

Using Astragalus to Model Body Mass, Habitat Preference, and Population Density of Prehistoric Bovid *Duboisia santeng* (Dubois, 1891) in Eastern Java island in The Early Pleistocene

Andri Wibowo*

Keywords:

astragalus, body mass, Bovid, Pleistocene, population density

*U. o. Indonesia (UI),
West Java, 16424.
Indonesia.
Correspondence email:
paleobio2020@gmail.com
andri.wibowo
@sc.ui.ac.id

Abstract

Astragalus bone is one of the most important fossil records as it can reconstruct the prehistoric life. Respectively, this study aims to model the body mass, habitat preference, and population density of prehistoric bovid *Duboisia santeng* (Dubois 1891) in eastern Java island in the early Pleistocene. The astragali from 9 specimens were used to estimate the body mass and population density. Likewise regression models are used to analyze the relationship between astragalus lateral length, width, and body mass compared to the astragalus of extant Bovid species. The result revealed the body mass average was 60.3 kg (95%CI: 58.9-61.7) and this indicates the *D. santeng* belongs to large herbivores. While the population density was estimated at about 5.39 individuals per km² (95% CI: 3.18-7.6).

Introduction

Astragalus bones have been used extensively in paleoecology studies. The studies of astragalus are also growing recently considering the astragalus can be used to model many aspects of extinct mammals and environments as well. Those aspects including body mass, population size, abundance, and habitat preferences. In southwestern Ethiopia Barr (2015) has used Bovid astragalus to reconstruct the paleoenvironments of the Shungura formation during Plio-Pleistocene from 3.4–1.9 million years (Ma) ago. Previously, it has been hypothesized that the paleoenvironments of the Shungura has experienced significant habitat change at 2.85 Ma caused by environmental changes. However, Barr (2015) found the facts that the astragalar data do not support major habitat change at this time. Based on the astragalar data, it was found that there are significant fluctuations in inferred habitats with more open habitats indicated at 2.56 Ma and just after 2.36 Ma. This was known as sub-unit fluctuations caused by local factors including spatial habitat heterogeneity around the river channel and in its floodplain which is can be the contributing role.

Astragalus of mammals from Bovid groups is one of the most commonly preserved bones in the fossil record. Each Bovid astragalus is specific to its habitat related to the bony anatomy. The habitat preferences of Bovids can be modeled using their astragalus bone morphology. A relatively short astragalus is belonged to the highly cursorial Bovids which are living in structurally open habitats. The short astragalus is required to maintain rotational speed throughout the camming motion of the rotating astragalus. In fact, the astragalus of Bovids living in open habitat is different to the Bovids inhabit the closed habitat. In this habitat, the Bovids are belonged to the less cursorial groups. Hence, Barr (2014) conclude that the morphology of the Bovid astragalus is related to habitat-specific locomotor ecology.

Java island is known as one of island with high diversity of Bovids from Pleistocene era. One of Bovids that the fossil records have been found in central and eastern parts of Java island is *Duboisia santeng*. This antelope like Bovids were originated from south east Asian land and migrated to south to Sundaland during Pleistocene era 1.2-1.5 Ma. The migration routes of *D. santeng* have resulted in the presence of this Bovid species in several paleohabitats including Satir, Ci Saat, Trinil, Kedung Brubus, Ngangdong, Punung, and Wajak (Leinders et al. 1985, Theunissen et al. 1990, van den Bergh et al. 2001). Considering the widely distributed of *D. santeng*, this study aims to model the body mass and paleo habitat related population density of *D. santeng* using astragalus studies in eastern part of Java island.

