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Sex allocation and secondary sex ratio in Cuban boa (*Chilabothrus angulifer*): mother's body size affects the ratio between sons and daughters

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Abstract Secondary sex ratios of animals with genetically determined sex may considerably deviate from equality. These deviations may be attributed to several proximate and ultimate factors. Sex ratio theory explains some of them as strategic decisions of mothers improving their fitness by selective investment in sons or daughters, e.g. local resource competition hypothesis (LRC) suggests that philopatric females tend to produce litters with male-biased sex ratios to avoid future competition with their daughters. Until now, only little attention has been paid to examine predictions of sex ratio theory in snakes possessing genetic sex determination and exhibiting large variance in allocation of maternal investment. Cuban boa is an endemic viviparous snake producing large-bodied newborns (~200 g). Extremely high maternal investment in each offspring increases importance of sex allocation. In a captive colony, we collected breeding records of 42 mothers, 62 litters and 306 newborns and examined secondary sex ratios (SR) and sexual size dimorphism (SSD) of newborns. None of the examined morphometric traits of neonates appeared sexually dimorphic. The sex ratio was slightly male biased (174 males versus 132 females) and litter sex ratio significantly decreased with female snout-vent length. We interpret this relationship as an additional support for LRC as competition between mothers and daughters increases with similarity of body sizes between competing snakes.

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Introduction

Secondary sex ratio contributes considerably to sex allocation of the maternal investment. Thus, the sex ratio has been extensively studied in many animal taxa. The sex ratio theory (Cockburn et al. 2002; Uller et al. 2007; Wild and West 2007) predicts that in species with almost equal maternal costs of son and daughter production, the investment in sons and daughters is typically balanced and thus close to the parity (Fisher 1930). Moreover, presence of the sex chromosomes genetically determining sex of the offspring provides a simple proximate mechanism enabling parity of the primary sex ratio (of zygotes). Nevertheless, empirical studies have reported numerous deviations from expected parity of the sex ratio in diverse vertebrate taxa: humans (e.g. Kemkes 2006; Almond and Edlund 2007), mammals (e.g. Phalangeridae: Johnson et al. 2001; Johnson and Ritchie 2002; Isaac et al. 2005; primates: vanHooff 1997; White 2009; Rapaport et al. 2013; ungulates: Hoefs and Nowlan 1994; Blanchard et al. 2005; Holand et al. 2006; rodents: Frynta and Žižková 1994; Shibata and Kawamichi 2009; for review see Rosenfeld and Roberts 2004; Robert and Schwanz 2011), birds (e.g. Passeriformes: Hjernquist et al. 2009; Bowers et al. 2011, 2014; Psittaciformes: Heinsohn et al. 2011; for reviews see Sheldon 1998; Pike and Petrie 2003) and reptiles (e. g. Crocodylia: Zhao et al. 2013; turtles: Lovich et al. 2014; Squamata: Colubridae: Luiselli et al. 1996; Elapidae: Shine and Bull 1977; Reichling and Gutzke 1996; Scincidae: Wapstra et al. 2004; for review see Wapstra and Warner

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2010). These deviations are usually interpreted as adaptive maternal manipulations of the sex ratio of the progeny.

The most popular hypothesis is that originally proposed by Trivers and Willard (1973) suggesting that mothers under good conditions tend to produce sons while the remaining ones produce daughters. As males are the sex exhibiting larger variance in reproductive success (Clutton-Brock 1990), it is advantageous to produce sons when a high quality of the offspring is to be expected. Nevertheless, the gain from such a manipulation depends upon additional conditions. There has to be, e.g. a positive correlation between maternal investment (measurable as the body weight at birth) and reproductive success at adulthood (Trivers and Willard 1973; Stanley and Shultz 2012; English et al. 2013; Piedrahita et al. 2014).

Another adaptive model of the maternal manipulation of the secondary sex ratio represent local resource competition hypothesis (Clark 1978). In matrilocal species, daughters compete with the mother for food and other resources while sons disperse. Mothers may avoid this cost by selective production of the male offspring.

