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# A Reevaluation of the Paleoenvironmental Reconstructions Associated with *Homo erectus* from Java, Indonesia, Based on the Functional Morphology of Fossil Bovid Astragali

Daniel Charles Weinand  
*University of Tennessee - Knoxville*

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To the Graduate Council:

I am submitting herewith a dissertation written by Daniel Charles Weinand entitled "A Reevaluation of the Paleoenvironmental Reconstructions Associated with *Homo erectus* from Java, Indonesia, Based on the Functional Morphology of Fossil Bovid Astragali." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Anthropology.

Andrew Kramer, Major Professor

We have read this dissertation and recommend its acceptance:

Lyle Konigsberg, Walter Klippel, Sally Horn

Accepted for the Council:

Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Anne Mayhew  
Vice Chancellor and  
Dean of Graduate Studies

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ASSOCIATED WITH *HOMO ERECTUS* FROM JAVA, INDONESIA, BASED ON  
THE FUNCTIONAL MORPHOLOGY OF FOSSIL BOVID ASTRAGALI

A Dissertation  
Presented for the  
Doctor of Philosophy  
Degree  
The University of Tennessee

Daniel Charles Weinand  
August 2005

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## ABSTRACT

The Middle Pleistocene sites of Trinil and Kedung Brubus, Java, Indonesia have provided extensive faunal remains that are classified as part of a larger biostratigraphic framework. Paleoenvironmental reconstructions, associated with early hominids on Java, have been constructed based on the composition and perceived shared habitat preference of fossil and modern animal taxa. Research of the African members of the family Bovidae has shown that a more effective way of examining past environments is through the study of morphological traits that are characteristic of functional adaptations to different environmental conditions. This research represents the successful extension of this method by testing several parametric and nonparametric statistical models for habitat prediction based on bovid astragali from Southeast Asia. The results of the fossil analysis indicate the paleoenvironment at the Trinil site (ca. 1 Ma) was dominated by densely vegetated river valleys and upland forests, broken by open grasslands. These grasslands probably expanded during the period associated with the Kedung Brubus locality, approximately 0.8 Ma. This environmental change, coupled with the immigration of new species, was important to the appearance and future evolutionary success of *Homo erectus* during the Middle Pleistocene.



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## NOMENCLATURE

Ar	argon
astragalus (plural = astragali)	one of the bones making up the ankle joint
bovid	member of the mammalian Order Artiodactyla, Family Bovidae (cattle, buffalo, sheep, and goats)
BP	calibrated “years before present” (AD 1950)
CP	complexity parameter
ka	French “kiloan” equal to 1,000 years
LDA	linear discriminant analysis
Ma	“megannum” equal to one million years
rpart	recursive partitioning program
1 SE	one standard deviation of the minimum cross-validated error rate
Xerror	cross-validated error rate
X-val	cross-validation

# CHAPTER 1

## INTRODUCTION

An increasing amount of research indicates that the environment holds the key to understanding hominid morphological and behavioral adaptations (Vrba, 1995; Spencer, 1997; Potts, 1998; DeGusta and Vrba, 2003). By examining the paleontological record, it is possible to reconstruct the environments encountered by early hominids and to create inferences of behavior based on these reconstructions. Studies of the African members of the family Bovidae have shown that an effective way of examining past environments is through the study of morphological traits that are characteristic of functional adaptations to different environmental conditions, also known as ecomorphology (Kappelman, 1986, 1988, 1991; Plummer and Bishop, 1994; Kappelman et al., 1997; DeGusta and Vrba, 2003). Ecomorphological analyses are based on the assumption that an animal's locomotor anatomy has adaptations based on the substrate or terrain that the animal must navigate. Selection for these locomotor traits is based on predation and the ability of individuals to avoid this predation by successful locomotor evasion. This selection may result in relatively specialized functional anatomy. Bovids are specifically well suited to this type of study due to their predator avoidance strategy. Additionally, bovids are frequently preserved in paleontological contexts.

The earliest attempts to reconstruct past environments relied on taxonomic affinity of fossil species and an extension of the habitat preference of extant relatives to these fossil counterparts. While this method is useful, DeGusta and Vrba (2003:1010)

point out that in addition to requiring a particular level of certainty in the taxonomic and phylogenetic information, methods of this kind “rely on the assumption of temporal stasis in habitat preferences within a lineage over evolutionary time.” The identification of complete crania is often used to achieve the highest level of taxonomic and phylogenetic confidence. The cranium, however, is frequently fragmented or incomplete in paleontological contexts. Therefore, the need for a method of inferring paleoenvironments from the more frequently encountered post-cranial bones was recognized. A primary feature of ecomorphological analysis is that it is an empirical test that does not require the identification of fossil bovid postcranial remains to the genus or species level.

The role of phylogenetic relationships, however, cannot be completely ignored. DeGusta and Vrba (2003:1010) note that “[t]he morphology of an organism is constrained and shaped by its evolutionary history, and is not engineered specifically and solely for its current habitat.” This phylogenetic relationship can affect the ability to identify morphological characters that are indicative of habitat use. It is therefore necessary for the researcher to isolate those features that represent morphological differences exclusive of phylogeny. This is accomplished through the accumulation of metric and non-metric morphological characters from a variety of modern taxa and using statistical methods to identify those characters that are indicative of habitat, exclusive of phylogeny. Specifically, these methods test how well these characters predict habitat preferences compared to the known habitats of the modern taxa.

The manner in which these tests work can best be explained by example. In the case of Southeast Asian bovids, the morphological characters shared by *Bos javanicus*

and *Bos sauveli*, but not shared by the species *Bos frontalis* from the same genus, are most likely due to a common adaptation of the first two species to open habitats. In contrast, *Bos frontalis* possesses morphological characters indicative of its adaptation to heavily forested hills. If the characters observed were solely associated with phylogeny, all three species would be expected to display similar morphology.

Regardless of the characters chosen, some type of habitat-grouping scheme must be employed. Habitat classes are originally assigned based on published literature for the extant species being studied. Many animals, however, navigate a variety of habitat types. These published accounts may vary from the results of the statistical analyses. To minimize this effect, Kappelman et al. (1997) have proposed a four-class habitat designation system (Open, Light Cover, Heavy Cover, and Forest). This is an improvement to the three-class system originally used by Kappelman (1986; 1988) and Plummer and Bishop (1994), in which Light Cover and Heavy Cover were grouped as Intermediate. Once the chosen habitat model is constructed for a series of modern species from one taxonomic family, the results can be applied to the fossil record of specimens from the same family regardless of species identification.