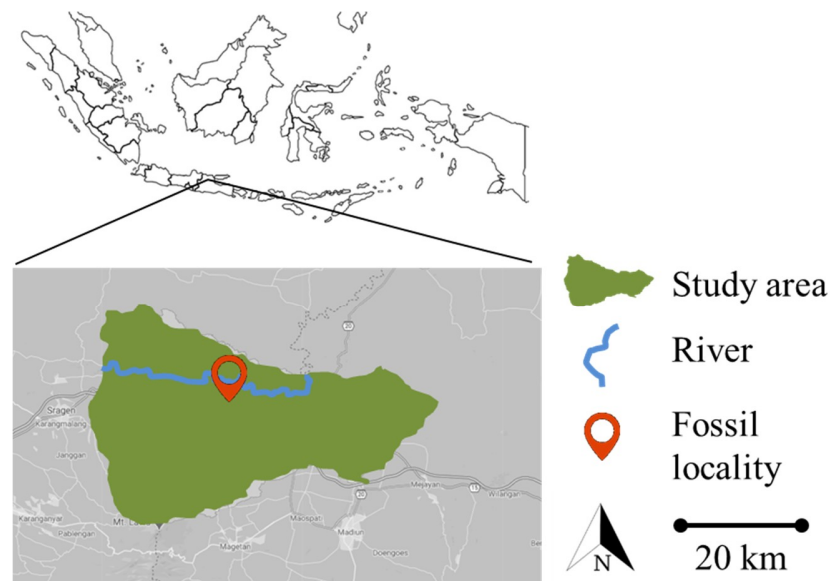


Figure 1. Study area within eastern parts of the Java island in Ngawi. The *D. santeng* fossils were found in Trinil.

Methods

The study area was a landscape known as Ngawi located in the eastern parts of Java island (Figure 1). This landscape was bordered by 3265 m mount Lawu (Figure 2) in the south and 84 m width Solo river in the north (Astirin et al. 2019). The landscapes in the north near the river were dominated by patches of lowland forests, plantations, paddy fields, and pastoral areas. Forest areas were common in the southern parts especially near the mount Lawu. The size of forests in mount Lawu is 54 Km².

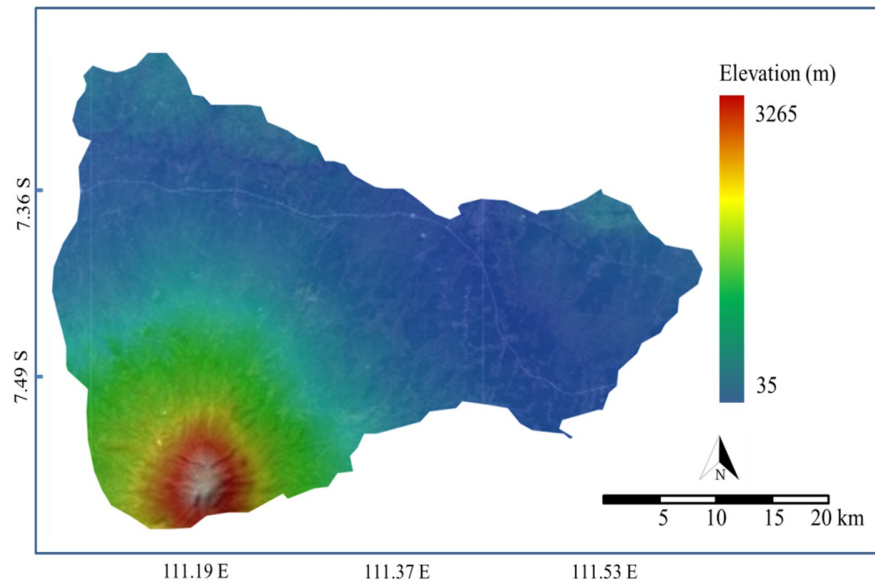


Figure 2. The elevation (m) of Ngawi with mount Lawu in the south.

The fossils in the form of astragalus bones were found in Trinil area located near the river bank (Figure 1) in the north of Ngawi. The bones then were measured following Degusta and Drba (2013). The parameters taken from the bones measurements were width (W) and lateral length (LI) in mm (Figure 3).

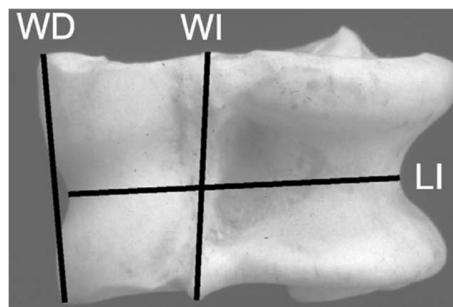


Figure 3. Measurements of astragalus fossils (W: width, LI: lateral length). (Degusta and Drba 2013).

