens

A total of 160 specimens of *C. v. viridis* were selected from Laurence Klauber's large "Platteville series" collected from Platteville County, Colorado (see material examined). Body size dimorphism was previously studied in the population selected: out of 858 specimens (459 males, 399 females) maximum adult length was 863 mm for females and 1015 mm for males (Klauber, 1956). The mean length of males from this population is 776 mm ($n = 224$ specimens), 5.3% larger than the average female size of 737 mm ($n = 170$ specimens) (Klauber, 1956). Most species within *Crotalus* exhibit sexual size dimorphism, with males reaching larger body sizes than do females (Klauber, 1956). Specimens were selected that could be divided easily into sex and size classes, to facilitate statistical analyses. They reach sexual maturity at approximately 530 mm snout-vent length (SVL) depending on locality (Aldridge, 1979; Macartney and Gregory, 1988; Macartney et al., 1990). For our analyses, an arbitrary cut-off point of 375 mm was used. Specimens 375 mm or longer were classified as "large" and included both sub-adults and adults; snakes less than 375 mm in length were classified as "small" and were immature. A total of 40 specimens were examined from each of the following four size-sex classes: small male, small female, large male, and large female. Sex was determined by examining relative tail length and presence or absence of hemipenes.

Dissection techniques

Specimens were prepared for dissection following the techniques of Wallach (1985, 1991). First, a single ventrolateral incision from the cloacal region to the gular area of the neck was made with a pair of scissors. Then the head was secured to a dissection board with pins placed on either side of the head posterior to the jaw articulation (pins were not placed through the head). The body was then stretched as straight as possible, followed by securely pinning the tail to the board with the specimens laid ventral side up. After exposing the pleuro-peritoneal cavity of the specimen, the posterior tip of the thin and often translucent right lung was located. If it was not apparent upon first inspection, the posterior tip was located by inserting a small pipette into the lung and gently inflating. An incision then was made on the ventral surface of the lung to expose the vascular and avascular components.

Measurements were recorded on the most anterior points of the dense vascular portion (DVP), sparse vascular portion (SVP), and the avascular (saccular) portion (AVP) (fig. 1). We use the term “point measurement” to refer to specific reference points on which measurements were recorded and they represent the proportional distance from the snout. In *C. v. viridis* the transition zone between the DVP and the SVP was taken to be the point where the DVP walls decreased in size and thickness based on visual inspection. The beginning of each lung region and the caudal end of the right lung were recorded as the distance in mm from the snout. From these data we also calculated the midpoint for each lung region, yielding a total of seven point variables. We also derived the following length variables from our data: vascular (DVP + SVP), avascular, and total length of the lung as proportions of snout-vent length, and total vascular length (DVP + SVP) as a proportion of total lung length.

Statistical analyses

Data were log-transformed to satisfy the assumptions of normality and homogeneity of variances for the statistical procedures we employed. We first tested for the presence of ontogenetic variation in lung morphology in each sex. Because there is no overlap in body lengths between our “small” and “large” size classes, the assumptions of analysis of covariance (ANCOVA) could not be met. Therefore, the most appropriate way to test for the presence of ontogenetic variation was to express each midpoint measurement as a proportion of snout-vent length and use one-way analysis of variance (ANOVA) to compare the mean ratio values. While there are theoretical problems associated with the use of ratios in statistical analyses, they are often the only meaningful way to investigate biological data (Sokal and Rohlf, 1973). Atchley et al. (1976) found that there were minimal problems when univariate statistics were performed on ratio variables. To test for the presence of sexual dimorphism within size classes we performed one-factor ANCOVA’s on the log transformed data with snout-vent length as the covariate and sex as the factor. ANCOVA’s were preceded by Homogeneity of Slopes tests.

Results and discussion

Sexual dimorphism

Homogeneity of Slopes tests showed that all slopes within each analysis were not significantly different ($P > 0.05$). Analysis of covariance revealed that point measurements are significantly more caudad in males than in females at the same body size in all variables except the location of the most anterior extremity of the respiratory system (table 1; see fig. 2a for an example). These sexual differences were evident in both small and large snakes. Thus, vascularity begins in the same location in both sexes; however, the position of demarcation lines between lung components lies farther down the body in males, trans-

Table 1. Summary of statistical results testing for the presence of sexual dimorphism and allometry in the lung morphology of a population of prairie rattlesnakes, *Crotalus v. viridis*. Data are expressed as proportions of snout-vent length (SVL) for ease of presentation. Analyses were performed on log transformed data, rather than on the raw ratio variables shown. DVP = dense vascular portion, SVP = sparse vascular portion, AVP = avascular portion, MP = mid-point, TTL = total lung length. $n = 40$ for each size/sex class.