Irrespective to the ultimate factor favouring maternal sex ratio manipulation, there is also its cost. In mammals where the sperm determines the sex of the zygote, any deviation from the primary sex ratio is done by selective mortality of zygotes, embryos and/or foetuses. This makes maternal sex ratio manipulation costly. The researchers dealing with large samples of mammalian secondary sex ratios typically disagree whether the maternal manipulation is present or not (Festa-Bianchet 1996; Silk et al. 2005; Nováková et al. 2010; Polák et al. 2015) or attribute the observed effects directly to proximate factors as are the glucose levels (Cameron 2004; Cameron et al. 2008), steroid hormones (James 1997, 2000; for review Navara 2013) and presence of parasites (Kaňková et al. 2007a, b). In contrast, adaptive explanations were repeatedly considered in birds (Komdeur et al. 1997, 2002; Ležalová et al. 2005) where chromosomal setting of the egg determines the sex of the embryo and thus a female has a potential to directly manipulate the sex of the offspring (Alonso-Alvarez 2006; Rutkowska and Badyaev 2008).

Although many papers focused on sex-specific allocation and/or manipulation with the sex of the progeny in mammals and birds, squamate reptiles, i.e. lizards and snakes, were currently proposed as an ideal model group for the study of sex allocation (Wapstra et al. 2007). Moreover to other reasons, the authors argue that (1) lizards and snakes exhibit simple ways of parental investment consisting almost exclusively from maternal investment to eggs and pregnancy; (2) they show wide plasticity in life history strategies and phenotypic trajectories; (3) some species can be reliably sexed shortly after hatching or birth and (4) they cover a great variation of sex determining mechanisms including both temperature and genotypic sex determination (further referred to as TSD and GSD, respectively). Many lineages of this group, including snakes, share the sex determination pattern with birds (ZW chromosomes) and consequently have a potential for maternal manipulation of the sex of the progeny than those with XY mode of GSD. Thus, snakes are especially promising for testing prediction of the sex ratio theory.

In this paper, we studied a Cuban boa, *Chilabothrus angulifer* (Bibron, 1843), a viviparous snake species with an extremely heavy investment in each newborn. (1) We analyse long-term data from captivity and demonstrate factors predicting deviations from the balanced investment into the sons and daughters. (2) In order to complete the pattern of sex allocation, we also assessed the sexual size dimorphism (further referred to as SSD) of the neonates. (3) We propose a modified local-resource competition hypothesis to explain the observed patterns of sex allocation in the studied snake species.

Material and methods

Chilabothrus angulifer is endemic to Cuba and surrounding small islands (Sheplan and Schwartz 1974). It is the largest species of the Antillean boids with specific life history. Females of this species are giving birth to a small number of extremely large-bodied (~200 g) and thus expensive newborns which are able to accept mice and bats soon after the first ecdysis. This strongly contradicts the other species which produce a great number of small (<20 g) newborns that is typical for the other nine species of this genus inhabiting other islands of the Great Antilles, e.g. *Chilabothrus striatus* (Fischer, 1888) of Hispaniola; *Chilabothrus inornatus* (Reinhardt, 1843) of Puerto Rico; *Chilabothrus subflavus* (Stejneger, 1901) of Jamaica (Tolson 1987). Juveniles of these species feed on anoles or *Eleutherodactylus* frogs and then switch to mammalian or avian prey at subadulthood (Henderson et al. 1987, but see Knapp and Owens 2004). The genus *Chilabothrus* of the Great Antilles (for phylogenies see Tolson 1987; Kluge 1989; Burbrink 2005; Reynolds et al. 2013) is a close relative of the South American anacondas of the genus *Eunectes* (see Dirksen 2002) and rainbow boas of the genus *Epicrates* sensu stricto (Passos and Fernandes 2008; Rivera et al. 2011), both producing newborns of an intermediate size (see Tolson 1987) which are able to accept mammalian or bird prey (Pizzatto et al. 2009).

