

Hyoid Bone Size and Its Implications for Social Organization and Sexual Selection in *Alouatta pigra* and the Elusive *Alouatta macconnelli*

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The purpose of this research paper is focusing on the hyoid bone in *Alouatta pigra* and *Alouatta macconnelli* and determine its role in affecting the social organization and sexual selection of the individuals in these species. This includes the discussion on the dimensions of the hyoid between the males and females as well as an analysis of observed social behaviour patterns and the sexual selection process. It was found that female *Alouatta pigra* had a larger hyoid than males of the species and that *Alouatta macconnelli* males had a hyoid nearly twice the size of females. The hyoids were measured from the Mammal Biodiversity collection at the Royal Ontario Museum. The bones dimensions were taken using plastic calipers and their circumference measured using a soft tape measure. Based on the sexual selection and social organisation of *Alouatta pigra* which is multi-male/multi-female with the occasional unimale with multiple females, the null hypothesis must be accepted as the larger hyoid is not found in males but in females and the size of the hyoid does not affect the social organization in this species. In *Alouatta macconnelli*, there is little information on this species but the null hypothesis is rejected as males have much larger hyoids than females and the social organization is that of a uni-male with multiple females.

Keywords: hyoid bone; howler monkey; sexual selection; *alouatta pigra*; *alouatta macconnelli*; social organization

Known for their deafening calls, *Alouatta* spp. is a world famous genus that include platyrrhine monkeys capable of producing a howl that can be heard 500 to 1000 metres away (Van Belle et al., 2013). Their calls, howls, barks and roars are due to a highly specialized bone in the laryngeal areas called the hyoid (Bergman et al., 2016 p.756; Dunn 2018, p.32). Howler monkeys species have large bloated cup-like hyoid bones that increases their calls vibrancy. The hyoid bone in *Alouatta* spp. ranges from very large to small across the species and among the sexes. This specialized adaptation is unique to the *Alouatta* genus as other genre do not have this feature. This paper will be looking at two species of howler monkeys, *Alouatta pigra* and *Alouatta macconnelli* and their hyoid bones and how their hyoid bone size relates to their social organization and sexual selection.



Figure 1. *Alouatta macconnelli* hyoid bone from the male specimen 31715, from the Royal Ontario Museum Mammal Biodiversity collection.

The hyoid bone is normally small in most species, with *Alouatta* spp. being the exceptions. The bone is connected lateral ventricular to the air sacs in our throats that allows us to make noise. The cup-like feature on a howler hyoid is called a bulla and is absent in anatomically modern humans. All great apes other than *Pongo* and *Homo sapiens* have a bulla, though it is greatly reduced in size (Dunn 2018, p.30). The bulla in howlers is a thin-walled cup shaped features on the anterior part of the hyoid. The hyoid is connected through muscles and ligaments to the mandible, tongue, laryngeal cartilage, pharynx and cranial base. The air sac will actually go into the bulla making a balloon shape (Youlatos et al., 2015). The extreme enlargement forms a resonating chamber for the air sac producing booming calls. The bulla takes up almost all of the hyoid in howlers and is also a sexual dimorphic trait as there is differences in size and shape among different species and sexes (Dunn 2018, p.23). Among the 9 species of howlers, *A. macconnelli* is the least researched yet it has the largest and most bulbous hyoid shape in male individuals. On the other hand, *Alouatta palliata* has the smallest hyoid in male (Dunn 2018).

Variation in the howls is strong enough for individual males to be identified through their sounds alone. The hyoid bone is responsible for shifts in the frequency and pitch of the noises the monkeys are making (Bergman et al., 2016, p.759). It was found that *Alouatta pigra* average roar has a frequency of $3,319 \pm 17$ Hz (Bergman et al., 2016 p.761). *A. pigra* was also found that a male will have an average roaring bout of 14.8 ± 0.6 minutes long, one of the longest sessions among the howler genus (Bergman et al., p.760; Van Belle et al., 2013, p.1209). There are many reasons why a howler may roar, it's been observed that at the crack of dawn *A. pigra* will be up howling to let everyone else know that this is his territory (Van Belle et al., 2013, p.1210; Carpenter 1934, p.55). One of the only things known about *Alouatta macconnelli* behaviour is that males are very territorial and will park themselves at the edge of their range and call out to proclaim their control of the area (Van Belle et al., 2013, p.1211). Howlers are known to use