Measurement	$\bar{x}(s)$	Range	F values for one factor ANCOVA testing for sexual dimorphism within age classes	Slope	F values for one way ANOVA testing for intrasexual ontogenetic variation
Point measurements			df = (1,77)		df = (1,78)
DVP ANT. TIP/SVL					
Large male	8.40 (1.15)	6.18-10.19	2.64 (NS)	0.923	80.03****
Large female	8.03 (1.02)	5.57-9.92		0.734	125.07****
Small male	10.81 (1.21)	8.28-13.43	3.95 (NS)	0.466	
Small female	10.41 (0.73)	8.49-11.84		0.868	
DVP MP/SVL					
Large male	23.82 (1.00)	22.21-26.16	20.99****	0.900	170.19****
Large female	22.87 (1.21)	20.20-25.37		0.821	169.97****
Small male	26.70 (0.97)	24.76-28.92	23.70****	0.819	
Small female	25.91 (0.77)	24.13-27.27		0.852	
SVP ANT. TIP/SVL					
Large male	39.24 (1.39)	36.77-42.78	25.76****	0.898	113.10****
Large female	37.72 (1.84)	33.78-42.13		0.841	100.87****
Small male	42.60 (1.44)	39.29-44.72	17.36****	0.909	
Small female	41.40 (1.40)	39.08-44.05		0.849	
SVP MP/SVL					
Large male	43.22 (1.33)	40.76-46.26	39.86****	0.905	128.71****
Large female	41.31 (1.87)	37.02-46.03		0.843	120.02****
Small male	46.65 (1.38)	44.07-49.66	31.10****	0.924	
Small female	45.19 (1.18)	42.88-47.49		0.864	
AVP ANT. TIP/SVL					
Large male	47.19 (1.41)	44.43-49.74	44.53****	0.912	99.98****
Large female	44.91 (2.01)	40.24-50.52		0.846	103.71****
Small male	50.69 (1.73)	47.16-55.25	28.02****	0.935	
Small female	48.98 (1.34)	46.30-51.65		0.877	

Table 1. (Continued).

Measurement	$\bar{x}(s)$	Range	F values for one factor ANCOVA testing for sexual dimorphism within age classes	Slope	F values for one way ANOVA testing for intrasexual ontogenetic variation
AVP MP/SVL					
Large male	61.78 (1.40)	58.67-65.36	47.75****	0.960	30.78****
Large female	59.13 (2.29)	54.51-63.88		0.880	58.74****
Small male	63.99 (2.06)	58.77-67.08	17.74****	1.004	
Small female	62.36 (1.34)	58.63-65.00		0.902	
AVP POST. TIP/SVL					
Large male	76.38 (2.22)	70.04-82.73	26.24****	0.990	1.75 (NS)
Large female	73.34 (3.22)	66.08-78.94		0.900	15.79***
Small male	77.29 (3.39)	67.33-81.48	5.32*	1.050	
Small female	75.75 (2.11)	70.96-81.79		0.917	
HEART APEX/SVL					
Large male	43.38 (2.64)	40.49-55.53	30.33****	0.811	60.46****
Large female	41.30 (1.89)	37.36-45.93		0.797	118.70****
Small male	46.93 (1.51)	43.59-51.79	29.73****	0.839	
Small female	45.43 (1.45)	43.01-49.60		0.845	
Length measurements					
VASCULAR LENGTH/SVL					
Large male	38.79 (1.53)	35.83-42.38	29.41***	– 0.087	8.28**
Large female	36.89 (1.92)	32.73-41.34		– 0.129	19.57****
Small male	39.88 (1.86)	36.16-44.75	12.28**	0.066	
Small female	38.57 (1.45)	35.20-41.27		– 0.118	
AVASCULAR LENGTH/SVL					
Large male	29.18 (2.45)	21.34-35.49	1.51 (NS)	0.122	14.13***
Large female	28.43 (2.92)	21.75-34.99		– 0.023	7.45**
Small male	26.59 (3.46)	17.13-31.56	0.32 (NS)	0.297	
Small female	26.77 (2.32)	22.53-33.57		– 0.014	

Table 1. (Continued).