Subjects Breeding females were 42 captive born Cuban Boas (*Chilabothrus angulifer*) of the first, second or third generation born in captivity. Their age ranged from 6 to 27 years old. The colony had multiple unrelated founders (legally imported from Cuba in the 70s and the early 80s), and inbred mating was not allowed. Variation in mitochondrial cyt b revealed high degree of genetic variation (unpublished data).

Housing The breeding females were kept together with their mating partners, by pairs or groups of up to six individuals. The terrariums were 1300 × 1200 × 1000 mm in size provided with water pool, shelves and heating places allowing local basking. The neonates and juveniles were kept in similarly equipped glass terrariums. The size of the terrarium was adjusted to the actual body size of the growing individual. The temperature of breeding rooms was set to 26–27 °C. The adults were fed with chickens (entire bodies of 4-day-old chickens and/or necks and wings of slaughter-weight chickens). The minerals and vitamins were provided by addition of Nutri Mix (Trouw Nutrition Biofaktory s.r.o., Czech Republic).

Data collection In breeding females, we assessed their snout-vent length (further referred to as SVL) and body weight. Nevertheless, due to extension of mating and birth seasons, reliable body weight at the time of conception was available for only a minority of litters ($n = 32$). Body condition of the mother at the time around conception was expressed as a residual from the allometric relationship between SVL and body weight ($r = 0.670$; equation: ln (body weight) = 2.697 * ln (SVL)–11.713; $df = 1.30$, $F = 24.42$, $P < 0.0001$). We categorized the components of the litter on newborns, dead embryos and non-developing eggs. We could not distinguish non-fertilized eggs and eggs that had been fertilized but had died during early embryogenesis; therefore, these were further referred to as non-developing eggs. As we were unable to ensure that no undeveloped egg or dead embryo was cannibalized by the mother prior to the detection of the litter by the keepers, we prefer to rely on data concerning living newborns. After birth, we recorded the newborns' birth body weights and their body weights after the first shed when the yolk was already absorbed and thus the juvenile body form completed. After the first shed, we also assessed neonates' SVL, tail lengths and counted the number of ventral and subcaudal scales. We determined also their jaw lengths and interorbital widths (the shortest distance along the straight line between the lateral margins of the supraocular shields).

Sexing The sex of the snakes was assessed using metallic probes that were inserted into the cloaca. The distance of penetration of the probe was expressed as a number of subcaudal scales. The statistical distribution of this value was clearly bimodal; the snakes in which the probe penetrated to the distance exceeding five subcaudal scales were considered to be males (Fig. 1). The sexing procedure was performed in neonates. Low mortality rates allowed us to confirm the results by repeating this procedure later on in 105 individuals. The probing was confirmed as a reliable method to determine the sex of the individual even in neonates and/or juveniles, only 7 misclassifications were recorded. All of them were due to gentle probing and consequent incomplete penetration of the probe,
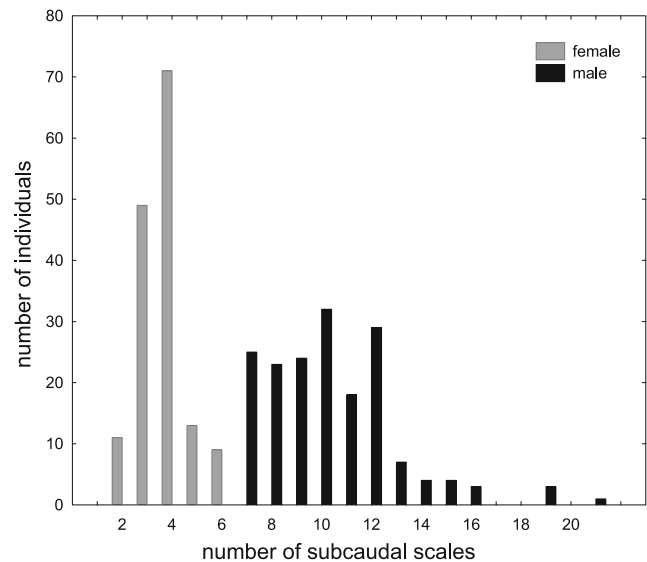

Fig. 1 Distribution of subcaudal scales numbers in examined Cuban boas (*Chilabothrus angulifer*)

which results in erroneous classification of the male subject as a female.