Research has confirmed the success of this method for various post-cranial elements from African bovids. The earliest attempts to combine postcranial skeletal metrics with habitat prediction were performed by Kappelman (1986, 1988). Kappelman (1988) initially demonstrated the relationship of femoral morphology and adaptation to predator avoidance using a three-habitat grouping scheme of Plains, Broken cover, and Forest. He later expanded this work (Kappelman 1991) to show its utility for habitat prediction of fossil African bovids from the Fort Ternan site in Kenya. The resulting



three-habitat models for the complete femur and the proximal femur analyses of the extant bovids had a prediction accuracy of 73% for each of the models. These original prediction accuracies were later improved with the introduction of a four-habitat classification model (Kappelman et al., 1997). The analysis of the complete femur improved to 85%, whereas the proximal femur improved to 81%. Plummer and Bishop (1994) applied a three-habitat grouping scheme, similar to Kappelman's scheme (1991) for African bovid metapodials, with prediction accuracies ranging from 62-89%. The results of all of these analyses demonstrated that habitat could be accurately predicted from the femur and metapodial skeletal elements; however, the highest accuracy percentages were obtained from complete elements. As with cranial elements, these postcranial bones are frequently incomplete in paleontological contexts.

Therefore, DeGusta and Vrba (2003:1011) applied these techniques to the astragalus, which is "likely to almost always be better represented [in paleontological contexts] than relatively complete femora or metapodials." Further, since the astragalus is one of the bones that make up the ankle joint, its morphology is also adapted to locomotion. DeGusta and Vrba (2003) used the four-habitat grouping scheme created by Kappelman (1991) in their analysis of African bovid astragalai. Their analysis resulted in a habitat prediction accuracy of 67% (DeGusta and Vrba, 2003). This is less than the accuracies associated with the complete femora and metapodials but is still 2.7 times greater than chance (25%).

While these researchers have clearly demonstrated the technique's usefulness, these studies have been limited primarily to African species. One exception is the work of Scott et al. (1999). They expanded the African dataset of bovid femora to include

three additional species found in Asia. This dataset was used to predict the paleohabitats associated with *Sivapithecus parvada*, a Middle Miocene ape (Scott et al., 1999). They regard their conclusions of the paleoenvironmental interpretations with caution, however, due to concerns with sample size (Scott et al., 1999:264). This further strengthens the argument made by DeGusta and Vrba (2003) for the use of the astragalus.

The study presented here will further expand the work of these previous researchers by examining the astragalus from members of the family Bovidae from Southeast Asia. This represents the first attempt to predict habitat, based on functional morphology, from this region. In addition to utilizing the four-habitat model created by DeGusta and Vrba (2003) for the astragalus, a five-habitat model will also be tested for its applicability to habitat prediction. Several mountain-dwelling bovids are found in Southeast Asia. Therefore the inclusion of this additional category may prove necessary for accurately describing the morphological adaptations to the unique substrates encountered by these species.

Previous ecomorphological research has relied on the parametric statistical method known as linear discriminant analysis (LDA) to categorize the modern species into their respective habitat groups. The extant species models are then used to predict the most likely habitat category for unknown fossil specimens. The use of this method, however, relies on adherence to certain assumptions about the modern dataset to be used. The primary assumptions are that the data should be normally distributed and the associated covariance matrices should be equal. These assumptions are frequently violated. Kappelman (1991) found that the covariances for his test of the proximal femur were not equal. This minimizes the confidence of the classifications obtained. A

preliminary examination of the datasets used in the present study also indicates that these assumptions are violated.

No test has yet been performed to identify whether discriminant analysis is robust to the violation of these assumptions. Therefore, in addition to discriminant analysis, the data studied here will be tested using a nonparametric statistical method known as recursive partitioning (rpart). Rpart does not rely on adherence to the above assumptions to classify specimens into their respective habitat categories (Feldesman, 2002). In addition, rpart can identify which of the two techniques is most applicable by testing a combination of the discriminant variates calculated by LDA and the specimen measurements (Steinberg and Colla, 1997). Each of these techniques will be described in greater detail in Materials and Methods.

Another important consideration when constructing ecomorphological models is the issue of body size. Much attention has been given to whether or not body size is actually driving the classifications of the species studied. It has been found that femoral length is significantly correlated with body size (Scott, 1985). Kappelman (1991) minimized this effect by eliminating those bovids from his study that exceeded 250 kg. Several bovid species from Southeast Asia exceed this body weight, thus it is concluded that this is probably not the best approach for this study. DeGusta and Vrba (2003) have also identified a strong correlation ( $R^2 = 0.91$ ) between their measurements of the astragalus and body weight. They, however, argue that the complete elimination of size may not be the ideal solution if habitat prediction is the ultimate goal (DeGusta and Vrba, 2003). To verify what effect the elimination of body size would have on habitat prediction, this study examines the use of size-corrected measurements in each of the

constructed models. The methodology for obtaining these size-corrected measurements follows the work of Darroch and Mosimann (1985) and is presented in the Materials and Methods chapter.

Once the models for the extant bovids have been created, each will be used to interpret the paleohabitats of two Pleistocene collections of fossils from Java, Indonesia, associated with the early hominid, *Homo erectus*. The two fossil collections are part of the Dubois Collection, housed in The Netherlands National Natural History Museum in Leiden, and represent two distinct faunal units from Java. The specific faunal units studied here are the Trinil H.K. (“Haupt-Knochenschicht”) and Kedung Brubus (new spelling) faunas. These units are part of the larger biostratigraphic framework composed of the Satir, Cisaat, Trinil H.K., Kedung Brubus, Ngandong, Punung, and Wajak faunas. *Homo erectus* fossils have been recovered from contexts associated with both the Trinil H.K. and Kedung Brubus faunas. Therefore, the identification of the paleoenvironments at each of these sites may provide paleoanthropologists with additional behavioral insight regarding this extinct hominid species.