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their calls as a way of intra-group communications for infant protection, mate guarding and resource defending (Van Belle et al., 2013, p.1211). Males tend to go on howling bouts alone or sometimes a group of multiple males will howl together (Van Bella et al., 2008, p.1491). In groups with multiple males, the dominate male, who spends the most time around the females, has more howling bouts than the beta or below males. When two neighboring groups of howlers are each at the edge of their territory, they will take turns howling at each other in long sessions (Carpenter 1934, p.82). *Alouatta macconnelli* are known to furiously defend their territories border and howl at anyone who approaches (Van Belle et al., 2013, p.1211). Females can also howl but not as loud and for as long as the males due to a smaller hyoid bone. Darwin even theorized the difference in the howling between males and females is due to a sexual selective adaptation, which is the hyoid size (Bergman et al., 2016, p.756).

Howler monkeys are known to live in a variety of different group settings. The majority of the troops are multi-male/multi-female groups (Lecompte et al., 2017, p.2; Van Belle et al., 2006, p.131). Some groups are physically separated through physical barriers which mark the boundaries of their territories (Van Belle et al., 2013, p.1210). In a large study of *Alouatta pigra* in Mexico that included 801 individuals, found that most groups are made of 2 to 12 individuals with a mean of 6.57 ± 1.20 members. In the most common group arrangement for *A. pigra* there were 2.07 ± 0.41 adult males, 2.26 ± 0.33 adult females, 1.28 ± 0.48 juveniles and 0.96 ± 0.44 infants in a group. In these multi-male/multi-female groups, there can be 1 to 5 males but all mixed-sex groups had a minimum of 2 females, making them polygynous species. (Van Belle et al., 2006, p.126 & 134). *A. pigra* is also known to have groups of lone males of up to 5 individuals (Van Belle & Estrada 2006, p.130). As mentioned before, *A. macconnelli* is extremely understudied and very little is known about them. There is some evidence of *A. macconnelli* being a species with predominantly unimale groups, yet it is unclear how many females there would be in the charge of the single male (Dunn et al., 2015, p.2841).

The highly advertised study on howler monkeys that came out in recent years, shows the connection of the hyoid bone size to the size of the males testicals. It was found that *Alouatta* males living in a single male group with many females will have smaller testes and a large hyoid. This is because the single male needs to attract many females into his polygynous social group and will be the only male mating with the females. He will not need large testes to outcompete other males. On the reverse, males living in a multi-male/multi-female group will have smaller hyoid bones and larger testicals. This is because the males do not need to attract the females in their group but need to be able to outcompete post-copulation with other males. Large testes produce more sperm and larger ejaculations making their sperm more likely to fertilize the female's ovum (Dunn et al., 2015, p.2839). This study did include a comparison of the hyoid bone size and the testes for *A. pigra* but not for *A. macconnelli*. The study shows that *A. pigra* has an average of 1.7 to 2.4 males per group, a hyoid volume of 60cm^3 and testes size of 11 to 13cm^3 . *A. pigra* fits with the model of multi-males/multi-females with the need of smaller hyoids and larger testes. By comparison, *A. palliata* which is the sister clade species to *A. pigra* has 2.7 to 3.4 males in a group, a hyoid volume of 10cm^3 and testes 20 to 25cm^3 . *A.*

palliata is on the extreme end of the spectrum with many males trying to out do the others through post-copulatory competition (Kelaita et al., 2011, p.179). This study does not include the testes size for *A. macconnelli* but it does show a group having 1 male and a hyoid volume of 110cm^3 (Dunn et al., 2015, p.2841). When following the trend of this theory, *A. macconnelli* will have very small testes as it has the largest hyoid, a complete opposite to *A. palliata*.

Females in *Alouatta pigra* groups chose to mate predominantly with the central or dominant male in the group, even if they lived in a multi-male/multi-female group. In groups with many males, the male who spends the most time around the females was more likely to be the dominant male of the group. He maintains much closer proximity to the females even if they were not in a period of estrous. While many females created a monopoly by only mating with the dominant male in the group, others tried to create paternity confusion by mating with a non-dominant male of the same group or with the dominant male of a neighboring group. Females were the majority instigators of sexual interactions as she would present her genitals to the males, establish eye contact and flick her tongue (Van Belle et al., 2009, p.154). The male may occasionally show sexual initiation by grooming the female and sniffing her genitals (Van Belle et al., 2009, p.156). Overall, female *Alouatta pigra* will choose to mate with the central male an overwhelming majority of the time and only mate with others to create paternity confusion (Van Belle et al., 2009, p.160). There is no record of any sexual behaviour study being conducted on *A. macconnelli* so any information regarding their sexual behaviour is purely speculative based on the evidence from other species of *Alouatta* and the data collected from the osteological analysis of the hyoid bones from the ROM collection.