The body mass (kg) estimation using astragalus parameters were done in 2 steps. First, this step is by comparing the *D. santeng* width and lateral length with other extant Bovid species. By using this comparison, *D. santeng* can be compared whether the body mass related to which living Bovids. Then, the body mass was estimated by using allometric equation developed by Tsubamoto (2014). The astragalus lateral length (LI) – body mass linear model was using slope value of 2.789 and intercept of 2.078. In this linear model, the lateral length was used as the predictor and the body mass was the result.

The linear model was also used to estimate the population density of *D. santeng*. The model was followed model developed by Damuth (1981). The body mass – population density linear model was using slope value of -0.75 and intercept of 4.23. In this linear model, the body mass was used as the

predictor (Tsubamoto 2014) and the population density (individuals/km²) was the result. The spatial model of the population density in Ngawi landscape was the function of forest covers. The whole process of population density using the astragalus bones can be seen in Figure 4.

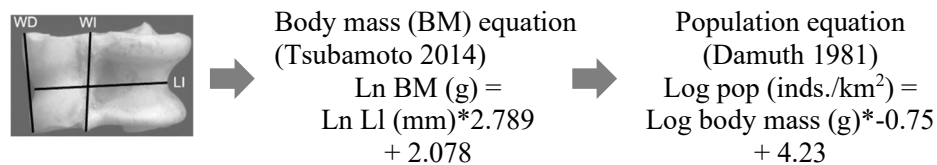


Figure 4. Flow of population density estimation using astragalus lateral length.

Results

The LI and W measurements on 9 specimens of *D. santeng* astragalus have been done. From the obtained LI and W, the estimated body mass (kg) have been calculated. The results of LI, W, and body mass were available in Table 1. From the model, it is estimated that the *D. santeng* originated from Trinil in Ngawi has average body mass equals to 60.3 kg (95%CI: 58.9-61.7).

The obtained LI and W data of *D. santeng* astragalus were compared to the extant Bovid species to study in which body mass classes of *D. santeng* (Ds). Four extant south east Asia Bovids were selected including *Bos frontalis* (Bf), *Bos javanicus* (Bj), *Bubalus mindorensis* (Bm), and *Bubalus depressicornis* (Bd). From the Figure 5, it can be seen that *D. santeng* has proximity of body mass to *Bubalus mindorensis* and *Bubalus depressicornis*. While *D. santeng* was separated with large Bovids including *Bos frontalis* and *Bos javanicus*.

The Ngawi landscape was consisting of varied forest covers (Figure 6). The high covers were observed in 2 parts. Those parts including near river banks were the *D. santeng* fossils were found. Then dense covers were also observed in the southern parts near the mount Lawu. Landscape between the mount Lawu and the rivers was having low covers. The forest covers and body mass then were used to estimate the population density.

Table 1. *D. santeng* astragalus measurements and body mass estimations

Parameters	n	mean	95%CI	
			Lower	Upper
Lateral length (mm)	9	34.9	34	35.8
Width (mm)	9	20.9	20.4	21.4
Body mass (kg)*	9	60.3	58.9	61.7

*Estimated from the model (Tsubamoto 2014).

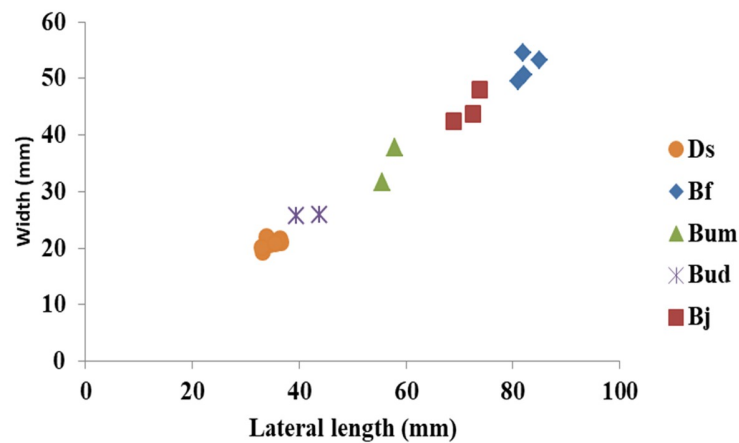


Figure 5. The comparison of astragalus lateral length (x axis) and width (y axis) of *D. santeng* (Ds) with extant south east Asia Bovids: *Bos frontalis* (Bf), *Bos javanicus* (Bj), *Bubalus mindorensis* (Bm), and *Bubalus depressicornis* (Bd).