For Java, environmental reconstructions have been limited primarily to comparisons of the overall faunal compositions within this current biostratigraphic framework (de Vos, 1983, 1987, 1995; de Vos et al. 1994; Sondaar 1984; Van den Bergh et al., 2001). As already mentioned, this type of environmental reconstruction relies on the assumption of temporal stasis of the species in question. The current study, therefore, represents the first attempt at an empirical means of examining paleohabitat using the functional morphology of fossil bovid remains from Java.

## CHAPTER 2

### BACKGROUND

Interpretations of Quaternary environmental change for Java are currently based upon the large-scale comparisons of biostratigraphic units. These biostratigraphic units and the currently accepted faunal succession, from oldest to most recent, are Satir, Ci Saat, Trinil H.K., Kedung Brubus, Ngandong, Punung, and Wajak (de Vos et al., 1994; Aziz, 2000). The current paleoenvironmental reconstruction for each component of this succession, and all subsequent tables, appears in Appendix A (see Table A.1). This study examines the bovid astragalai recovered only from the Trinil and Kedung Brubus type-sites excavated by Eugene Dubois between 1891 and 1892, along the Solo River and in the Kendeng Hills, respectively; however, a review of the environmental setting associated with the entire faunal scheme is warranted. A map indicating the site localities is presented in Appendix B (Figure B.1), as are all remaining figures.

#### FAUNAL SUCCESSION FOR JAVA

##### *Satir Fauna*

The Satir Fauna is the earliest recognized fauna on Java. This fauna is referred to as unbalanced, meaning that there are only a few genera of herbivores while carnivores are absent, and is believed to suggest island conditions (Sondaar 1984; De Vos *et al.* 1994). The primary faunae associated with this group are *Tetralophodon bumiajuensis* (mastodont), *Hexaprotodon simplex* (early hippopotamus), cervids, and the giant tortoise

(*Geochelone* sp.). The dates presented indicate that this fauna is between 2 and 1.5 million years old, and the association of these species has been interpreted to suggest isolated island conditions during this time (Sondaar, 1984; de Vos et al., 1994; Van den Bergh et al., 2001). The pollen sample from the site of Sangiran associated with this fauna indicates that swamp conditions prevailed (Semah, 1982; de Vos et al., 1994). Prior to this time, no mammals occur on Java. It is argued that Java was not emerged from the sea until the Late Pliocene (Van den Bergh et al., 2001), but other research demonstrates that parts of Java may have been emerged as early as the Late Miocene (see Weinand et al., 2005).

#### *Ci Saat Fauna*

The Ci Saat fauna is represented by *Stegodon trigonacephalus* (triangular-headed stegodont), *Hexaprotodon sivalensis* (Sivalik hippo), cervids, bovids, a possible felid (*Panthera* sp.), and *Sus stremmi* (Stremm's pig). The elephantid and hippopotomid appear to have replaced the early species. Cervids become abundant while bovids are poorly represented. De Vos et al. (1994) interpret this fauna as a species-poor isolated fauna, though the presence of the felid indicates a mainland connection. The giant tortoise also becomes extinct during this period. The Sangiran fossil pollen assemblage analyzed by Semah (1982) indicates slightly drier conditions than the preceding Satir stage, with an increase in grasses. An age of 1.2 million years BP has been assigned to this fauna (Leinders et al., 1985; Suzuki et al., 1985).

### *Trinil H.K. Fauna*

The Trinil H.K. fauna comprises fossils from the Trinil type-site located on the Solo River and the Lower Bapang Formation, including the Grenzbank, at Sangiran (see Figure B.1). This fauna is the first to contain remains of *Homo erectus*. It also includes the primates *Macaca fascicularis* (macaque) and *Trachypithecus cristatus* (silvered-leaf monkey), as well as rodents, felids, canids, *Stegodon* (an elephantoid), *Rhinoceros*, cervids, bovids and a suid. *Hexaprotodon* (hippopotamus) is absent but not considered extinct. This fauna is notably more diverse than previous ones, though it is still considered to be poor in species (de Vos et al., 1994). The environment is interpreted as open woodland (de Vos et al., 1982,1994). This is supported by the dominance of grasses during this period (Semah, 1982). It should be noted, however, that the pollen record at Sangiran also indicates an abundance of ferns that may reflect the local fluvio-lucustrine conditions at this time (Semah, 1982). Based on fission track dating, Suzuki et al. (1985) concluded that the Trinil H.K. Fauna is 1 million years old, however,  $^{40}\text{Ar}/^{39}\text{Ar}$  dating performed by Larick et al. (2001) for this lithostratigraphic layer at Sangiran indicate that it may be 1.5 million years old. Mean glacial eustatic sea level during this time, based on foraminifera, were 70m below present day sea levels (Vrba et al., 1989; Van den Bergh et al., 2001), but sea level greatly decreased around 800 ka, which permitted a major faunal immigration event (Van den Bergh et al., 2001).

### *Kedung Brubus Fauna*

The Kedung Brubus fauna is described as having a more mainland character than the previous fauna, resulting from a maximum faunal exchange with mainland Asia (de Vos et al. 1994). *Hyaena*, tapir, *Elephas*, and *Rhinoceros kendengindicus* mark new arrivals to the island fauna. A dry, open woodland environment is interpreted from the lack of primates, except for hominids, and the large number of bovid species present. There are, unfortunately, no pollen data reported for this time period. Remains of this fauna have been recovered from the Kedung Brubus type-site located east of Trinil in the Kendeng Hills of Central Java (see Figure B.1), the upper portion of the Bapang formation at Sangiran, the Bumiayu area of West Java, and north of the villages of Djetis and Pening (de Vos et al., 1994). The age for this fauna is inferred as 800 ka (Leinders et al. 1985).

### *Ngandong Fauna*

The Ngandong fauna is poorly understood, and it, as well as the following faunas described, are not represented at Sangiran. It is presumed to be similar to the Kedung Brubus fauna, though younger. *Macaca*, however, returns. The environment is also presumed to be similar, with open woodland dominating. Very young ages for the Ngandong fauna have been reported (Swisher, et al., 1996) although the conservative estimate of 135 ka argued by Van den Bergh et al. (2001) is followed here.



