

## Agonistic behaviour in captive Babirusa (*Babyrousa babyrussa*)

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### Abstract

The agonistic behaviour of captive babirusa (*Babyrousa babyrussa celebensis*) was studied at zoos in Indonesia, Belgium, and the Channel Islands. Observations were carried out on ninety-five babirusa of which 25 males and 21 females were kept in Surabaya Zoo, Indonesia. Male-male, male-female and female-female interactions were analysed with respect to body size, shape of upper canines, age and sex. The agonistic behaviour was described and could be categorised. "Threat at a distance", "surprise rush", and "the lying lunge" were used frequently by both males and females. The submissive babirusa generally lowered its head and vocalised its submission by means of a repeated, breath-long, rumbling squawk. The canine teeth were never seen to be used as weapons. "Boxing" was the ultimate form of agonistic behaviour exhibited between male babirusa. Body size was the most important factor determining the outcome of a "boxing" match. "Boxing" between females was never observed. Female agonistic behaviour was mainly aimed at biting the forelimb of the opponent. Adult females were submissive to adult males, but adult females were dominant over sub-adult males. Large females were dominant over smaller females.

### Introduction

The babirusa is endemic to the Indonesian islands of Sulawesi, Buru and the smaller Sula and Togian islands. Very few observations have been made of babirusa in the wild. One study of the behaviour of five animals was performed on the Togian island of Pangempan (SELMIER 1983) and recently video recordings of wild babirusa were made on the northern mainland of Sulawesi (PATRY and CAPIOD 1989; PATRY 1990). Several other behavioural studies have been made on captive animals. These either describe the social behaviour of very small numbers of captive animals, are preliminary accounts of observations on larger groups or are detailed accounts of reproductive behaviour (GEOFFROY-ST-HILLAIRE and CUVIER 1842; SELMIER 1978, 1983; BOWLES 1986; MACDONALD et al. 1989; LEUS et al. 1992).

The few studies of the babirusa in the wild and in captivity suggest that they are social animals, one or more adult females living together with young and juveniles, the adult males solitary or singly associated with family groups. They appear to employ a range of behaviours, to obtain or maintain dominance and position. This study reports on a variety of agonistic behaviour found between individual babirusa.

### Material and methods

Observations were made largely at Surabaya Zoo, Indonesia with additional observations recorded on the Channel Islands at the Jersey Wildlife Preservation Trust, at the Royal Zoological Society of Antwerp, Belgium, and in Ragunan Zoo, Jakarta, Indonesia. In July and August 1987 and 1988 between 0500 h (one hour before sunrise) and 2200 h (four hours after sunset) observations were carried out on 25 male and 21 female babirusa in six adjacent and inter-connecting pens in Surabaya Zoo. The main enclosure housed up to 35 animals, and details of the layout and sizes of the pens were published earlier (MACDONALD et al. 1989). Vocalisations were recorded on tape and subsequently analysed and described in relation to the behaviour with which they were associated.



The results of 220 of the agonistic encounters observed in 1988 at Surabaya Zoo were grouped in the following way. A sample of 142 observations of the outcome of fighting behaviour (boxing) between male babirusa was analysed. Precise ages were unknown, but the males were classified into four subgroups, according to the following criteria:

- juvenile: (small sized body, upper canines are just appearing)
- sub-adult: (body smaller than the adult male, canines narrow and upper canines tightly curved)
- adult: (large body size, canines thick, the upper canines curved back towards the head or are broken and more straight, dewlap present)
- old adult: (large body size, skin is scarred, creased and folded, upper canines usually broken and more vertical).

A further sample of 32 observations listed the results of agonistic male-female behaviour which were analysed according to sex and 'age' subgroups. A third sample of 50 observations examined the outcome of confrontations between female babirusa which were classified into three subgroups; juveniles, small adults and large adults.

In 1991, Surabaya Zoo moved its remaining 13 males and 16 females to a single new pen 35 m × 15 m in area. The animals were observed in December 1991 and January 1992 between 0500 h and 1500 h. Particular attention was paid to the agonistic behaviour in its different component parts shown by the dominant male of the group. In addition, the agonistic behaviour shown by the females towards one another and to the males was examined. Additional observations, which were gathered from a further forty-nine babirusa are included in this report; these were collected during studies of behaviour at the Jersey Wildlife Preservation Trust from 1983–1987, at Ragunan Zoo, Indonesia during the months of July and August 1987 and at the Royal Zoological Society of Antwerp, Belgium from July 1989–91.

## Results

The agonistic behaviour could be allocated to seven different categories by using the terms "threat at a distance", "surprise rush", "nose in the air", "head under jaw submission", "front half supported", "boxing", and "the lying lunge".

### Male-male interactions

#### *"Threat at a distance"*

The dominant male needed only look, or make an upward thrust or toss of the head in order to threaten another male. The threatened animal moved cautiously in relation to the dominant male though not necessarily far from him and seemed to keep a close eye on his movements. When a threat was perceived the submissive animal lowered his head and uttered a breath-long rumbling squawk, which may be repeated.