Statistical treatment A simple binomial test was applied to prove deviation of overall sex ratio from parity. In order to examine the effects of the body length, the body condition and the age of the mother, as well as the number of newborns, dead embryos, non-developing eggs on sex ratio of the litter and to avoid pseudoreplications, we employed marginal models (geepack package, geeglm function, binomial distribution, logit link function) accounting for identities of the mother.

The effects of sex on morphometric traits and scale counts were examined by linear mixed models (LMMs, package nlme, function lme, normal distribution, identity link function) accounting for mother and litter identities. The calculations were performed in R environment (R Development Core Team 2014).

Principal component analysis as implemented in STATISTICA 6.0 (StatSoft Inc. 2001) was employed to inspect the relationships among the following morphometric traits and scale counts: SVL, tail lengths, jaw lengths, interorbital widths, the number of ventral and the number subcaudal scales.

Results

In 62 examined litters produced by 42 females, we recorded 174 males and 132 females, thus the overall secondary sex ratio was significantly male-biased (56.9 % of males, 95 % CI = 51.1–62.5, $P = 0.0189$). Marginal models revealed that fixed factors significantly contributing to the sex ratio were the mother's body length (ANOVA: $\chi^2 = 19.88$, df = 1,

$P < 0.0001$) and the number of stillborns and non-developing eggs in the litter (ANOVA: $\chi^2 = 7.20$, df = 1, $P = 0.0073$). No effect of the number of living newborns (ANOVA: $\chi^2 = 0.58$, df = 1, $P = 0.4480$) and mother's age (ANOVA: $\chi^2 = 0.25$, df = 1, $P = 0.6137$) on the sex ratio of the progeny was found. Besides this, we also failed to prove the effect of the mother's condition on the litter sex ratio (ANOVA: $\chi^2 = 0.01$, df = 1 $P = 0.9780$), but the mother's body condition was available only for a limited number of litters ($n = 32$). Thus, these variables were removed from the final reduced model which contains only two predictors of litter sex ratio: the body length of the mother and the number of stillborns and/or non-developing eggs. The sex ratio, i.e. the representation of males, decreases with the increasing body length of the mother (geeglm: intercept = 4.4287, SE = 0.9259, coefficient = −0.0025, SE = 0.0005, $P < 0.0001$, see Fig. 2). The number of stillborns and/or non-developing eggs also predicts male bias of the litter (geeglm: coefficient = 0.4152, SE = 0.1547, $P = 0.0073$).

Principal component analysis revealed that the morphometric traits and scale counts measured in neonates were mutually closely correlated. PC1 explaining 47.3 % of total variation may be interpreted as a multivariate body size, while PC2 explaining 18.2 % reflects ratio between the counts of subcaudal scales and the newborn body weight (Fig. 3). Next, we performed LMMs accounting for the identities of the litter and the mother. The effect of the sex was not detected in any of the examined traits (Table 1). We also found no effect of the offspring's sex (ANOVA: $F = 1.49$, df = 1, $P = 0.2233$), the mother's SVL (ANOVA: $F = 0.66$, df = 1, $P = 0.4300$) and the interaction between these two variables (ANOVA: $F = 0.93$, df = 1,

$P = 0.3352$) on the newborn's SVL. Main part of the total variation in newborn's SVL was nested between litters (64.2 %) and in within-litter residuals (35.8 %), while the effect of mother identity was negligible (<1 %).

Discussion

Several authors reported no significant deviation from balanced sex ratios in snake hatchlings or neonates, e.g. in *Austrelaps superbus*, *Pseudechis porphyriacus* (Shine and Bull 1977), *Nerodia sipedon* (Weatherhead et al. 1995), *Trimeresurus stejnegeri stejnegeri* (Wang et al. 2003), *Tropidonophis mairii* (Brown and Shine 2004), *Thamnophis sauritus* (Weatherhead et al. 2006), *Thamnophis sirtalis* (Weatherhead et al. 2006; Krause and Burghardt 2007), *Pantherophis obsoletus* (Blouin-Demers and Weatherhead 2007), *Hydrophis cyanocinctus* (Karthikeyan et al. 2008), *Vipera ursinii* (Baron et al. 2010a) and *Thamnophis gigas* (Halstead et al. 2011). This conforms to the view that secondary sex ratio in snakes is typically balanced due to its predestination by genotypic sex determination mechanism.