### *Punung Fauna*

The Punung Fauna is a composite fauna that is recent in character although it represents the Late Pleistocene, presumably the last interglacial. The fauna has been described from fossils recovered from fissure deposits near Punung, Java and associated fossils from Sumatra. New immigrants include *Hylobates* (siamang), *Pongo* (orangutan), *Elepha maximus*, *Capricornus* (serow), *Sus vittatus* (East Indian pig), *S. barbatus* (bearded pig), and *Ursus* (bear). *Homo sapiens* also occurs. *Stegodon*, *Elephas hysudrindicus*, and *Sus macrognathus* disappear. The presence of large numbers of *Hylobates* and *Pongo* fossils in this fauna suggests a humid, tropical forest environment (de Vos, 1983). The presence of these exclusive tropical forest species indicates that their arrival must have occurred after the dry conditions of the penultimate glaciation at 135 ka. During this period, tropical species may have been displaced southward toward the then exposed Sunda Shelf and survived in refugia until spreading further south to Java between 110 – 70 ka (Van den Bergh et al., 2001). Therefore, the accepted age estimation of the Punung fauna at approximately 80 ka is considered a reasonable estimate (Van den Bergh et al., 2001).

### *Wajak Fauna*

The Wajak fauna is a modern Holocene composite fauna. After the latest glacial event, there appears to be an impoverishment of Javanese fauna (Van den Bergh et al., 2001). During this time climatic changes led to an increase in grass pollen and a decrease in fern spores (Van der Kaars, 1991; Van den Bergh et al., 2001). *Pongo* and *Tapirus* also disappear from the faunal record from Java. This is interpreted as evidence of the

end of tropical forest conditions and a return to open woodland environments (Van den Bergh et al., 2001).

#### THE TRINIL AND KEDUNG BRUBUS SITES

Dubois originally considered the fossils recovered from Trinil and Kedung Brubus to be of the same age (Dubois, 1908; de Vos et al., 1982). Later researchers agreed with this claim and referred to the grouped fossils as the 'Trinil' fauna (Stremme, 1911a, b; von Koenigswald, 1934; Hooijer, 1952). It was later argued that the fossils from these two sites actually represent two distinct faunal units, Trinil H.K. and Kedung Brubus (de Vos et al, 1982; Sondaar, 1984). Still others state that the Trinil site is comprised of two separate depositional histories spanning the Middle Pleistocene to the Holocene, thus arguing that the fossils recovered from this site cannot be considered a distinct fauna (Bartstra, 1983; Hooijer, 1983). Finally, in 1994, de Vos et al. published the results of a joint research effort to correlate the fossils from the various paleontological sites on Java with a detailed examination of dates and fossils from the Sangiran dome in Central Java. The results represented the first attempt to place all of the hominid-bearing deposits of Java into an ecological context under the biostratigraphic framework presented above.

The currently accepted ages for the Trinil H.K. and Kedung Brubus faunas are based on fission-track dating and estimate that these faunas are one-million and 800,000 years old, respectively. Other researchers, however, have argued that these faunas are much older (Larick et al., 2001). Using  $^{40}\text{Ar}/^{39}\text{Ar}$  dating, Larick et al. (2001) calculated that the age of the lithostratigraphic layer associated with the Trinil fauna is closer to 1.5-

million years. Their study did not include a revision of the Kedung Brubus fauna. The Kedung Brubus fauna is still believed to be 800,000 years old. Regardless of the absolute age of these fauna, there is no question that the strata associated with the Trinil H.K. fauna are older than those associated with the Kedung Brubus fauna. For the purposes of this study, a relative age of Middle Pleistocene for Trinil H.K. and Upper/Middle Pleistocene for Kedung Brubus is acceptable.

To ensure that only those astragalai associated with these two units are studied, it is important to identify the geospatial context of the fossils. Dubois collected over 2,000 post-cranial bovid fossils from several Pleistocene contexts throughout eastern and central Java. However, the fossils used to define the Trinil H.K. and Kedung Brubus faunal units are only from localities of known provenance (de Vos et al., 1982). These type localities are identified in the Dubois Collection as “Trinil” and “Kedoeng Broebroes.” According to de Vos et al. (1982:208), “The fossils were found mainly in situ” and the “materials come from one locality and one level.” Although as previously mentioned, Bartstra (1983) argues that the Trinil fossils may actually come from more than one distinct stratigraphic level. There is, unfortunately, no way to know for certain if the excavated collection represents one or multiple geospatial contexts. Therefore, for the purposes of this study, the context argued by de Vos (1982) is assumed, and only those astragalai identified by the locality designations “Trinil” and “Kedoeng Broeboes” are examined.

The paleontological importance of these sites is emphasized by the fact that Dubois collected over 40,000 plant and animal fossils from the Trinil site alone (Leakey and Slikkerveer, 1993). The anthropological importance of these sites, however, cannot

be ignored. The Trinil site represents the type-locality of *Homo erectus* on Java. Dubois recovered the remains of a calotte and molar fragment during his 1891 excavation, and in 1892, the remains of a femur were discovered. It wasn't until 1893 that Dubois concluded that these fossils all belonged to a single hominid he named, "*Pithecanthropus erectus*." A hominid mandible was also collected at the Kedung Brubus site, which Dubois additionally classified as *Pithecanthropus* in 1924 (de Vos et al., 1994). This species designation has since been revised as *Homo erectus*. Other *Homo erectus* fossils associated with the Trinil H.K. and Kedung Brubus faunas include Sangiran 2 (= *Pithecanthropus* II), Sangiran 3 (*Pithecanthropus* III), Sangiran 12 (= *Pithecanthropus* VII), and Sangiran 17 (= *Pithecanthropus* VIII) (de Vos et al., 1994). One of the goals of this study is to place *Homo erectus* into an empirically derived paleoenvironmental framework that may contribute to the understanding of the behavioral and logistic challenges faced by this early hominid.

## THE FOSSIL BOVIDAE OF JAVA

In his thorough examination of the cranial remains of the bovids from the Dubois Collection, Hooijer (1958) identified only four Pleistocene species. Two of these species, *Bibos palaesondaicus* Dubois and *Bubalus palaeokerabau* Dubois, are ancestral to the modern banteng (*Bos javanicus*) and the domesticated water buffalo (*Bubalus bubalis*), respectively (see Figures B.2a and B.2b). There are currently no qualitative diagnostic criteria and only limited quantitative criteria (see Hooijer 1958) for the identification of post-cranial elements, including astragalus elements, for these species in the literature. The quantitative criteria that do exist for the fossil specimens are only for complete atlas,

metapodial, and tibia elements, which are rarely found complete in paleontological contexts.

