
DIFFERENCES IN SIZE AND BEHAVIOUR DUE TO SEX-DIFFERENCES IN SNAKES.

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INTRODUCTION

With many animals males are larger than females. Difference in size - apart from sex governed differences - is often a result of intra sexual competition (rivalry within sexes). That is to say, competition takes place between females mutually, or between males mutually. Most familiar in this connection are the fights between males over females. Usually the strongest (and this often is the largest) male will win such a fight and mate with the female. In this way the strongest male will pass on his congenital qualities, which increases the likelihood of large males in the offspring.

You would expect this would result in ever larger males within the species, but this of course is not the case: there are many other factors that influence growth. Within many snakes the phenomenon of ritual fights is known between males ("male combat"). These fights are termed "ritual" because they are not really true fights in that sense but a type of symbolic battle following fixed patterns, which settles who is the strongest and who can mate with the females.

Shine has tested the supposition that these ritual battles within snakes in fact lead to larger males.

To be able to test this hypothesis, Shine conducted a literature search to find species where one sex is consistently bigger and determined if ritual fights occurred in such species. For many species however, there is no knowledge as to whether ritual fights occur.

RESULTS

Of the 224 species that were examined in 148 (66%) the female proved to be bigger than the male. Ritual fights are only known in 33 of the examined species. Differences in size between sexes and ritual fights do exist within all families.

Of the 33 species that are known to engage in ritual fights more species have larger males than would be expected on the grounds of coincidence.

This supports the hypothesis that ritual fights do eventually lead to the phenomenon of larger males.

DISCUSSION

The above mentioned research results make one suspect that with snakes the differences in size between sexes are the result of the same principle known in warmblooded animals, that is to say intra sexual competition (rivalry between males mutually and females mutually).

Although the correlation between having ritual fights and the appearance of larger males is strong this in no way is one hundred percent.

The exceptions can be described in two groups:

- a. Species that have fighting males and larger females (3% of the 224 species)
 - b. Species that have no battling males but where the males are bigger than the females (18% of the researched species).
- Both groups are described separately below.

FIGHTING SMALL MALES

This phenomenon appears for instance with the adder, *Vipera berus berus*. Shine concludes that ritual fights alone are not enough to get larger males. He explains this as follows; within certain species ritual fights can lead to larger males but at the same time other factors dictate that females grow even larger. The males do get bigger but don't catch up with the females. An example of such a restraining factor is the following. Within the adder in males for instance two colour variations are known; the normal colour with a silver-grey background and completely black individuals. The black males can take up heat more quickly and effectively and so apparently grow faster than the ones with a "wild colour". The black males do grow bigger. Adder females mate every other year in most areas. There are as many males as females, but more sexually active males than females! Males often fight amongst one another to get the opportunity to mate. It appears that black males (who are heavier) usually win the fights and due to that mate with the females. In this way the number of black males should increase all the time. But there is a restraining factor however, black males do attract more attention and due to that more often fall prey to preda-

tory birds than "wild colour" males. What they gain by more often winning a ritual fight is again lost by a much bigger chance of falling prey to natural enemies.

LARGE MALES THAT DO NOT FIGHT

On average this seems to appear often (18% of all cases). However, the facts are unreliable. It is almost certain that ritual fights do occur in more species than is known up to now.

Of the forty species from group B, 26 are coming from genera from which ritual fights are known among other species of this genus. All these 26 species do probably show ritual fights. The fourteen remaining species are all from Asia and little is known of them. It could be quite possible that larger males develop only due to ritual fights.

CONCLUSION

Shine's studies show us that the appearance of larger males most probably is caused by intra sexual competition. Apart from that it is striking that in most species females are larger than males.

Two interesting suggestions are given by Shine who could explain this phenomenon. The first suggestion is that natural selection is in favour of larger females because they produce more (or as much as but bigger) offspring.

The second suggestion is that natural selection favours smaller males because they are more mobile and in this way can reach females more often and quicker.