#### *"Surprise rush"*

Males often made sudden, and apparently unprovoked charges at other males. This startled the attacked male into facing the onrushing animal, lowering his head and uttering the rumbling squawk sound of submission. Usually these attacks were not carried through to physical contact; the attacking male charged forward with his head held high for a short distance only. However, in those few instances when the charge was carried through, the mandibular canine of the attacker struck the upper and/or lower canines or the shoulder of the submissive animal. If the attacked male was not intimidated the attacker became the attacked. The dominant male ended a standing confrontation by walking away.

#### *"Nose in the air"*

Two or more animals approached each other with their heads raised and their noses held in the air. They manoeuvred with their heads held high and at 60 to 240 degrees to one another (Fig. 1). The animals backed off slowly and then suddenly rushed several steps forward, again with heads raised and noses elevated. This complex of circling and feinting manoeuvres could either develop further, or the animals wandered away from each other.



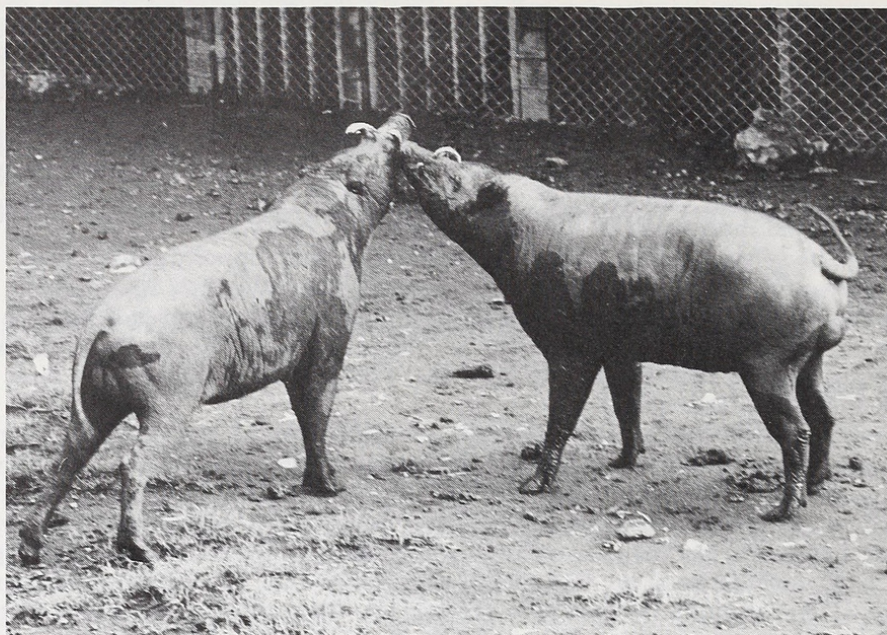


Fig. 1. Two adult male babirusa demonstrating the "nose in the air" agonistic behaviour

*"Head under jaw submission"*

When two males were in close proximity the submissive animal took up a position at an angle, often at about 90 degrees, to the head of the dominant animal, lowered its head such that its nose was positioned under the mandible of the superior male and uttered a very short squawk or a continuous rattling stream of sound, the pitch and intensity of which increased as the animal seemed to perceive increased threat. The dominant male made a sucking "tuh" sound apparently by lowering its mandible and then pulling its tongue off the upper palate. Both males circled one another with the subordinate animal usually in the middle. Even after being nipped in the nose or mouth, the subordinate male did not give up but remained where he was, often complaining noisily. In some instances the dominant male turned rapidly to face another male in close proximity and the behaviour was repeated. Usually the dominant male seemed to be the one to break off the confrontation by ignoring his opponent and wandering off.

*"Front half supported"*

Two males approached one another such that their heads were held side by side and pointing in the same direction. Their bodies were often held at 60 degrees to one another. The animals manoeuvred side by side until one male mouthed the tusks of the other and layed his head on the snout of the other. If this manoeuvre was successful, the male whose head was highest leant his head on the head of the other male (Fig. 2). The two animals could be at an angle or facing one another. Often the upper male seemed to be actively pushed upwards by the lower animal until his forefeet were off the ground. Sometimes he actively climbed until his chest was on the head of the inferior animal (Fig. 3). The upper male paddled with his front legs against the back and shoulders of the lower animal. The position of the canine teeth of the lower animal was such that they rubbed on the exposed neck and chin of the upper animal (Fig. 2), but without causing damage. This position was maintained for a variable length of time, the lower animal sometimes uttering the submissive squawk. It was the superior male which ended the behaviour by dismounting and walking away from the other male.