Measurement	$\bar{x}(s)$	Range	F values for one factor ANCOVA testing for sexual dimorphism within age classes	Slope	F values for one way ANOVA testing for intrasexual ontogenetic variation
TOTAL LUNG LENGTH/SVL					
Large male	67.97 (2.50)	60.13-73.80	26.24****	0.990	4.95*
Large female	65.31 (2.99)	59.53-71.92		0.900	0.01 (NS)
Small male	66.47 (3.47)	56.87-72.17	5.30*	1.051	
Small female	65.34 (2.26)	60.55-71.07		0.918	
TOTAL VASCULAR LUNG/TLL					
Large male	57.11 (2.52)	51.84-64.52	1.25 (NS)	− 0.088	18.05****
Large female	56.55 (3.19)	49.26-63.82		− 0.049	15.49***
Small male	60.13 (3.76)	53.64-70.35	2.22 (NS)	− 0.079	
Small female	59.08 (2.54)	52.76-64.24		− 0.044	

*= $P < 0.05$, **= $P < 0.01$, ***= $P < 0.001$, ****= $P < 0.0001$.

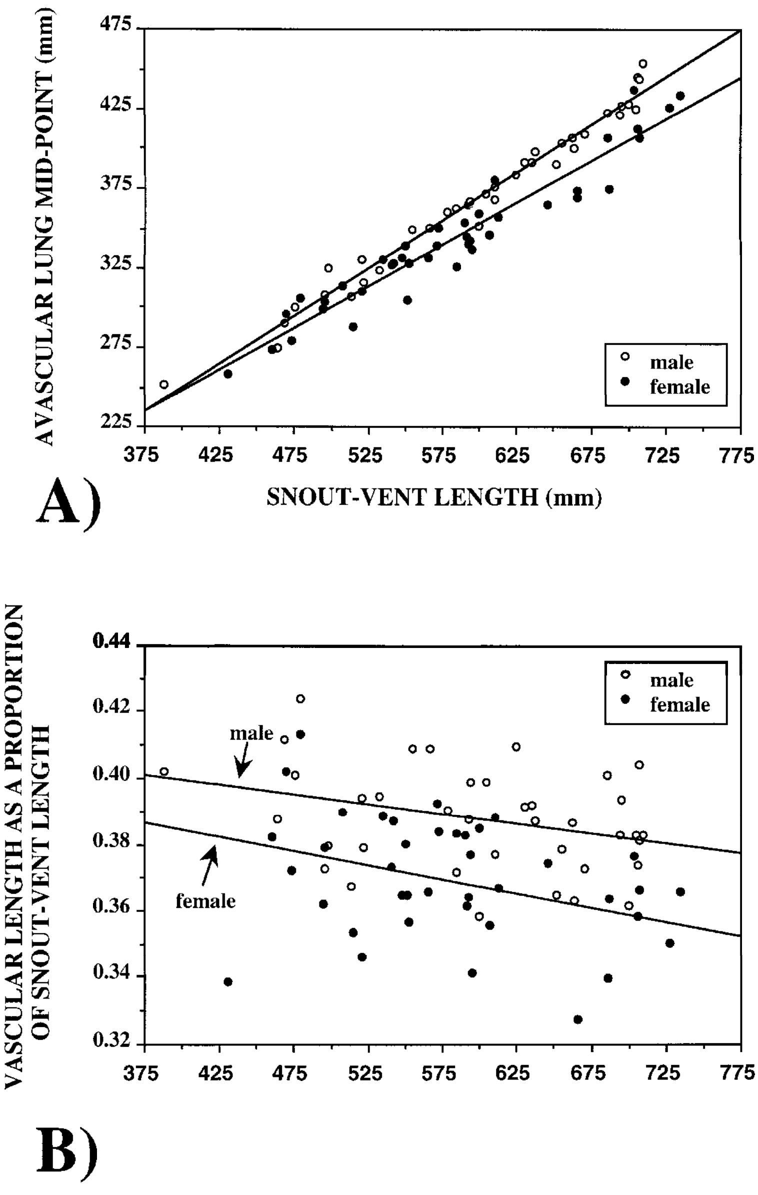

Figure 2. (A) Sexual dimorphism in midpoint position of the avascular (saccular) lung in sub-adult and adult prairie rattlesnakes. This figure is representative of the relationship of all other sexually dimorphic lung morphology variables examined in both juvenile and sub-adult and adult specimens in that the positions of all measurement points are significantly more posterior in males. (B) Sexual dimorphism in right lung vascular length (dense vascular portion + sparse vascular portion) expressed as a proportion of snout-vent length in sub-adult and adult prairie rattlesnakes. As the snakes grow the proportion of vascular length in relation to snout-vent length decreases at a similar rate in both males and females. However, males have a significantly longer vascular portion than females at the same snout-vent length.

lating into greater total lung length in males at all body sizes. The vascular component as a proportion of total lung length is similar in both sexes; however, in absolute terms males have a longer vascular lung at all body sizes (fig. 2b), while there is no difference in avascular lung length between the sexes in either size class. Thus males have longer lungs than females throughout ontogeny due to the longer vascular component. Sexual dimorphism is summarized in fig. 3a.