A goal of this paper is to use the results from an osteological study at the Royal Ontario Museum to shed some light on the phantom *Alouatta macconnelli* based on the size of the hyoid bone. However this is not the focus of the paper as no behavioural study has been conducted on *A. macconnelli* and therefore I can not prove or disprove any of my hypotheses for it. I can only make interpretations from the data but it still would need to be further tested. The thesis of the paper is the look at the hyoids size in its social organization in its relationship to sexual selection in *Alouatta pigra* and *Alouatta macconnelli*. My first hypothesis is that males will have larger hyoid bones than females due to larger body size and this would allow them to produce louder calls. My second hypothesis is that in species with males having a larger hyoid bone, these species are uni-male/multi-female social groupings as females will choose males with large hyoid bones and louder calls.

Methods

This study of the hyoid bone in platyrrhines was conducted at the Royal Ontario Museum (ROM), under the supervision of Dr. Burton Lim. The platyrrhine skeletons in the Mammal Biodiversity Collection were combed through in hopes of finding a hyoid bone among the remains. Unfortunately, almost all the remains were either purley cranial with just the cranium and mandible or were a full skeleton with the hyoid missing. The only non-howler monkey hyoids found were that of *Pithecia pithecia*, *Cebus apella*, *Ateles paniscus* and a fragment from *Cebus olivaceus*, with only one hyoid per

species listed. *Ateles* is the only other genus used in this study as an outgroup comparison in hyoid bone dimensions. As the hyoid in many species is small, as well as fragile, the bone rarely preserved and is underrepresented in collections.

The Mammal Biodiversity Collection at the ROM was accessed on February 28th, 2019. I was given access by Dr. Burton Lim. As said above, only a few hyoid bones were found. These included one from *Ateles paniscus*, one from *Alouatta belzebul*, 8 from *Alouatta macconnelli* and 6 from *Alouatta pigra*. There are 16 hyoids included in this study with a focus on the ones from *A. macconnelli* and *A. pigra*. Plastic calipers were used to take measurements of the hyoid, including the horns, bulla, the opening mouth of the bulla and the circumference of the body was taken at its widest point using a soft tape measure. The measurements were taken from areas that cover the majority of the shape for the hyoid bone (lateral) and its superior connection the laryngeal area (superior). The key areas include the total body height, body height without the bump after the mouth opening, the lateral width of the bone (taken from a lateral view), the mouth dimensions, the width and length from a superior view and the horn length are all included in Table 1. A reference picture of where the measurement were taken can be found in Figure 2.

The range, mean, median, mode and standard deviation were calculated for the male and female individuals of *A. macconnelli* and *A. pigra*. *Ateles* and *A. belzebul* statistics were not calculated as there is only one hyoid bone of each species found at the ROM. Their measurements are included in Table 1 to be a outgroup comparison size. The median and mode were calculated but are not shown in the result section as there is such a small data set they are almost exactly the same as the mean.

Table 1. Key measurements taken of the hyoid bone in millimeters taken from the right lateral side and a superior view.

Species	Specimen	Sex	Body Circumference (mm)	Horn Height (mm)		Lateral View (mm)			Superior View (mm)			
				Left	Right	Total Body Height	Body Height	Body Width	Mouth Width	Mouth Length	Body Width	Body Length
<i>Ateles paniscus</i>	106634	Female		13	14	7	6	5			15	5
<i>Alouatta belzebul</i>	91212b	?	80	30		31	11	21	18	13	20	21
<i>Alouatta pigra</i>	33487	Male	66			19	14	12	11	11	15	11
	33500	Male	60		10	17	8	11	9	11	13	12
	33495	Female	76	14	15	23	17	11	15	19	16	19
	33497	Female	76			22	10	15	13	20	19	21
	33498	Female	75	17	16	21	10	15	13	21	19	25
	33499	Female	77		15	21	17	11	15	25	17	24
<i>Alouatta macconnelli</i>	31715	Male	162	25	31	53	34	46	22	19	31	42
	31930	Male	176	26	31	65	41	49	10	15	30	49
	32322	Male	183	38	43	70	51	50	23	11	54	49
	32328	Male	166	26	26	54	31	40	23	13	43	41
	32444	Male	187			65	46	52	25	14	49	53
	31672	Female	98	21	21	33	24	23	14	10	21	14
	31742	Female	86			33	20	19	14	8	18	21
331788	Female	99	20	25	34	21	23	14	13	23	23	