On one occasion, when two relatively young (2–3 years) males were squabbling in a narrow corridor, the hind legs of the upper male slipped and he lost the grip of his forefeet





Fig. 2. Two adult male babirusa engaging in an early stage of the "front half supported" behaviour. Note that the maxillary canines of the lower male are in contact with the neck of the superior animal

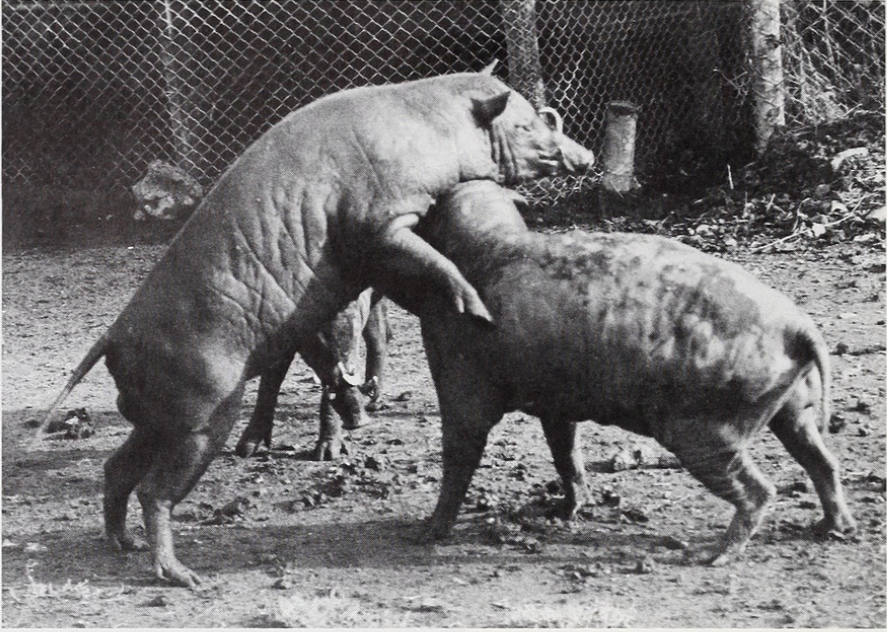
on the back and shoulders of the lower male. The two animals had manoeuvred into a 90 degree angle with each other and as the superior animal lost his balance the inferior animal tossed his head. The left lower canine of the lower male struck the neck of the falling male and penetrated about 3 cm. The upper male became locked on the tusk of the lower male and started a loud, continuous, high pitched scream. The lower male persisted in making upward movements with his head. He made no attempt to end the confrontation. The animals were eventually separated by the keepers. The animal with the pierced neck behaved in a very submissive fashion for weeks thereafter.

#### *"Boxing"*

Only about 5 % of interactions resulted in boxing behaviour. Boxing usually started from the "nose in the air" behaviour with both animals facing each other and each trying to place his head on top of that of the other animal. Each raised himself off the ground until both were standing on their hind legs facing one another. Once in this position they leant and paddled against the chest and shoulders of their opponent (Fig. 4). Their snouts were held as high as possible. The animals seemed able to remain on their hind legs for about one minute at a time. If one of the animals fell onto all four legs it reared up again and the boxing continued. The boxing match usually lasted for 2 to 5 minutes, but could extend for up to 20 minutes. The pushing and shoving could lead to large distances being covered within the pen. During the boxing the animals often fought with their mouths open but there was little or no vocalisation.

The superior animal often appeared to be the one that raised his head the highest; he also had his ears pointed forward. The dominant male usually broke off the confrontation by ignoring his opponent and wandering off. The submissive animal may or may not lower his head below that of the dominant animal when they both came back onto all fours but rarely did he vocalise his submission with the short squawk or continuous rattling stream

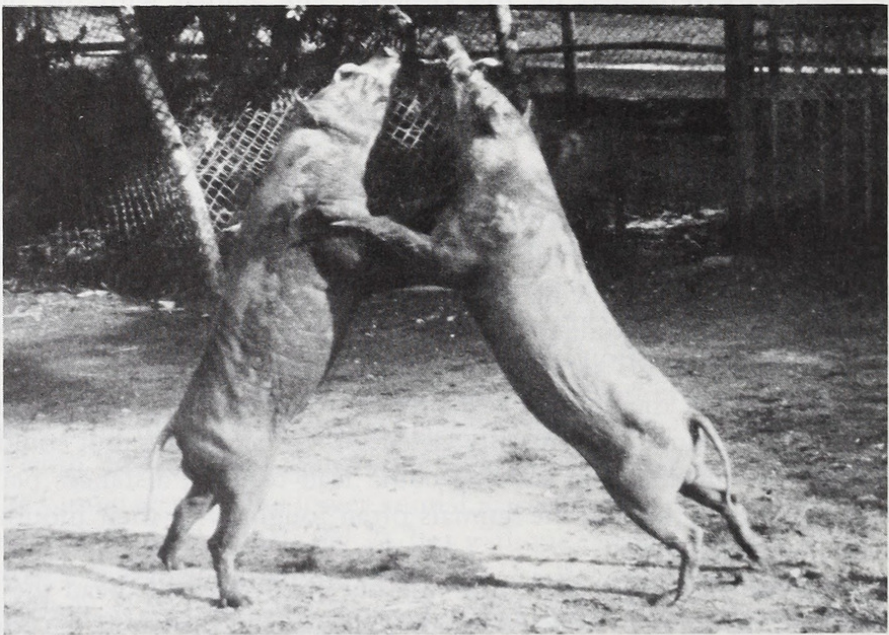




*Fig. 3.* The final stage of "front half supported" behaviour as exhibited by two male babirusa. The neck and chest of the upper male rest on the face and teeth of the lower male

of sound described above. Occasionally a third male intervened by raising his head between the competing animals and causing the boxing match to stop. In some instances, the intruder himself began boxing with one of the two combatants. It also happened that the intruding male would join forces with one of the two combatants and the third animal would then back off in the face of the two advancing males.