The direction of sexual dimorphism in lung morphology is consistent with the few other studies in which it has been examined. Bergman's many studies (e.g., Bergman, 1949, 1962) on the lungs of 22 species of Asian snakes show that the posterior tip of the right lung is more caudad in males than in females in all but one (reviewed in Wallach, 1998). The right lungs of male garter snakes (*Thamnophis sirtalis*) are significantly longer and end more posteriorly than those of females (Parsons and Djatschenko, 1983). However, Collins and Carpenter (1970) found that the tracheal lung length plus right lung length was longer in female copperheads (*Agkistrodon piscivorus*) and Thorpe (1989) found no sexual dimorphism in the posterior tip of the right lung in grass snakes (*Natrix natrix*). Wallach (1991) and Wong (1994) studied sexual dimorphism in some of the same lung variables that we have investigated (i.e., avascular portion posterior tip, avascular length, and total lung length). Though sample sizes were small, they found similar trends in sexual dimorphism in lung morphology in most of the 48 species of African Aparallactinae and Atractaspidinae (Wallach, 1991) and two of the three species of Typhlopidae (Wong, 1994) studied. The position of the heart also showed significant sexual dimorphism. The posterior tip of the ventricle lies more caudally in males than in females of the same body length. This finding is consistent with other studies on heart position in snakes (Collins and Carpenter, 1970; Rossman et al., 1982; Thorpe, 1989).

Allometry

Both males and females display significant allometric changes in all point variables with increasing body length, except for the AVP posterior tip in males (table 1). With increasing body length, lung components are found more anteriorly. The relative lengths of lung components also display an interesting shift through ontogeny. In both sexes the proportion of vascular length relative to SVL decreases with increasing size (fig. 2b), while the proportion of avascular length relative to SVL increases. However, total lung length as a proportion of SVL shows no allometry in females and only weak variation in males. Thus, total lung length increases isometrically with SVL, but the proportion of vascular lung decreases as the snakes grow. Even though males have a larger vascular component than females in both small and large snakes, vascularity decreases at the same rate (same slope) in both sexes. Allometric shifts are summarized in fig. 3b.

This anterior allometric shift is difficult to explain, but may be due to varying rates of growth in different regions of the body as has been described by Thorpe (1975, 1979, 1989) in *Natrix natrix* (it is worth noting that though Thorpe (1975) found that the measured