Included in Table 1 are some of the key measurements that were taken *Ateles paniscus*, *Alouatta belzebul*, *Alouatta pigra* and *Alouatta macconnelli* hyoid bones from the Royal Ontario Museum Mammal Biodiversity collection. A reference of where the measurements were taken on the hyoid bone can be found in Figure 2. Figure 3-5 are graphs depicting the ranges for *A. macconnelli* and *A. pigra* in total body height, body width and circumference measurements.

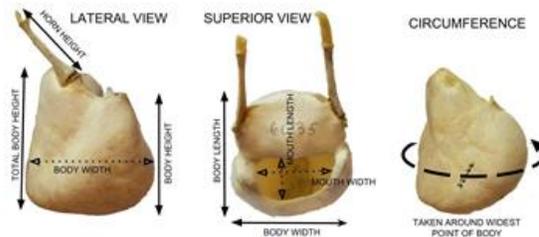


Figure 2. Diagram of where measurements were taken on the hyoid bone. Image of *Alouatta macconnelli* hyoid bone from specimens 31715.

Alouatta macconnelli males have a range of total height from 53 to 70mm and mean of 61 ± 7.31 mm (n=5). Females range is 33 to 34mm and mean of 33.33 ± 0.57 mm (n=3). Males have a body width range of 40 to 52mm and mean of 47.4 ± 4.67 mm (n=5). Females have range of 19 to 23mm and mean of 21.67 ± 2.31 mm (n=3). Males have a body circumference range of 162 to 187mm and mean of 174.8 ± 10.71 mm (n=5) and females range of 86 to 99 mm and a mean of 94.33 ± 7.23 mm (n=3).

Alouatta Pigra males have a range in total body height of 17 to 19mm and mean of 18 ± 1.41 mm (n=2). Females range is 21 to 23mm and mean of 21.75 ± 0.96 mm (n=5). Males have a range of body width of 11 to 12 and means of 11.5 ± 0.71 mm (n=2). Females range is 11 to 15 mm with a mean of 13 ± 2.31 mm (n=4). Males have a body circumference range of 63 to 65mm (n=2) and females' range is 75.75 ± 0.96 mm (n=4).

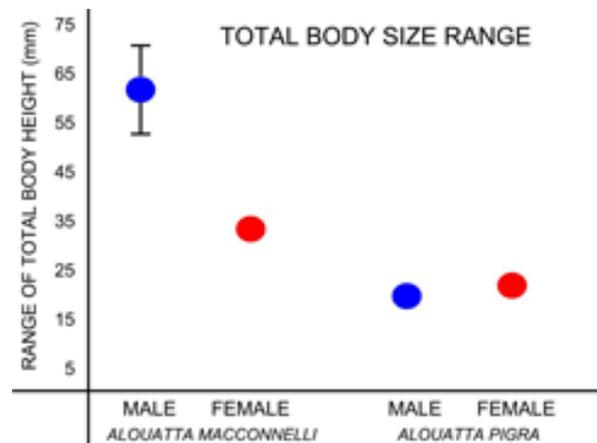


Figure 3. Total body height range for male and female *A. pigra* and *A. macconnelli* hyoid bones.

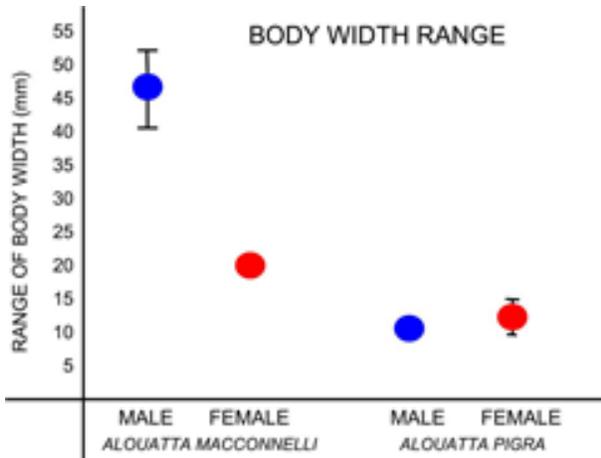


Figure 4. Body width range for male and female *A. pigra* and *A. macconnelli* hyoid bones