The deciding factor seemed to be the ability to stretch the highest and push your opponent off balance and onto all four legs. The tusks seemed to play little or no part in the contest (Fig. 4). The contests could become violent in which case the males made greater use of their strength and threw their weight at one another. In those instances the upper male uttered a rolling, deep-throated, low pitched growl and would often froth at the



*Fig. 4.* "Boxing" behaviour being demonstrated by two adult male babirusa. Both animals have reared onto their hind legs, faced one another, and are leaning and paddling with their forefeet against the chest and shoulders of their opponent. Note that their noses are being stretched as high as possible



mouth. These battles attracted the attention of other males which often interfered in the fight and broke it up.

An analysis of 72 boxing encounters between males of different size showed that the larger male was dominant on 71 occasions. In 28 further encounters where the males were evenly matched for size, straight tusked animals were dominant 16 times and those with curved tusks were dominant 12 times. When age of the animal was examined during another 38 encounters, sub-adult or adult males were dominant over elderly males on 30 occasions. No clear outcome was apparent in the remaining eight interactions, and in four other boxing matches no distinguishing feature was apparent between the animals.

Boxing was most common among the young adult males. Old males were never seen boxing and often seemed to ignore conflict except for vocalisation and biting at animals when food was available. In the winter of 1991/92 the alpha male, which was not the largest male in the group, was rarely seen boxing. However, he patrolled the pen almost constantly and showed the other types of intimidatory behaviour on many occasions. Infants of only a few days of age were seen pushing each other and attempting to get on top of each other. Siblings of either sex and aged from about two months until weaning were seen to rear up on their hind legs and playfully paddle against one another's chests with their forelegs. More serious boxing between males was observed when the juveniles were about one year of age, when the tusks were emerging. Boxing could take place at any time of the day but usually did so more often when it was cooler, in the early morning and late in the afternoon.

#### *"The lying lunge"*

When lying in the pen a male was sometimes seen to swing his head up and round towards an approaching animal which appeared to be about to lie down beside him. A loud shriek of short duration ( $< 1$  sec) was usually uttered by the submissive pig. The threat was sometimes followed by a nip at the nose, flank or leg of the threatened animal.

#### **Male-female interactions**

Intimidatory behaviour of the three types, "threat at a distance", "surprise rush" and "the lying lunge" were found between males and females in which either sex may be dominant. The "head under jaw submission" with squealing vocalisation was seen in association with both reproductive behaviour and perceived threat. The female tended to bite at the front legs during an attack and would do so also in defence. When the female nipped defensively at the feet of the male he uttered a low "gruff-gruff" sound. Only twice was an adult female seen to come to an adult male with her nose raised in the same way as was described between two adult males; when this happened they manoeuvred to face each other, and began boxing. Neither animal vocalised.

On one occasion the same female repeatedly climbed onto the front of the same male until her chest rested on his head. He terminated the interaction by moving away without a sound.

In 31 of 32 interactions between adult males and females, the male was dominant. When an adult female confronted either a sub-adult or juvenile male the adult female dominated in 11 out of 13 occasions. In five interactions between juvenile animals the males were dominant.

#### **Female-female interactions**

Examples of "distant threat", "surprise rush" and "the lying lunge" have been seen between females. Usually, when one female rushed at another, the attacked female ran off closely pursued for some distance by the attacking female. We often saw the dominant female chase the submissive female repeatedly over a period of about ten minutes.





Fig. 5. Typical agonistic behaviour between two adult females in which the female on the right is attempting to reach below the head and neck of the female on the left in order to bite the latter's front leg. The female on the left has anticipated this move and has lifted her right front foot away to prevent it from being bitten

Of the other four behaviours, "nose in the air" and "head under jaw submission" were seen rarely between adult females and "front half supported" and "boxing" behaviours were never seen. When two females confronted one another it was often quite violent, fast moving and noisy. Clear attempts were made to reach below the head and neck of one another; the objective seemed to be to bite the leg or foot of the opponent (Fig. 5). The female which had her head highest and allowed her fore or hind limb to be bitten lost the contest and uttered a high pitched squeal of short duration. The superior female often expressed a deep-throated growl during the contest. Fifty female-female interactions were observed and in 41 of these the larger animal was dominant. In only four occasions was the smaller female superior. On five occasions the interacting females were of the same size.