In contrast to this, some studies performed in fragmented populations of adders repeatedly reported female-biased secondary sex ratios and explained this bias by a strong local mate competition among brothers (Madsen and Shine 1992a, cf. Capula et al. 1992; Luiselli 1993). Female-biased sex ratios were also reported in newborns of *Regina grahami* (Seigel 1992) and *Charina bottae umbratica* (Hoyer and Stewart 2000). In the latter species, the authors interpret this bias as a mechanism compensating selective mortality of adult females at population level (Hoyer and Stewart 2000).

Fig. 2 Relationship between the litter sex ratio and the mother's body length in Cuban boas (*Chilabothrus angulifer*)
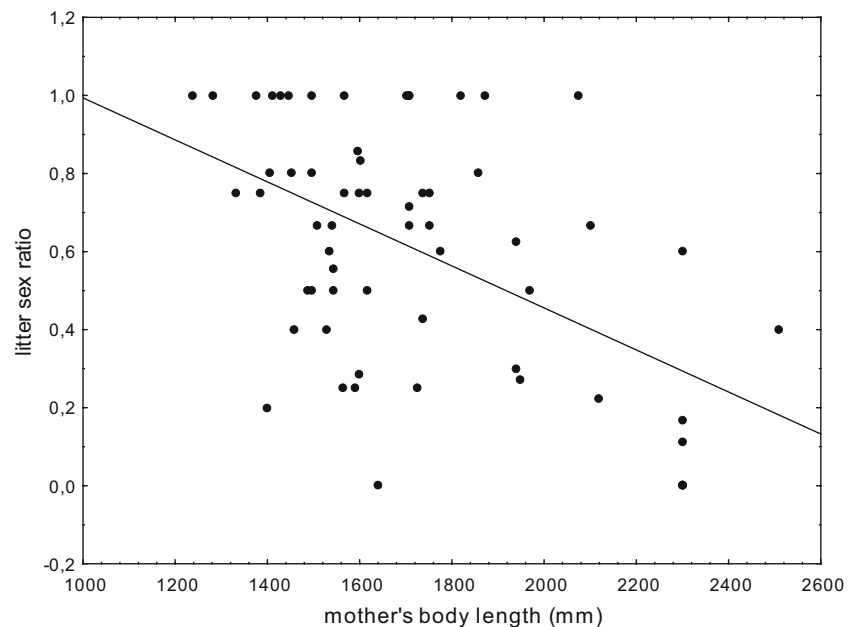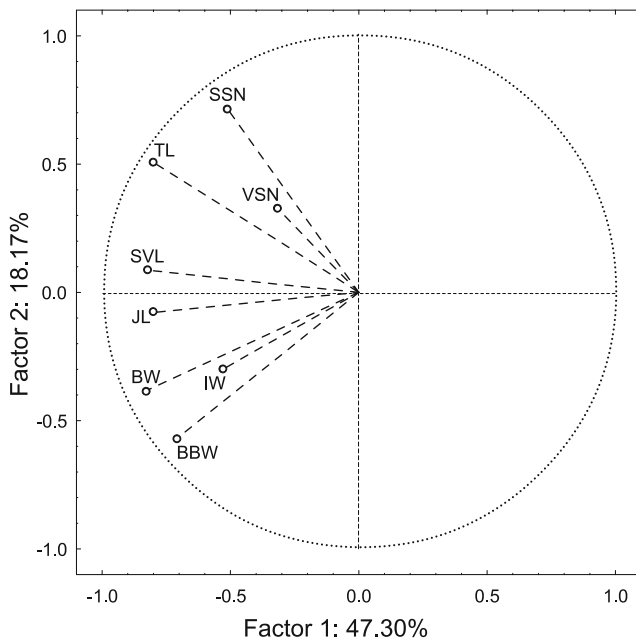
Fig. 3 Loadings of the first two factors as revealed by principal component analysis (PCA) of morphometric traits measured in the Cuban boas' neonates (*Chilabothrus angulifer*). Abbreviations: *SVL* snout-vent length, *SSN* number of subcaudal scales, *VSN* number of ventral scales, *TL* tail length, *JL* jaw length, *IW* interorbital width, *BW* body weight after first shed, *BBW* birth body weight