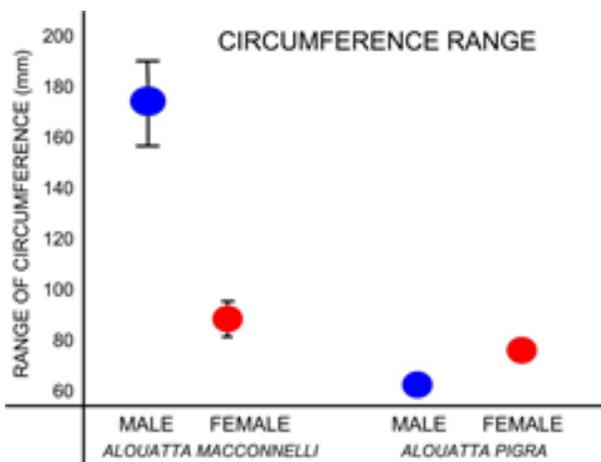


Figure 5. Circumference range for male and female *A. pigra* and *A. macconnelli* hyoid bones.

Discussion

A baffling realization is that while *Alouatta macconnelli* has the largest hyoid bone of any of the *Alouatta* ssp., it is perhaps the least studied (Dunn 2018). Extremely limited literature can be found on this species leading to many questions that can only be answered with in-field studies. The osteological measurements of the hyoid bone proved that my first hypothesis is correct, as males do have larger heads than females. Male *A. macconnelli* have almost double the circumference of the females. Males with a mean circumference of $174.8 \pm 10.71\text{mm}$ (n=5) and females with $94.33 \pm 7.23\text{mm}$ (n=3). There are strong sexual selective pressures working in this species. There is no information on the body size of *A. macconnelli*, yet it is known that in *Alouatta*, the larger the body the larger the lungs and therefore the louder the call (Bergman et al., 2016, p.762). Based on this, I theorize that due to the very large hyoid bone in males compared to the female, male *A. macconnelli* are much larger than females and there is sexual dimorphism in body size. The larger hyoid will allow for a deeper, louder and more powerful roar (Bergman et al., 2016, p.762). In accordance to the hyoid-testes theory, the

larger the hyoid the louder the call and smaller testes due to less competition between males. The male with a large hyoid and powerful call attracts the females and is more likely to be in a uni-male polygynous social group (Van Belle et al., 2008; Dunn 2018, p.32; Dunn et al., 2015). This fits with the small evidence about the social organization of male *A. macconnelli* living in groups consisting of one male and undetermined number of females (Dunn et al., 2016, p.2841).

I am able to accept my second hypothesis as *A. macconnelli* would be able to produce a dominating call that would attract females lead to living in a single male-multi female group. However, there are some problems with the rejection of my second null hypothesis. The first being there is no other information of the behaviour and social organization of *A. macconnelli* beyond Dunn et al., 2015. *A. macconnelli* is an extremely understudied species, yet they have the largest hyoid bone of all *Alouatta* (Dunn 2018). There is no information on the number of females in a social grouping. This means there is a possibility that *A. macconnelli* could be monogamous with only one male and one female per group. Overall, there is a lack of information to fully confirm my hypothesis, I can only make inferences based on the osteological data collected, the limited information available for this species and connections to other *Alouatta* species.