When single females were put in adjacent wire-sided enclosures two different reactions were observed. Some females appeared indifferent of one another whereas others would repeatedly show aggression towards each other. The latter would run back and forth along the separating fence with their heads elevated and ears pointed forward, making sharp upward thrusts of the head towards their opponent. They also often pushed side to side through the fence and growled at one another, nipping with their lower incisors in the direction of the legs and flanks of their opponent.

## Discussion

We have identified and described a series of agonistic behaviours of the babirusa. These results confirmed and extended the fragmentary observations reported for this species by SELMIER (1978, 1983), MACDONALD et al. (1989), and LEUS et al. (1992). The repertoire of behaviours exhibited by the babirusa fell within the broad classifications of threatening, display and fighting behaviour which are used for assessment between individuals of a wide variety of species (MAYNARD SMITH 1982). The babirusa seems to employ the behaviours "threat at a distance", "nose in the air" and "boxing" as the sequence of increasing level of threat.

The same classifications can be recognised in the range of agonistic behaviours described for a number of pig species including the wild boar (*Sus scrofa*), the bush pig (*Potamochoerus porcus*), the warthog (*Phacochoerus aethiopicus*) and the giant forest hog (*Hylochoerus meinertzhageni*) although it is clear from the published descriptions that the details of the behaviours exhibited vary between genera (FRÄDRICH 1965, 1967; BEUERLE 1975; CUMMING 1975; SKINNER et al. 1976; KINGDON 1989).



“Threat at a distance” as demonstrated by the babirusa with a slow or faint movement of the head upwards has also been reported for the wild boar, the warthog and the bushpig (FRÄDRICH 1965, 1967; CUMMING 1975; SEIDACK 1990). A more overt toss of the head into the air in the direction of the opponent is shown by all pigs (FRÄDRICH 1967).

Display is reported in the wild boar as the presentation of the body broadside to the opponent with the back arched, the front part of the body stretched out, the head elevated and the hair of the body erect (FRÄDRICH 1967; BEUERLE 1975). By way of contrast, bush pig opponents face one another, thereby presenting to one another their conspicuously marked head and erected dorsal main (SKINNER et al. 1976; SEYDACK 1990). The only behaviour exhibited by the babirusa which could be identified as the equivalent of display was stretching of the head and “nose in the air”. The animals will sometimes do this at a distance, but more usually close to their opponent and, like the warthog, may exhibit a range of positions from parallel head to head to frontal nose to nose (FRÄDRICH 1965; CUMMING 1975).

The subspecies of babirusa from Sulawesi, unlike the other two subspecies of babirusa, lacks the hair coat of the wild boar. The species also lacks the conspicuous facial colouration of the bush pig and the facial warts of the warthog. However, the male babirusa has prominent maxillary canines which grow upwards in such a way that they pierce through the skin of the snout and curve over in front of the forehead (Figs. 1–4 and 7). The lower canines grow upwards alongside the snout and curve more gradually caudally. Whether the canines are important to display is not known. Moreover, whether those babirusa subspecies with longer hair coats use these in display also remains a matter for speculation.

“Boxing” was the ultimate form of agonistic behaviour exhibited by the babirusa under observation in the zoos. This form of agonistic behaviour has not been reported for any other species of pig with the exception of *Sus scrofa cristatus*, on the island of Sri Lanka (BARRETTE 1986). One of the main differences between these two sets of observations

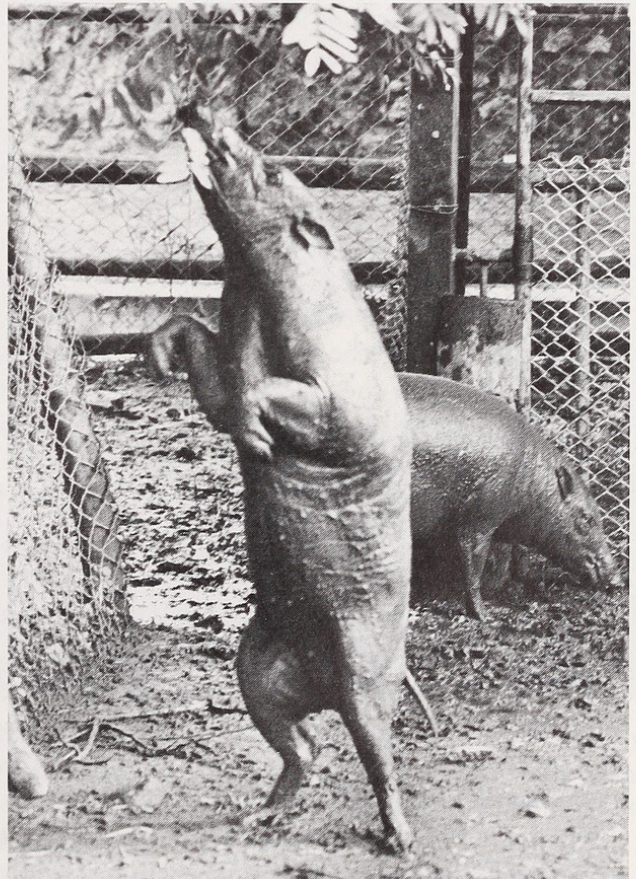


Fig. 6. An adult female balancing on her hind legs while browsing the leaves of a tree in the enclosure