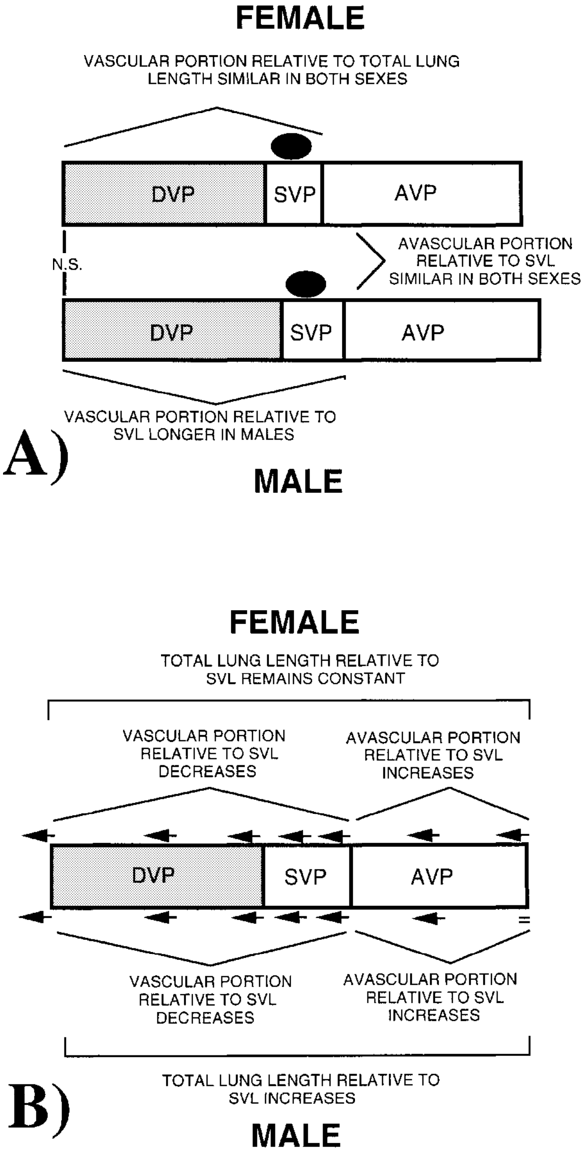

Figure 3. (A) Summary of sexual dimorphism in the lung morphology of sub-adult and adult prairie rattlesnakes. The anterior, mid-point, and posterior point measurements for each of the three lung sections are significantly different (one-factor ANCOVA, $P < 0.05$) between males and females (same pattern for juveniles) except for the position of the anterior point of the dense vascular portion (DVP). The oval shape represents the heart where the position of the apex also shows sexual dimorphism. (B) Summary of allometric shifts in lung morphology of prairie rattlesnakes. The arrows indicate the direction of significant differences in the point measurements for each of the three sections of the right lung with increasing age. The equal sign (=) indicates no significant difference in the point measurement. Except for the posterior tip of the right lung in males, all lung components are found relatively more anteriorly with increasing body size.

positions of internal organs varied allometrically, their segmental positions, in ventral scale units, did not). However, this does explain why the relative length of the vascular area gradually shrinks. Pough (1977a, b, c) found an unusual pattern in the blood physiology of garter snakes, *Thamnophis sirtalis* which offers one possible explanation. At birth, garter snake blood has high oxygen affinity, low hematocrit, and a high proportion of inactive hemoglobin, but larger snakes show a decrease in oxygen affinity, an increase in hematocrit, and a decrease in inactive hemoglobin with increasing size. Pough (1977b, 1980) hypothesized that the unusual shift in blood oxygen affinity through ontogeny may be attributable to the unique respiratory system of snakes. Breathing is relatively complex in snakes because they have no diaphragm, so ventilation of the lung occurs by contractions of intercostal muscles, moving the ribs in and out and the pressing of the liver into the lung (Rosenberg, 1973). Pough (1977c) found that the larger muscle mass of adult *Thamnophis sirtalis* facilitated better ventilation than in smaller snakes thus suggesting a possible explanation for the high blood oxygen affinity in juveniles. Adults are able to pass more oxygenated air over the vascular portion of the lung and therefore may not need the extra faveoli.

The highly unusual lung morphology of snakes and the data we present here suggest that the pursuit of answers which might explain why such allometric and sexual dimorphism patterns are displayed in the lungs of lungs are fruitful areas of further research. The data further suggest that intraspecific variation should be considered when characters derived from lung size are used in snake systematic studies.

Material examined

Crotalus v. viridis from prairie dog towns near Milton Reservoir in Sand Hills, 10 mi. E Platteville and 50 mi. NE Denver, Platteville Co., Colorado, collected by C.B. Perkins, 12-14 October 1930: SDSNH 3588, 3589,3596, 3597, 3600, 3604-3609, 3611-3614, 3619-3621, 3670, 3717-3719, 4521, 4527, 4528, 4537, 4542, 6157-6158, 6160, 6162, 6165-6167, 6169-6173, 6175, 6176, 6178, 6180-6182, 6184, 6186, 6187, 6193, 6195, 6196, 6202-6219, 6221-6232, 6235, 6237, 6239-6241, 6256, 6266, 6268, 6272, 6289, 6300, 6302, 6303, 6312, 6344, 6349, 6350, 6352, 6358-6361, 6363, 6366, 6411-6413, 6415-6420, 6428, 6430, 6431, 6433, 6436, 6437, 8129, 8131, 8138, 8140, 8144, 8145, 8147, 8149, 8152, 8157, 8162, 8164, 8166-8168, 8217, 8257-8259, 8295-8297, 8299, 8300, 8302-8305, 8309-8314, 8316, 8319-8322, 8751.

Acknowledgements. VW thanks T. Fritts, formerly curator at the San Diego Natural History Museum, for permission to dissect the series of specimens used in this study. Data were collected by VW as part of a Zoology Special Study for R. Etheridge at San Diego State University. JSK was supported by a Fulbright Fellowship from the American-Australian Education Foundation and an Overseas Postgraduate Research Scholarship during manuscript preparation. This manuscript was improved by the helpful comments of P. Doughty, C. Qualls, R. Shine and two anonymous referees.

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Received: November 3, 1998. Accepted: February 10, 1999.