My examination and measurement of the *Alouatta pigra* hyoid collection at the ROM revealed unexpected results. As seen in Table 1 and Figures 3-5, female *A. pigra* have a larger hyoid bone than the males of this species. The female circumference range is $75.75 \pm 0.96\text{mm}$ (n=4) while the males is $63 \pm 4.24\text{mm}$ (n=2). This is the opposite of my first hypothesis saying that males had larger hyoids than female. Therefore I must reject my first hypothesis and accept by null hypothesis for this species. The collection at the ROM has limited my reference data to only 6 individuals of *A. pigra*, which is an extremely small data set. As my data set is so limited, I can not fully show that all female *A. pigra* have a larger hyoid than the males, I can only show that this is the case for my data. As seen in Dunn’s pictogram (Figure 6), the male hyoid is very large but there is no female hyoid for *A. pigra*. The female *A. macconnelli* hyoid shown in the figure is smaller than that of the male *A. pigra* (Dunn 2018). According to my data, the female *A. macconnelli* is larger than male *A. pigra* hyoids. This calls into question the scale of these hyoid depictions and that the male hyoids in my data set may be from the smaller end of the spectrum for male hyoid size and that a much larger data set may reveal that male *A. pigra* hyoids are bigger than both female *A. pigra* and *A. macconnelli* hyoids. Another piece of evidence that my data set for male *A. pigra* hyoid size is of the lower end outliers is how body size affects the hyoid dimensions. *A. pigra* males have a body weight range of 11,113 to 11,590g and females have a range of 6,577 to 6290g (Ford & David 1992, p.16; Kelaita et al., 2011, p.182). Males are substantially heavier and therefore have a larger body size than females. As large bodied individuals would have a larger hyoid (Bergman et al., 2016, p.762), this shows that the males in the ROM collection may be subadult or on the smaller side of the weight range.

I must also reject my second hypothesis and accept the null hypothesis for *A. pigra*. As in this hypothesis I state that males have a larger hyoid bone than females and this leads to one-male polygynous social groups. This is not the case for *A. pigra* as my data shows females having larger hyoids and *A.*

pigra social groups are majority multi-male/multi-female (Lecompte et al., 2017, p. 2; Van Belle et al., 2013, p.1212; Van Belle & Estrada 2006, p.126). The average of adult males in a *A. pigra* group is 2.07 ± 0.41 and 2.26 ± 0.33 adult females in the group, which is not what I hypothesized (Van Belle & Estrada 2006, p.126). Based on my data and the reversal of my first hypothesis (i.e. females have larger hyoids) it would make more sense if *A. pigra* was a monogamous species with very little sexual dimorphism or they are polyandry with one female and multiple males in a group. Upon first examination of the *A. pigra* hyoid bone, I had theorized that this was a polyandry species.

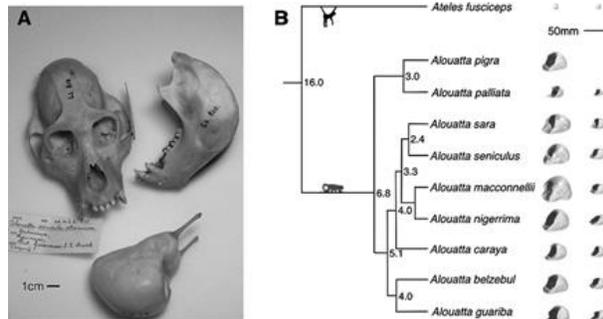


Figure 6. Picture of male *Alouatta macconnelli* hyoid, cranium and mandible along with a taxonomic cladistic of the *Alouatta* genus from the paper *Sexual Selection and the Loss of Laryngeal Air Sacs During the Evolution of Speech* by Jacob Dunn.

Conclusion

My hypothesis for *A. pigra* and *A. macconnelli* was that males would have a larger hyoid bone than females, and that due to the larger hyoid size, are able to attract more females through their calls and be living in a single-male/multi-female polygynous social group. However the data from my ROM osteological study and the lack of behaviour studies has led to my rejection of some of my hypotheses. *A. pigra* has a smaller hyoid bone than the females of this species. This means I must reject my first hypothesis. As well, *A. pigra* lives in a social group of multi-males/multi-females and the males must post-copulatory compete rather than attract females in being apart of a polygynous social group (Lecompte et al., 2017, p.2; Dunn et al., 2015). Therefore I must accept both null hypotheses in the case of *A. pigra*. For *A. macconnelli*, there is extremely limited evidence for behaviour of this species which makes my acceptance of my second hypothesis challenging. I accept my first hypothesis for this species as a male *A. macconnelli* nearly has twice the size of a female hyoid bone. I am accepting my second hypothesis but am cautious as there is little evidence supporting the social organization of this species as a polygynous unimale social group and there is no evidence on how many females there are in each group (Dunn et al., 2015, p.2841). The study of *A. macconnelli* should be continued as there is much to learn about the sexual dimorphism, sexual selection and social organization of the species. As well, larger datasets are needed to further the analysis of *A. pigra* in its hyoid size and sexual dimorphism.

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