The two remaining fossil species are endemic to Java and existed only briefly during the Middle Pleistocene. One of these species, *Duboisia santeng*, is thought to be closely related to the Indian Siwalik species *Boselaphus tragocamelus* and is known from the Trinil H.K. and Kedung Brubus Faunas (see Figure B.2c; de Vos et al., 1982). This species is noticeably smaller than either *Bibos palaesondaicus* or *Bubalus palaeokerabau*. Measurements taken by Hooijer (1958) indicate that the complete lower toothrow of *Duboisia santeng* measures 73 - 82 mm, whereas the lower P<sub>3</sub>-M<sub>3</sub> toothrow (the *Bibos paleosondaicus* specimen was lacking P<sub>2</sub>) for both modern and fossil species of *Bubalus* and *Bibos* measures 125 - 150 mm. The smaller size of *Duboisia* has made identification of its post-cranial skeletal elements possible, including the astragalus elements used in this study.

The other species, *Epileptobos groenveldtii*, is known only from the Kedung Brubus Fauna (see Figure B.2d; de Vos et al., 1982). The identification of the post-cranial bones of this species is more problematic due to its similarity in size to both *Bubalus paleokerabau* and *Bibos palaesondaicus*. One atlas and one left metacarpus, however, have been positively identified as *Epileptobos groenveldtii* based on their association with cranio-dental remains. Unfortunately, no astragalai have been positively identified for this species.

Bovids are first recognized in the fossil record as part of the Ci Saat Fauna, though no particular species has been identified. The first recognized bovid species appear in the succeeding Middle Pleistocene Trinil H.K. faunal stage. The small-bodied

endemic bovid, *Duboisia santeng*, first appears in the Trinil H.K. fauna but lasts only through the Kedung Brubus fauna. *Bubalus paleokerabau* and *Bibos palaeosondaicus* also appear during this time. The Trinil H.K. fauna has been described from the type-site of Trinil (de Vos et al., 1982). The environment has been interpreted by the dominance of bovids as being “relatively dry, presumably corresponding with a glacial period” (de Vos et al. 1994:131), though the reported presence of *Pongo pygmaeus* during the Early/Middle Pleistocene from the site of Sangiran would indicate a more tropical environment (Kaifu et al., 2002). The claims of Kaifu et al. (2002) have not been confirmed and the teeth they present as evidence of *Pongo* may, in fact, belong to *Homo erectus* (de Vos, personal communication, 2004). Therefore, this study assumes that the species composition was indicative of a dry, open woodland environment.

The Kedung Brubus Fauna represents the maximum faunal interchange with the Asian mainland (de Vos et al., 1994) and is first recognized at approximately 0.8 Ma. Van den Bergh et al. (2001:390) note that this faunal stage “coincides with the onset of a distinct mode of eustatic sea level fluctuations.” The extent of the drop in sea level, coupled with an interpreted dry environment and open woodland (de Vos et al., 1994), indicates that Java was connected to the mainland via the Sunda Shelf (the underwater continental shelf that connects mainland Southeast Asia to the Indonesian Archipelago and Borneo). The bovids of the preceding Trinil H.K. fauna are joined by *Epileptobos groeneveldtii* Dubois; however, both *Epileptobos* and *Duboisia* are extinct by the end of this stage. Therefore, for the purposes of ecomorphological analysis, only the Trinil H.K. and Kedung Brubus faunas were considered for use in this study.

## CHAPTER 3

### MATERIALS AND METHODS

#### MATERIALS

The studies of Kappelman (1988, 1991) and Plummer and Bishop (1994) achieved their highest prediction accuracies using complete femur and metapodial elements. These bones are less-frequently recovered as complete fossils. This was found to be particularly true for the fossil collection from Java examined here. For this reason, the astragalus was chosen for use in this study.

Measurements from the modern Southeast Asia bovid astragalai used in this study were collected from specimens housed at the American Museum of Natural History (AMNH), the Field Museum (FMNH), and the Smithsonian National Museum of Natural History (NMNH). Unfortunately, these institutions provided too few specimens for statistical analysis. Therefore, additional bovid specimens from Africa and North America were added. The additional measurements for the African species *Connochaetes taurinus*, *Damaliscus lunatus*, *Cephalophus monticola*, and *Madoqua kirki* were obtained from David DeGusta at the Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, and Department of Integrative Biology, University of California, Berkeley, CA. Three *Bison bison* specimens from the University of Tennessee Zooarchaeology Collection were also measured.

A list of the modern specimens, their common names, and the associated measurements appear in Appendix C. One astragalus from each of the 81 specimens was

measured, with no preference of side or sex. Specimens with readily evident pathological deformation were excluded. In most cases, only adult, wild animals were utilized. In some cases, missing locality data prevented confirmation of collection method. Due to its perceived taxonomic relationship to possible species found in the fossil assemblage, one captive animal (*Boselaphus tragocamelus*) was included in the study.

The fossil specimens utilized were obtained from the National Museum of Natural History in Leiden, the Netherlands. The fossil specimens and their associated measurements are found in Appendix D. These specimens are part of the Dubois Collection of fossils excavated from the Trinil and Kedung Brubus sites, Central Java, Indonesia and represent two distinct faunal units. The bovid sample associated with the Trinil H.K. faunal unit comprised 95 astragalai. Most of these specimens are identified only to the family-level Bovidae; however, 14 astragalai are from the species *Duboisia santeng*. The Kedung Brubus sample comprised 21 specimens identified to family and one *Duboisia santeng* specimen.

## METHODS

Seven measurements were taken from each astragalus examined (see Figure B.3) and follow those outlined by DeGusta and Vrba (2003), though two of their original measurements were excluded here. The measurements used in this study are as follows:

- 1) Medial length (LM): The maximum proximal-distal dimension of the medial surface taken parallel to the main proximal-distal axis of the astragalus (Figure B.3a).