Male-biased sex ratio was reported in *Notechis scutatus* (Shine and Bull 1977) and in those litters of *Coronella austriaca* which are either extremely large or containing stillborns (Luiselli et al. 1996). We also detected slight but significant male-biased sex ratio in the neonates of Cuban boa. As in the case of *Coronella austriaca*, this sex bias may be

Table 1 Means, SE and results of analysis of deviance (*F* and *P* values) revealed by linear mixed models testing the effect of sex on particular traits of newborns of Cuban boa (*Chilabothrus angulifer*) and accounting for litter identity

Examined traits	Sex	Mean	Std. Dev	F	P value
SVL	Female	565.44	37.01	1.12	0.2908
	Male	554.87	43.03		
Tail length	Female	68.57	7.22	0.21	0.6511
	Male	64.18	8.67		
Birth body weight	Female	157.63	24.80	0.40	0.5295
	Male	154.04	22.67		
Shed body weight	Female	149.47	22.77	0.04	0.8336
	Male	148.12	24.16		
Ventral scales	Female	283.41	5.44	1.16	0.2834
	Male	283.05	5.07		
Subcaudal scales	Female	49.28	4.82	0.81	0.3695
	Male	47.58	5.31		
Interorbital width	Female	11.59	0.57	0.19	0.6643
	Male	11.56	0.48		
Jaw length	Female	29.04	1.35	0.04	0.8475
	Male	28.87	1.43		

attributed to selective mortality of the embryos or foetuses, which was reported also in some oviparous elapids (*Aspidelaps*: Reichling and Gutzke 1996, *Naja atra*: Ji et al. 2009). Although we have no direct evidence for this interpretation, it is remarkable that 10 of 13 all-male litters included stillborns or non-developing eggs.

Besides the male bias in the overall sex ratio, we demonstrated that sex ratio of the litter is influenced by the mother's body size; large mothers of Cuban boas tend to produce daughters, while smaller ones tend to produce sons. Dependence of the secondary sex ratios on the mother's age (which is usually closely correlated with body size in snakes) were previously reported in *Vipera ursinii* (Baron et al. 2010a). In this case, however, the proportion of males increased with the mother's age and the authors explained this relationship by maternal manipulation helping to avoid incestuous mating with sons. Other studies failed to prove any relationship between the mother's body size and/or age and sex ratio of the litter (e.g. Madsen and Shine 1992a, Wang et al. 2003; Halstead et al. 2011).

Sex differences in body size at birth, moreover to the litter sex ratio, contribute to the sex allocation of the maternal investment. Female newborns are heavier or longer than males are in several snake species (e.g. *Regina grahamii*: Seigel 1992; *Acrochordus arafurae*: Houston and Shine 1994; *Thamnophis sirtalis*: King et al. 1999; Krause and Burghardt 2007; *Acanthophis praelongus*: Webb et al. 2006; *Hydrophis cyanocinctus*: Karthikeyan et al. 2008). Male neonates typically possess longer tails and/or higher numbers of the subcaudal scales than females do (e.g. *Pantherophis obsoletus*: Blouin-Demers and Weatherhead 2007; *V. ursinii*: Tomović et al. 2010; *Natrix tessellata*: Werner and Shapira 2011). These differences in the body shape may be easily attributed to the presence of the male copulatory organs (hemipenises; for the evolutionary hypotheses, see King 1989) and have almost no effect on sexual size dimorphism and thus sex allocation of the maternal investment.