Both hypotheses are complementary to one another and in principle can be put to the test. Because the evolution of body-size is hardly understood it is meaningful to re-search Shine's hypotheses. Research best could take place with species from the genera *Crotalus*, *Elaphe*, *Naja* and *Vipera*.

APPENDIX: LIST

Remarks:

1. In the list below the following code is used; a 1 is used when males grow bigger than females; when females grow bigger a 2 is used; and a 3 when no difference in size occurs.
2. A small star behind the figure means that in this species ritual fights do occur.
3. A small star following the name means that this mention does not come from Shine's list but has been added by Hans van de Rijst or Ton Steehouder.
4. Of course the list is not complete.

Boidae

<i>Boa constrictor</i>	2
<i>Charina bottae</i>	2
<i>Chondropython viridis*</i>	2*
<i>Eryx conicus</i>	2
<i>Eryx colubrinus</i>	2
<i>Eryx johni</i>	2
<i>Lichanura t. roseofusca</i>	2

Colubridae

<i>Achalinus spinalus</i>	2
<i>Amphiesma stolata</i>	2
<i>Aspidura brachyorros</i>	2
<i>Aspidura trachyprocta</i>	2

<i>Boaedon fuliginonus</i>	2
<i>Boaedon lineatus</i>	2
<i>Boiga blandingii</i>	3
<i>Calamaria septentrionalis</i>	2
<i>Calamelaps unicolor</i>	2
<i>Carphophis amoenus</i>	2
<i>Carphophis vermis</i>	2
<i>Cerberus rhynchops</i>	2
<i>Coluber constrictor</i>	2
<i>Coluber spinalis</i>	2
<i>Coronella austriaca</i>	3*
<i>Crotaphopeltis hotamboeia</i>	2
<i>Dasypeltis medici</i>	2
<i>Dasypeltis scabra</i>	2
<i>Dendrophis pictus</i>	2
<i>Diadophis punctatus</i>	2
<i>Dinodon flavozonatum</i>	1
<i>Dipsadomorphus ceylonensis</i>	1
<i>Dipsadomorphus trigonatus</i>	1
<i>Dryophis mycterizans</i>	2
<i>Duberria lutrix</i>	2
<i>Elaphe dione</i>	2
<i>Elaphe longissima*</i>	*
<i>Elaphe obsoleta</i>	1*
<i>Elaphe quadrivirgata</i>	1*
<i>Elaphe rufodorsata</i>	2
<i>Elaphe scalaris*</i>	*
<i>Enhydris bocourti</i>	2
<i>Enhydris jagorii</i>	2
<i>Eurypholis major</i>	1
<i>Farancia erythrogramma</i>	2
<i>Fordonia leucobalia</i>	2
<i>Haplocercus ceylonensis</i>	2
<i>Helicops schistosus</i>	2
<i>Heterodon nasicus</i>	2
<i>Heterodon platyrhinos</i>	2
<i>Holarchus formosanus</i>	1
<i>Holarchus violaceus</i>	1
<i>Homalopsis buccata</i>	2
<i>Lampropeltis triangulum</i>	1*
<i>Lamprophis inornatus</i>	2
<i>Lycodon aulicus</i>	2