- 2) Intermediate length (LI): The minimum proximal-distal dimension of the astragalus taken parallel to the main proximal-distal axis of the element (Figure B.3c).
- 3) Lateral length (LL): The maximum proximal-distal dimension of the lateral surface taken parallel to the main proximal-distal axis of the astragalus (Figure B.3b).
- 4) Intermediate width (WI): The minimum medial-lateral dimension on the anterior surface at the junction of the proximal and distal articular facets. Projections or tubercles are included (Figure B.3c).
- 5) Distal width (WD): The medial-lateral dimension of the distal end at its distal-most point (Figure B.3c).
- 6) Intermediate thickness (TI): The minimum anterior-posterior dimension of the lateral surface at the junction of the proximal and distal articular regions (Figure B.3b).
- 7) Distal thickness (TD): The anterior-posterior dimension of the distal end of the lateral surface (Figure B.3b).

All measurements were taken with digital calipers and recorded to the tenth of a millimeter. Weinand took all measurements of the modern and fossil Southeast Asian specimens, as well as the *Bison bison* specimens. D. DeGusta provided the African specimen measurements (personal communication, 2004). To eliminate concerns of intraobserver error for the Southeast Asian specimens, a total of four specimens were measured twice with a separation of at least two days between measurements. The

results of this test are presented in Table A.2. All seven measurements were taken for each of the modern specimens but not necessarily for all of the fossil specimens. In some cases, damage to these fossils prevented measurement.

Previous studies have indicated that body size is a potential complicating factor in habitat classification. Some researchers have attempted to utilize measurement ratios to eliminate body size (see Plummer and Bishop, 1994) but, as argued by DeGusta and Vrba (2003), the complete elimination of size may not be the ideal solution if habitat prediction is the ultimate goal. They do, however, note that it is important to explore the relationship between the raw measurements and body weight. In their study of the astragalus in modern African species, DeGusta and Vrba (2003) performed a multiple regression of the natural log of body weight against all of the raw measurements and found a strong correlation between the measurements and body weight ( $R^2$  of 0.91). To test the effects of body size on habitat predictions in this study, a different approach is utilized.

Based on the high correlation found between the measurements and body weight for the astragalus in African species, a comparison of raw measurements versus size-corrected measurements is performed to test the effects of eliminating size from the analyses. Therefore, for each specimen measured, all seven measurements are converted to log-scaled values following the methodology of Darroch and Mosimann (1985). First, the log of each measurement is taken. The seven resulting log values are then averaged to obtain a grand size variable. Since the goal is to eliminate size from the analysis, this grand size variable is then subtracted from the log of each of the original logged measurements to obtain a shape value, based on the following equation:

$$\text{Log}(X_1) - [\sum_i \text{Log}(X_i)] / n$$

Where  $X_1$  is the first raw measurement,  $[\sum_i \text{Log}(X_i)]$  represents the sum of all logged, measurements, and  $n$  is the total number of measurements used in the study (in this case,  $n = 7$ ). This equation is then used for the subsequent remaining six raw measurements.

All ecomorphological analyses require some form of habitat classification. These classifications represent an arbitrary finite sample of the continuous range of habitats, or the relative density of understory vegetation, encountered by the taxonomic group being studied. Early ecomorphological studies used a three-habitat grouping scheme that consisted of ‘open / plains,’ ‘intermediate / broken cover,’ and ‘closed / forest’ habitats (Kappelman 1986, 1988, 1991; Plummer and Bishop, 1994). The ‘intermediate / broken cover’ category was later split into ‘light cover’ and ‘heavy cover’ creating the now common four-habitat grouping scheme (DeGusta and Vrba, 2003; Kappelman et al., 1997; Scott et al., 1999). The four-habitat scheme utilized by DeGusta and Vrba (2003) for the astragalus of African species was part of this study, though Weinand assigned the bovids from Southeast Asia to their habitat categories. A new five-habitat scheme was also created and tested in this study, with the addition of a ‘mountain’ category.

All of the habitat classifications used in this study are based on the observation of behavior for each of the species as defined in *Walker’s Mammals of the World, Fifth Edition, Volume II* (Nowak, 1991). The ‘Open’ taxa include those animals that frequent edge or ecotone, open country, and arid country (Kappelman et al., 1997). ‘Light Cover’ taxa are those that frequent light bush, tall grass, and hilly areas (Kappelman et al., 1997). The ‘Heavy Cover’ taxa frequent bush, woodland, swamp, and near-water habitats

(Kappelman et al., 1997). ‘Forest’ taxa are naturally, forest-dwelling taxa (DeGusta and Vrba, 2003). ‘Mountain’ taxa have been defined in this study as those animals found in a variety of habitats within high-altitude settings but flee to rocky slopes when startled by predators. The habitat classifications were primarily conducted independently of the statistical analyses, with two notable exceptions.

The species *Bos javanicus* and *Bubalus bubalus* are problematic. Based on the literature (Nowak, 1991:1429), *Bos javanicus* is “usually found in drier, more open areas than *B[os] gaurus* . . . [but] it depends on dense thickets and forest for shelter.” Since this animal inhabits what is considered an ecotone, it has been classified as Open in this study. This classification was confirmed in early attempts to place this species into other classification categories. In each of these cases, the specimens were misclassified as Open. The same results were found for the *Bubalus bubalis* specimens. *Bubalus bubalis*, however, is “associated with wet grasslands, swamps, and densely vegetated river valleys” (Nowak, 1991:1420). It seems that this species should be classified as Heavy Cover, according to the above classification scheme. It may be, however, that both of these species benefit from their large body size as a predator avoidance strategy that reduces selection pressures related to habitat, as suggested by Scott et al. (1999) for the large African species *Syncerus caffer*. Another possibility is that these animals were not truly wild individuals when obtained, but the effects of domestication on the functional anatomy of the astragalus has not been analyzed and is beyond the scope of the current study.

In addition, for comparative purposes, species classified as ‘Mountain’ taxa in the five-habitat scheme studies have been assigned different habitat classifications in the

four-habitat studies, respective of their specific habitats within mountain settings. It must be emphasized that each of these classification schemes are arbitrary divisions of a continuous range and that bovid taxa may actually inhabit a range of habitat types. Therefore, the specific assignments represent a ‘best fit’ designation rather than an exclusive one, as noted by DeGusta and Vrba (2003:1014), and are a simplification of actual habitat ranges.