concerns the female animal; adult female babirusa were never seen to box with one another whereas this did occur between female wild boar. Female babirusa did have the ability to balance on their hind limbs, and were seen browsing in this position (Fig. 6). They were also occasionally seen to box with male babirusa whereas adult male and female wild boar were never observed boxing with one another (BARRETTE 1986). Another difference was that the babirusa would repeatedly rear up on their legs if they slipped or were toppled momentarily, whereas the first occasion that the wild boar was knocked off balance decided the competition (BARRETTE 1986). The third main difference between the two species was the lack of retreat shown by the babirusa when defeated; the superior animal, which was usually the largest and the one which stretched the tallest on its hind limbs, walked away from the loser. This is in marked contrast to the pursuit of the loser shown by the wild boar (FRÄDRICH 1967; BEUERLE 1975; BARRETTE 1986).

It is possible that "boxing" may not represent the most extreme form of fighting behaviour in babirusa. BARRETTE (1986) suggested that the behaviour shown by the wild boar in Sri Lanka was a mechanism allowing delay or avoidance of the relatively high risks inherent in a tusk fight between wild boar, as has been described for this species by BEUERLE (1975). Male babirusa have large canine teeth (Fig. 7) which are either absent or rudimentary in the female (MOHR 1960). It has been suggested that the upper canines may be used by one animal to hook one of the lower canines of his opponent; in this way the sharp maxillary canine of the opponent would be disarmed while he was free to inflict injury with his own lower canine to the opponent's eye, the side of his face or throat (GEIST 1966; MACKINNON 1981).

Our study of the anatomy of the maxillary canine showed that conflict of this sort is unlikely. The maxillary canine has a relatively shallow socket, whereas that of the lower canine occupies a large proportion of the length of the mandible (Fig. 7). This implied that large leverage forces would be placed on the root of the upper canine by the well anchored lower canine of the opponent during this suggested hooking manoeuvre (MACKINNON 1981; WHITTEN et al. 1987) which the socket of the upper tooth would not be competent to withstand. Moreover, the upper canine has been described as loose in its socket (MOHR 1960) and not very strong, being liable to split or break (HEINSIUS and VOGT 1916; MOHR 1960; SCHAFTENAAR 1991). On no occasion did we observe the interlocking of tusks in any of the zoos.

The use that the adult male babirusa makes of his canine teeth during agonistic behaviour remains incompletely known. GRAAFLAND (1898) suggested that the animals deliberately break their upper canines in order to make them better weapons. On the contrary, the evidence of the present study would indicate that the curved maxillary canine teeth are not used as weapons but as a shield preventing the lower tusks from reaching or deeply penetrating the opponent's body in most instances. With every upward thrust of the head towards the body of the opponent, it will be the curved upper tusks that first make contact with the opponent's body. The sole occasion that we witnessed one animal impaled on the lower canine of another was the result more of an accident than a deliberate attack. Indeed both animals seemed confused by the situation. The babirusa in Surabaya sometimes showed superficial scratch wounds on their shoulders, back and sides but we never saw how these were inflicted.

Ritualised fighting behaviours among other wild pigs have been divided into two categories; 1) frontal fighting involves head to head pushing and is shown by bush pig, warthog and giant forest hog and 2) lateral fighting which involves shoulder to shoulder pushing (either nose towards tail or head to head) is shown by wild boar (FRÄDRICH 1965). The presence of elaborate tusks, and the wear pattern on the upper tusks of *B. b. babyrussa* have been interpreted as evidence that frontal fighting might be used by this subspecies (FRÄDRICH 1965; MACKINNON 1981). Alternative explanations, such as the movement of stones and branches with the snout remain conceivable and may be preferable explanations