<i>Lycodonomorphus rufulus</i>	2
<i>Macropisthodon plumbicolor</i>	2
<i>Macropisthodon rudis</i>	2
<i>Malpolon monspessulanus*</i>	1*
<i>Masticophis taeniatus</i>	1*
<i>Mehelya capense</i>	2
<i>Mehelya poensis</i>	2
<i>Meizodon semiornatus</i>	2
<i>Natrix maura</i>	2
<i>Natrix</i>	2
<i>Nerodia</i> (9 spp)	2
<i>Oligodon ornatus</i>	1
<i>Opheodrys aestivus</i>	2
<i>Opisthotropis balteata</i>	2
<i>Opisthotropis latouchii</i>	2
<i>Oxybelis aeneus</i>	2
<i>Pareas carinatus</i>	1
<i>Passerita prasina</i>	2
<i>Philothamnus irregularis</i>	2
<i>Pituophis melanoleucus</i>	3*
<i>Psammodynastes pulverentulus</i>	2
<i>Psammophis condanarus</i>	2
<i>Psammophis subtaeniatus*</i>	1
<i>Pseudoxenon fukiensis</i>	2
<i>Pseudoxenon macrops</i>	1
<i>Pseudoxenon striaticaudatus</i>	1
<i>Prosymna ambigua</i>	2
<i>Pseudaspis cana</i>	2/3*
<i>Ptyas korros</i>	1
<i>Ptyas mucosus</i>	1
<i>Regina grahami</i>	2
<i>Regina septemvittata</i>	2
<i>Rhabdophis tigrinus</i>	2
<i>Rhadinea flavilata</i>	2
<i>Rhamphiophis oxyrhynchus</i>	3
<i>Scaphiophis albopunctatus</i>	2
<i>Seminatrix pygaea</i>	2
<i>Sibynophis chinensis</i>	2
<i>Sibynophis collaris</i>	2
<i>Sinonatrix</i> (India, 19 spp)	2
China, 8 spp)	2
Maleisië, 4 spp)	2

Sonora episcopa	3*
Spalerosophis cliffordi	2
Storeria dekayi	2
Storeria occipitomaculata	2
Thamnophis (7 spp)	2
Trirhinopholis styani	2
Virginia striatula	2
<i>Crotalidae</i>	
Agkistrodon contortrix	1*
Agkistrodon halys	2/3
Agkistrodon hypnale	3
Agkistrodon piscivorus	1*
Crotalus adamanteus	1*
Crotalus atrox	1*
Crotalus cerastes	2*
Crotalus durissus	1*
Crotalus horridus	1*
Crotalus lepidus	1*
Crotalus mitchelli	1*
Crotalus ruber	1*
Crotalus scutulatus	1*
Crotalus viridis	1*
Crotalus (20 spp)	1
(Klauber)	
Sistrurus miliarius	1*
Trimeresurus (12 spp)	2
<i>Elapidae</i>	
Austrelaps superbus	1
Bungarus candidus	1*
Bungarus fasciatus	1
Dendroaspis jamesoni	2*
Dendroaspis polylepis	2
Hemiaspis daemellii	3
Hemiaspis signata	3
Maticora intestinalis	1
Naja haje	1*
Naja	2*
Naja tripudians	1*
Notechis scutatus	3*
Pseudechis porphyriacus	1*

<i>Pseudonaja nuchalis</i>	3
<i>Pseudonaja textilis</i>	3*
<i>Unechis gouldii</i>	1
<i>Hydrophiidae</i>	
<i>Enhydris chinensis</i>	2
<i>Enhydris plumbea</i>	2
<i>Lapemis curtus</i>	3
<i>Pelamis platurus</i>	2
<i>Laticaudidae</i>	
<i>Laticaudus colubrina</i>	2
<i>Typhlopidae</i>	
<i>Typhlina nigrescens</i>	2
<i>Viperidae</i>	
<i>Atractaspis irregularis</i>	2
<i>Amblyodipsas unicolor</i>	2
<i>Atheris nitschei</i>	2
<i>Atheris squamiger</i>	2
<i>Bitis arietans</i>	2*
<i>Bitis gabonica</i>	2
<i>Bitis nasicornis</i>	2
<i>Echis carinatus</i>	2
<i>Echis coloratus</i>	1
<i>Pseudocerastes fieldi</i>	3
<i>Vipera ammodytes</i>	1*
<i>Vipera aspis</i>	2*
<i>Vipera berus</i>	2*
<i>Vipera latastei</i>	3
<i>Vipera lebetina</i>	1
<i>Vipera ursinii</i>	2
<i>Vipera xanthina</i>	1