Once the astragalus measurements, both raw and size-corrected, were obtained and habitat classifications assigned, a method for determining the degree to which habitat could be predicted for the modern specimen measurements was applied. Most ecomorphological analyses rely on linear discriminant analysis (LDA) for this purpose and this procedure is one of two used in this study. Discriminant analysis is designed to characterize the relationship between a set of predictor variables and a grouping variable. In the case of ecomorphology, the predictor variables are the measurements taken from the bones and the grouping variable is the constructed habitat classification scheme. The various statistical programs employed then create a linear combination of the predictor variables that best characterizes the differences among the groups, thus the name, “Linear Discriminant Analysis.” By constructing this discriminant rule from existing data, the resulting model can be used to predict the classification of new data whose membership is unknown.

The discriminant model has the following mathematical formula for each of the functions created:

$$F_K = D_0 + D_1X_1 + D_2X_2 + \dots + D_pX_p$$

where  $F_K$  is the score on function  $K$ ,  $D_i$  are the discriminant coefficients, and  $X_i$  are the predictor variables. The maximum number of functions  $K$  that can be derived is equal to the minimum number of predictors ( $p$ ) or the quantity (number of groups – 1). In the case of the ecomorphology studies, there are more predictors than groups and, therefore, the number of functions is limited by the latter value. For a four-habitat model, LDA constructs three classification functions (four groups – 1). Further, LDA calculates a discriminant score for each function. This score is used to classify the cases into one of the group variable categories.

There are three methods for classifying cases into groups. These are maximum likelihood methods, linear classification functions, and distance functions. The method used in this study is a maximum likelihood method based on Bayesian statistics that creates a rule to classify cases. The principle is that a case is assigned to a particular group if its probability of membership to that group is greater than the probability of belonging to any other group. This is accomplished with the use of two probability estimates. Prior probability is an estimate of the probability that a case belongs to a particular group when no information from the predictors is available. Prior probabilities can either be determined by the number of cases in each category of the grouping variable or by assuming that the prior probabilities are all equal. The posterior probability is the probability of obtaining a specific discriminant score given that a case belongs to a specific group. These values can be used to determine the confidence of the calculated predictions.

In addition to these prediction probabilities, the validity of the constructed model can be ascertained by the use of cross-validation. LDA calculates a cross-validated

accuracy of the model based on a leave-one-out classification system. Using this system, LDA eliminates one specimen from the analysis and constructs a model based on the remaining specimens. The held-out specimen is then tested against this new model. LDA continues this process with each specimen in the dataset until all have been held-out and tested. The number of correct classifications, divided by the total specimens in the sample, gives the cross-validated accuracy of the overall model.

The methodology followed here for the discriminant analysis portion of this study primarily follows that of DeGusta and Vrba (2003) for their work with African bovid astragalai. The statistics program used here, however, is the Statistical Package for the Social Sciences (SPSS 12.0 for Windows, Release 12.0.0, SPSS inc., 2003). SPSS uses a discriminant function to calculate probabilities that describe the likelihood that an individual case belongs to a specific habitat group. To find the best discriminant model for the data, all seven raw measurement variables were used for both the four-habitat and five-habitat schemes, followed by all seven size-corrected values for both habitat schemes.

The accuracy of the constructed model, however, ultimately depends on adherence to certain assumptions about the dataset. LDA relies on two primary assumptions about the population to be studied. LDA assumes that each group is drawn from a multivariate normal population. This assumption is often violated but can be particularly problematic if the groups are not well separated in the space of the predictor variables. The second assumption is that the covariance matrices of the various groups are equal. The covariance matrices are frequently not equal for large sample sizes. In most cases, LDA is robust to violations of these assumptions. A preliminary examination

of the data used in this study, however, demonstrated that the data was not distributed normally. Further, Box's M test of covariance equality indicated the covariance matrices were not equal ( $p < 0.001$ ). Therefore, the use of another statistical method was deemed necessary to create a usable classification model and to determine if LDA is robust to the violation of these assumptions.

Feldesman (2002) demonstrated an alternative classification method to LDA that does not rely on multivariate normality or equality of covariance matrices to determine group membership. The method is known as recursive partitioning (rpart), or classification trees. It is a nonparametric method specifically designed to classify predictor variables that do not demonstrate normality.

There are several advantages of using recursive partitioning for variable prediction. These are summarized from Feldesman (2002). The first of these is that rpart is nonparametric. It does not require a particular distributional form, such as normality. Secondly, it does not require advance variable selection. If certain variables do not contribute to the reduction of classification errors, these variables are simply not used in the construction of the classification tree. Thirdly, it is robust to outlier variables, which rarely define splitting nodes. Another advantage is that the resulting classification trees are not affected by variable transformations, such as logarithmic transformation. Rpart can also use any combination of categorical and continuous predictor variables. In this study, however, only measurements of astragalus morphological features are used. A sixth advantage is that rpart handles missing predictor variable values by developing splitting rules based on alternate measurements that exhibit "strong concordance with the primary splitting variable at any given point on the tree" (Feldesman, 2002:258). This is



particularly useful for paleontological studies when fossils are incomplete or damaged. Finally, cases in rpart with unknown response variables can be placed in their own group and participate in tree construction. This is not possible in LDA. Groups with one or only a few cases must be excluded in LDA because it is not possible to construct a meaningful covariance matrix with small classes.

Rpart uses the binary recursive partitioning algorithm (BFOS algorithm) developed by Breiman et al. (1984) to examine all possible univariate divisions of the dataset. It creates a maximum number of branch points, calculated by the number of cases times the number of measurements used, to find the one that produces the greatest increase in classification accuracy (Feldesman, 2002). At each branch, cases are either selected to move left or right on the tree based on whether or not the value is greater than or less than the splitting value. To find the best split, the BFOS algorithm calculates the Gini diversity index for each possible split. Using this criterion, rpart then computes the ‘improvement’ in classification accuracy resulting from the proposed decision rule. The best split combines the greatest reduction in the Gini diversity index with the greatest improvement in the number of correct assignments (Feldesman, 2002). The sample is then split at the midpoint between the actual ‘best’ value and the closest, but larger, recorded value from the same variable. For a detailed explanation of these calculations, see Feldesman (2002).

Rpart also calculates Bayesian probabilities for each of the nodes. The highest Bayesian probability at each node is used to determine the node classification for each of the terminal nodes for the completed classification tree. These values are reported by

rpart (yprob) and are the values used here to describe the confidence value of a particular classification prediction.