In the Cuban boas, we demonstrated the absence of sex difference in both the body size and shape. This result simplifying the picture of the maternal sex allocation in the Cuban boas conforms to the results reported in some other species belonging to diverse clades of snakes (e.g. *Vipera berus*: Madsen and Shine 1992b; *Coronella austriaca*: Luiselli et al. 1996; *Liasis fuscus*: Madsen and Shine 1996; *Crotalus atrox*: Taylor and DeNardo 2005; *Vipera ursinii ursinii*: Baron et al. 2010b; *Sistrurus*, *Nerodia* and *Thamnophis*: Pilgrim et al. 2011).

In the Australian water pythons (*Liasis fuscus*), juveniles initially living under high prey abundance succeeded to maintain their large body size to adulthood. Thus, the increment of the initial body size represents "a silver spoon" improving life-long fitness of the snake (Madsen and Shine 2000). Nevertheless, there are reptilian species exhibiting highly

efficient compensatory growth capable to fully eliminate differences in their initial growth and body size (e.g. *Bitis gabonica*: Bonnet et al. 2001; *Amphibolurus muricatus*: Radder et al. 2007). According to our previous unpublished results in captive Cuban boas, the body size of fully grown adults is uncorrelated or only weakly positively correlated with their neonate body size. Moreover, there was no relationship between neonate body size and mortality rate in the period from the birth to achievement of the sexual maturity. Thus, at least under laboratory conditions, an increased maternal investment in a given offspring has little effect on life-history parameters that may be viewed as predictors of life-long reproductive success. Taken together with the sexual monomorphism of the newborns, the variation in neonate sex ratios cannot be attributed to the mechanism proposed by Trivers and Willard (1973) due to violation of its assumption.

Following the logic of local mate competition hypothesis which has been successfully applied to vipers (Madsen and Shine 1992a; cf.. Capula et al. 1992; Luiselli 1993), excess of daughters in the litters produced by large-bodied mothers in Cuban boas may be viewed as prevention of the mate competition between sons of previous and current litters. Nevertheless, this hypothesis requires low dispersal of males.

More appropriate to the case of the Cuban boas is the local resource competition hypothesis (Clark 1978) suggesting that females avoid competition with their own progeny by a selective production of the dispersing sex. This hypothesis may be combined with other models of sex ratio evolution (cf.. Wild and West 2007). In snakes, males are usually the dispersing sex (e.g. Rivera et al. 2006; Keogh et al. 2007; Dubey et al. 2008). In order to search for receptive females, they exhibit higher mobility and spatial activity (Pernetta et al. 2011; Hofmann et al. 2012; but see Lane and Shine 2011). This was also reported in another species of Great Antillean boas (*Chilabothrus inornatus* and *Chilabothrus subflavus*: Puente-Rolón and Bird-Picó 2004; Miersma 2010) which are closely related to *Chilabothrus angulifer*. Compared to males, snake females are more philopatric (Madsen and Shine 1999; Rivera et al. 2006; Brown and Shine 2007) and have higher annual consumption rates (Bonnet et al. 2000; Madsen and Shine 2002; Jones et al. 2009). Moreover, species composition and size of the prey depends considerably on the body size of the snake (Shine et al. 1998). Therefore, it is reasonable to expect that it is advantageous for smaller females to avoid competition with their daughters and to selectively bias the sex ratio of their progeny in favour of males. As life spans of the Cuban boas may reach three decades and sexual maturation is achieved at the age of 3–5 years (Rehák 1996), there is enough time for parent-offspring competition for local resources. In addition, fully grown female Cuban boa is approximately two times heavier than the conspecific male and the food composition substantially differs between the sexes in snakes

exhibiting sexual size dimorphism (Dirksen 2002; Pearson et al. 2002).