The population density model of *D. santeng* is available in Figure 7. In Ngawi landscape the mean density of *D. santeng* is 5.39 individuals per km² with 95% CI: 3.18-7.6. High density was observed in the forest areas near the mount Lawu. While in the lowland between mount Lawu and river, the densities were observed lower than forest areas.

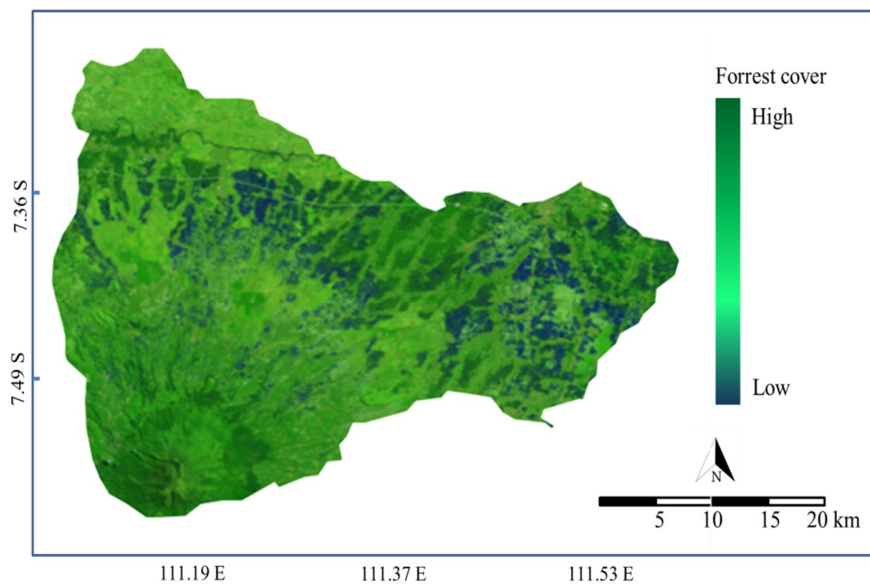


Figure 6. The forest covers of Ngawi with mount Lawu in the south.

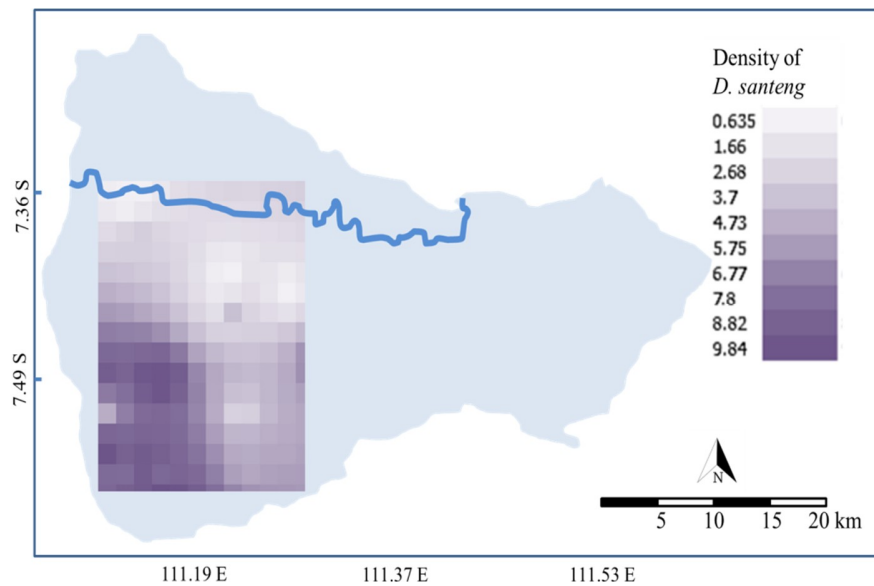


Figure 7. Spatially estimated density of *D. santeng* per km² depicted at 1 km² grids in Ngawi. The density ranged between 0.635 to 9.88 individuals per km².