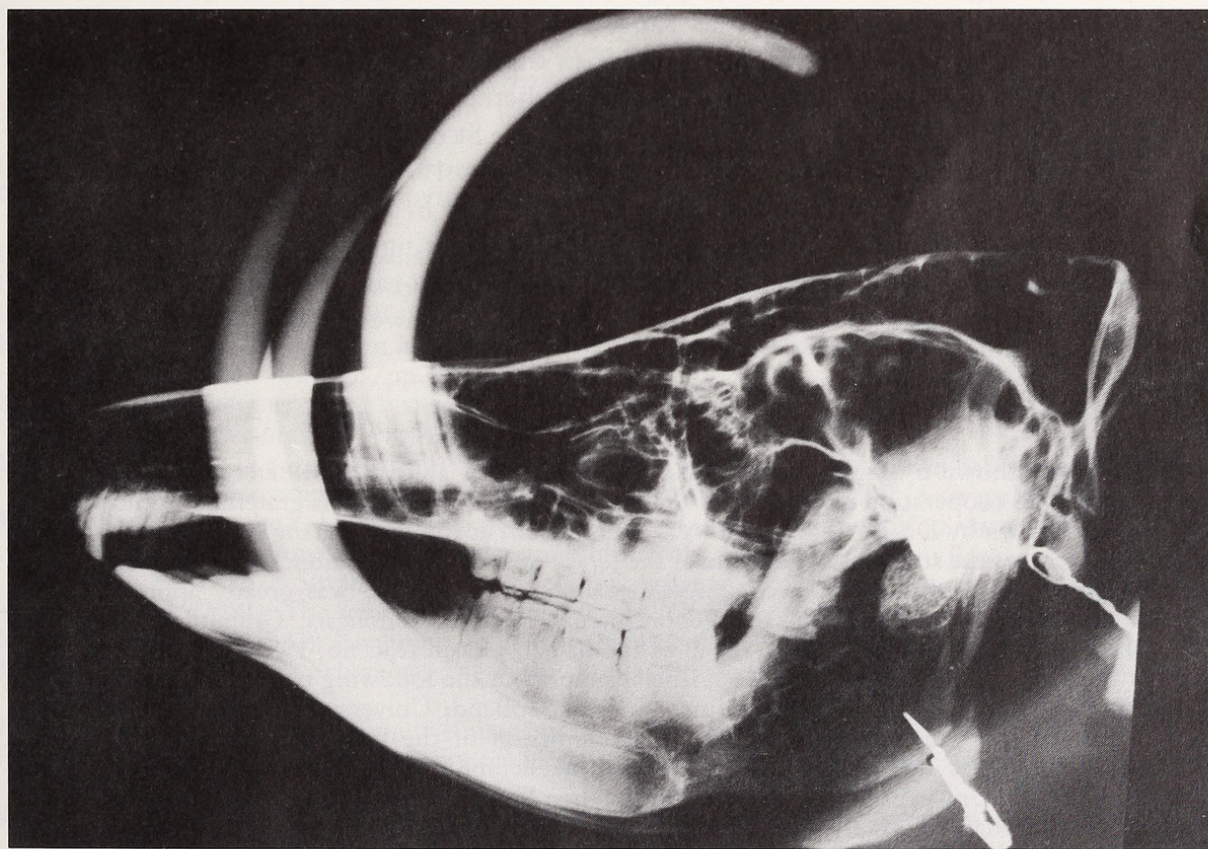
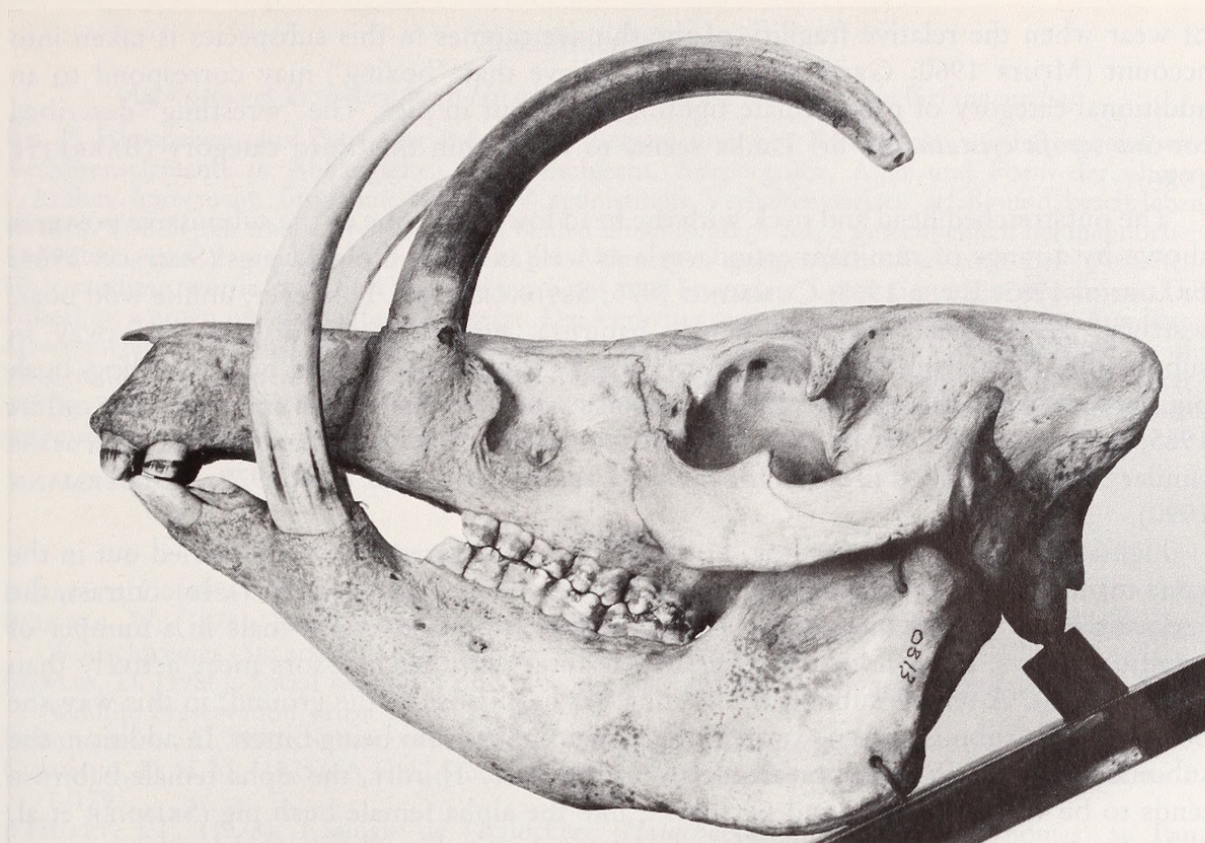