The explanation of the observed sex ratio variation in Cuban boa by the local resource competition requires a considerable food competition in the environment in which putative maternal manipulation of the sex ratio has evolved. Unfortunately, population densities of large Antillean reptiles were dramatically reduced during the last centuries (e.g. Tolson and Henderson 1993, Ricklefs and Bermingham 2008, Hastings et al. 2014). Moreover, food habits of the Cuban boas have undergone a strong shift when local endemic mammals were replaced by introduced rats and domestic animals (Sheplan and Schwartz 1974; Mancina et al. 2007; Borroto-Páez 2009). Thus, we can only speculate about the degree of competition for prey in the past. Nevertheless, boas were top predators (besides crocodiles) of the Great Antillean region in the pre-Columbian era (for absence of native carnivores see Taboada et al. 2007; Colten et al. 2009). It suggests that we can reasonably expect the ability of boa populations to reach the carrying capacity and to be limited by the abundance of prey species.

In contrast to mammals and birds, reptiles exhibit a great variation in modes of sex determination and this may affect sex ratios considerably. Currently, Rovatsos et al. (2015) confirmed that families of advanced snakes (caenophidians) possess ZW sex chromosomes and demonstrated that the mechanism of GSD has remained conserved for more than 60 ma. Nevertheless, they also showed that the remaining snake families including boids do not share these sex-determining mechanisms with advanced snakes. In these families, the genes corresponding to those localized on the sex chromosomes of advanced snakes are autosomal. This finding, together with the absence of homology of ZW sex-determining mechanisms in snakes and varanid lizards, may violate our presumption that Cuban boas exhibit ZW mode of GSD. ZW chromosomes were previously reported in another boid species (*Acrantophis dumerili*: Mengden and Stock 1980); however, data concerning sex-determination mechanisms in basal snakes are so scarce to allow exclusion of the other sex determination modes, i.e. XY mode of GSD and even TSD which represents an ancestral state in multiple reptilian lineages (Pokorná and Kratochvíl 2009).

Besides the sex-determination mechanisms, adoption of unorthodox reproductive strategies may distort sex ratios, e.g. parthenogenetic mothers produce exclusively either sons (varanids: Watts et al. 2006) or daughters (Darevsky 1958, cf. Jančúchová-Lásková et al. 2015). In recent decades, parthenogenetic reproduction was reported in multiple snake lineages (Booth et al. 2014 and references herein). Among boid snakes (Boidae), parthenogenesis was currently recorded in *Boa constrictor* (Booth et al. 2011a) as well as in two species of the genus *Epicrates* (*Epicrates maurus*: Booth et al. 2011b, *Epicrates cenchria*: Kinney et al. 2013) which is closely

related to the genus *Chilabothrus*. In both these genera, the parthenogenesis was initially detected in all-female litters. Booth et al. (2011a, b) supposed that these boids like colubroid snakes exhibit genotypic sex determination with ZW chromosomes in females. Accordingly, they deduced that daughters of the parthenogenetic females possess abnormal combination of sex chromosomes (WW). We never recorded parturition in a female not allowed to copulate in a given mating season. Nevertheless, we examined whether the observed overdispersion of sex ratios among examined litters found in our material can be explained by the presence of all-female litters. In spite of small litter sizes produced by Cuban boas, we recorded only 3 all-female litters (consisting of 8, 5 and 6 neonates) among 58 ones (singletons excluded). We recorded 13 all-male litters in this data set. We can conclude that the number of all-female litters was not elevated. In spite of this, without detailed genetic examination of each juvenile and further understanding of this reproductive strategy in boid snakes, the occurrence of the other forms of parthenogenesis than production of WW females cannot be entirely excluded as a proximate mechanism responsible for split sex ratios in the studied species.

In conclusion, in the examined population of captive Cuban boas, the overall sex ratios are slightly male-biased and sexual size dimorphism is entirely absent in the neonates. Nevertheless, the proportion of daughters increases with a body length of the mother. This may be attributed to specific variant of local resource competition hypothesis (Clark 1978) suggesting that the small-bodied females avoid producing daughters which, unlike smaller and putatively dispersing sons, would stay in the vicinity of their natal range until adulthood and become food competitors of their long-living mothers.

Compliance with ethical standards

Conflict of interests The authors declare that they have no conflict of interests

Ethical standards This article does not contain any studies with human participants performed by any of the authors. All applicable international, national and/or institutional guidelines for the care and use of animals were followed (see above).

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