Discussions

Astragalus bones have been used even in the Paleogene era, an era before Pleistocene (Martinez & Sudre 1995). In the study of paleomammals, astragalus bones have been used to estimate the mean body mass. The estimations were made based on allometric model. During Paleogene, the body mass of extinct *Dolichochoerus*, *Dremotherium*, and *Gelocus* were estimated to be 26 kg, 13.59 kg, and 7.5 kg respectively. The extinct body mass of *D. santeng* from Pleistocene era in this study was comparable to the extant Bovids. According to the comparisons based on LI and W data, *D. santeng* was estimated similar close to the extant *Bubalus depressicornis* and *Bubalus mindorensis*. *B. depressicornis* was known having body mass ranged from 90 to 225 kg (Mistari 1996). While *B. mindorensis* weighted from 180 to 300 kg (Cebrian et al. 2014). Based on the estimation, the *D. santeng* weight average equals to 60.3 kg is much more realistic. This weight is also supported with the fact that the order of LI and W data is $D. santeng < B. depressicornis < B. mindorensis$. *D. santeng* body mass is also smaller than 2 other extant Bovids including *Bos frontalis* and *Bos javanicus*. Those extant species were having heavy body mass even greater than *B. mindorensis* and *B. depressicornis*.

The habitat preference of *D. santeng* was also comparable to the *B. depressicornis* and *B. mindorensis* since those species having similar morphology, body mass, and length of LI and W. Among herbivores, body size has been previously implicated as a driver of spatial scales and habitat selection (Fisher et al. 2015). In Anthropocene era right now *B. depressicornis* was endemic to Sulawesi island and *B. mindorensis* endemic to Mindoro island. In Sulawesi island, *B. depressicornis* inhabited lowland forest with population density 1.6 inds./km². A subspecies *B. depressicornis quarlesi* was known inhabiting

montane forest at up to 2300 m above sea level (Burton et al.2005). Since extinct *D. santeng* LI and W data was closely related to the extant Bovid species, then the preferred habitat of *D. santeng* during Pleistocene area was estimated comparable to the habitat of extant species. In fact, the *D. santeng* fossils in Ngawi were found in riverbank which is surrounded by low land forests. South of Ngawi was also dominated by montane forests especially in mount Lawu. During Pleistocene, the forests in Lawu might be preferred by *D. santeng* since the extant *B. d. quarlesi* is also inhabiting montane forests.

The studies about relationships of body mass and population density have been documented (Ebenman et al. 1995, Johnson 1999). The population density in this study was estimated using a linear model with negative relationship with exponent of -0.75 (Polishchuk & Tseitlin 2001). During Pleistocene, population density of *D. santeng* was estimated ranged from 0.635 to 9.88 individuals per km². The data of estimated population density in particular south east Asian paleomammals are still limited. The only population density available is the estimated density of mastodon mammut (0.2-0.4 inds. per km²) in north America (Haynes 2014). This density was varied as a function of forest covers. The closely related extant species, *B. depressicornis* preferred forest covers with densities varied as low as 0.9 inds. per km² (Arini 2013) to as high as 1.6 inds. per km² (Ranuntu 2015). Lower density of extant species considering that at the current time there was a threat to the mammal habitats in the form of deforestation. While during Pleistocene this threat was absent. High population density of *D. santeng* in Ngawi was related to the body mass as well. This is in agreement that small animals are more abundant than large ones (Peters & Wassenberg 1983). *D. santeng* was estimated weighing around 60 kg and this allow this species to run escaping from predator and moving to hide. Second is related to the absence of competitors in grazing. Malhi et al. 2016 found that the existence of megaherbivores weighing >1000 kg can alter habitat structure through their high rates of consumption or through breakage and trampling. In Ngawi, there is no record yet about the existence of megaherbivores that can be potential competitors for large herbivore likes *D. santeng*.

Conclusion

This study has estimated the population density of *D. santeng* in Ngawi. The population density was interpolated and forest areas have more population than areas with low covers. The estimated body mass and population density are comparable to the extant Bovids. Using comparison with extant species, *D. santeng* is grouped as large herbivores.

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