Fig. 7. The skull of an adult male babirusa (*Babyrousa babyrussa celebensis*) from Sulawesi (above) photographed and (below) X-rayed to demonstrate the shape, relative position and socket size of both the mandibular and maxillary canine teeth. Note that the socket of the maxillary canine tooth is significantly smaller than that of the mandibular canine



of wear when the relative fragility of the thinner canines in this subspecies is taken into account (MOHR 1960; GROVES 1980). We believe that "boxing" may correspond to an additional category of pre-ultimate fighting behaviour in pigs. The "wrestling" described for *Sus scrofa cristatus* on Sri Lanka seems to fall within this third category (BARRETTE 1986).

The outstretched head and neck with the head lowered is one of the submissive postures shown by a range of ruminant artiodactyla as well as by all the wild pigs (SIMPSON 1964; FRÄDRICH 1965; EWER 1968; CUMMING 1975; SEYDACK 1990). However, unlike wild boar, warthog, giant forest hog, and female babirusa, male babirusa do not run away in submission (FRÄDRICH 1965; CUMMING 1975; KINGDON 1989). Wild boar, warthog, bush pig, and babirusa all make a submissive noise when threatened or cornered (FRÄDRICH 1965; BEUERLE 1975; CUMMING 1975; SEYDACK 1990). The noise made by the babirusa is similar to that described in detail for the wild boar (KLINGHOLZ et al. 1979; BRIEDERMANN 1990).

Fights between female warthog, bush pig, and giant forest hog were carried out in the same manner as between male animals (FRÄDRICH 1965; CUMMING 1975). In contrast, the agonistic behaviour of the female babirusa differs from that of the male in a number of significant ways. Most noticeably, the female bites with her incisors more actively than does the male. A female submits by holding her head close to the ground; in this way she both indicates submission and protects her lower limbs from being bitten. In addition, the submissive scream is more prevalent than in the male. Thirdly, the alpha female babirusa tends to be very aggressive and persistent, like the alpha female bush pig (SKINNER et al. 1976; SEYDACK 1990); the inferior females seem to actively seek to avoid her attentions.

In the wild, agonistic behaviour of pigs is found in association with reproduction and with environmental resources such as food, water, nesting sites and hiding places. The amount, distribution and availability of these to the babirusa is presently unknown. It is therefore not yet possible, for example, to say whether this species exhibits a territorial claim on food, like the bush pig (SKINNER et al. 1976; SEYDACK 1990), or not as shown by the wild boar, warthog and giant forest hog (BEUERLE 1975; CUMMING 1975; D'HUART 1978). It is likewise not clear whether or not babirusa in the wild engage in agonistic encounters within the context of territorial claim for mating partners and/or any of the other environmental resources. Additional studies, of home range, social organisation and habitat exploitation in the wild are required in order to answer these questions.

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## Zusammenfassung

### *Agonistisches Verhalten beim Hirscheber (Babyrusa babyrussa) in Gefangenschaft*

An 95 Hirschebern aus Zoos von Indonesien, Belgien und den Kanalinseln wurden agonistische Verhaltenselemente in Abhängigkeit von Geschlecht, Körpergröße, Alter und Form der oberen Eckzähne untersucht. Insgesamt konnten 7 agonistische Verhaltensweisen erfaßt und beschrieben werden. Von diesen traten 3 regelmäßig in beiden Geschlechtern auf, 2 ausschließlich bei männlichen Individuen und 2 weitere hauptsächlich bei Männchen, gelegentlich aber auch bei Weibchen. Unterwerfung wurde stets durch gesenkten Kopf und besondere Lautäußerungen signalisiert. Die Eckzähne wurden nie als Waffen eingesetzt. Die Verhaltensweise "Boxen" ist typisch für Auseinandersetzungen zwischen männlichen Individuen, wohingegen weibliche Tiere stets versuchen, in die Vorderläufe der Gegnerin zu beißen. Adulte Weibchen waren gegenüber adulten Männchen unterwürfig, aber gegenüber sub-adulten Männchen dominant. Große Weibchen waren auch dominant gegenüber kleineren.

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