In addition to these prediction probabilities, rpart also performs a ten-fold cross-validation of the complete rpart model. The program holds-out ten specimens at random and tests these held-out specimens against the model constructed from the remaining specimens. It only reports, however, the cross-validated error rate (xerror) at each of the nodes in the model. To determine a cross-validation for the model chosen, the total number of specimens 'misclassified' in the root node is multiplied by the xerror value. This gives the cross-validated number of misclassified specimens. To obtain the cross-validation for the model, the number of correctly classified specimens is then divided by the total number of specimens used in the model. Since rpart selects ten specimens at random each time the program is run, the xerror values will be slightly different each time. Therefore, to obtain a relative cross-validation for the model chosen, several of these cross-validations are calculated and an average cross-validation is computed.

Another feature of rpart is that the full classification tree, one that creates the most branches to minimize error, can be 'pruned' to balance the number of terminal nodes with the misclassification error rate. To determine if, or how much, pruning is necessary, Breiman et al. (1984) proposed the use of a cost-complexity parameter (CP) defined as:

$$CP = \text{Training Dataset Misclassification Rate} + \alpha * (\text{Number of Terminal Nodes}),$$

where  $\alpha$  is the penalty for each additional terminal node (Feldesman, 2002). In rpart, CP is computed as  $\alpha / (\text{root node relative error})$ . This actually makes CP and  $\alpha$  equivalent, since the root node relative error is normalized to 1.0 in rpart. The CP values can be interpreted as the improvement in fit compared to a tree with one less split (Feldesman,

2002). It also measures the accuracy lost by removing one or more terminal nodes, or ‘pruning.’

By comparing the calculated CP values against the cross-validated relative error, it is possible to make assertions regarding the appropriate size of the full classification tree. This is based on the idea that if an additional split does not improve the fit of a model enough to overcome the penalty of adding additional splits, a smaller tree may be appropriate. Rpart calculates a CP value for each of the nodes in the classification tree and can plot these values against the cross-validated error values described above. In addition, this CP plot also includes a horizontal line that indicates one standard deviation of the minimum xerror value. This 1 SE boundary is then used to decide if a model could benefit from pruning. The optimal tree can be chosen by identifying the largest tree with an xerror value that does not fall below this 1 SE line.

In this study, the Windows implementation of the binary recursive partitioning algorithm (rpart) created by Breiman et al. (1984) is used in conjunction with the open source statistical package, R (Ihaka and Gentleman, 1996). Both of these programs are available free for most operating systems at <http://www.r-project.org>. As with the discriminant analysis portion of the study, raw and size-corrected measurements were used for each of the habitat schemes to identify the best rpart model for the data.

To further examine the applicability of discriminant analysis for use in the ecomorphological study presented here, as well as to help choose which of the previous eight models may be most useful, the discriminant variates generated for each of the discriminant models were added to the raw and size-corrected measurements for each of the habitat schemes and run using rpart. As noted by Feldesman (2002) and originally

performed by Steinberg and Colla (1997), this type of combined model can help identify which type of statistical analysis is most appropriate for the dataset under study. If rpart chooses to use the discriminant variates as part of the resulting classification tree, LDA may be the better choice. Although, not mentioned in previous studies, if the resulting combined model is even more accurate than any of the previously examined exclusive models, it may also indicate that a combined model is the better choice overall for predicting classification of unknown data such as fossils.

Because accuracies assigned to each of these tests are the product of the dataset itself, the resulting accuracies represent a maximum. To thoroughly examine the accuracies of each of the resulting models, a series of validation tests were performed on each of the original models. In addition to the ‘automated’ cross-validations produced by SPSS for LDA and rpart, a similar jackknifing procedure is employed, following the method described by DeGusta and Vrba (2003), whereby one specimen from each species is held out. This procedure was repeated 24 times for each of the original models.

DeGusta and Vrba (2003) also performed further tests of the accuracy of each model in which a series of ‘generator tests’ were employed. Similar tests are utilized here. In the first of these tests, holding out all 24 specimens used in the jackknifing procedure created a ‘test’ sub-sample. The remaining specimens were then used as a ‘generator’ sub-sample to construct a model that was applied to the ‘test’ sub-sample. After completing this generalized ‘generator test,’ a series of ten randomized ‘generator tests’ were performed. In each of these, a random sample of 20 specimens (25% of the total sample) was held out as the ‘test’ sub-sample. The ten sets of random specimens were chosen by numbering the specimen list (1 - 81) and then using a randomized

sequence program available online at <http://www.random.org>. The ten randomized ‘test’ sub-samples were used for each of the classification models to maintain comparative consistency. The average of these ten generator tests is then compared to the automated cross-validated values obtained for each model to examine the validity of the automated tests.

As previously mentioned, the classification trees produced by *rpart* can be refined by what is called ‘pruning.’ Pruning simply removes those branches from the tree that may be superfluous. To assess which models may benefit from this procedure, the complexity parameter plots for each full model were examined. These figures plot the complexity parameter of the model against the cross-validated error and classification tree size. In addition, a horizontal line is placed on the graph at the value that represents one standard deviation from the cross-validation error for the largest tree. By visual inspection of this graph, it is possible to select a complexity parameter value at which to prune the full tree. In some cases, pruning is not necessary. Each of the full *rpart* models was subjected to this examination.

In addition to creating predictions for each of the known astragalus specimens, both LDA and *rpart* produce associated probability percentages. These confidence values are actually estimates that a particular specimen belongs to each of the habitat groups. The models then assign a specimen to the group with the highest probability. LDA also assigns a second most-likely habitat prediction for each of the specimens. In *rpart*, the probability value associated with the terminal node of the classification tree is the confidence value for that prediction. In an attempt to create a system for weighing each of these confidence values, a system proposed by DeGusta and Vrba (2003) is used here

for those specimens tested with the LDA models. They posed the question, “What confidence value would we have to use as the cutoff value to obtain a misclassification rate of less than 5%?” This value is equivalent to a  $p$ -value of 0.05 and, for this model, is equivalent to 4 of the total 81 specimens. The cutoff value is slightly different for each of the models tested. Specimens that fall below this cutoff value are considered ‘indeterminate.’ These ‘indeterminate’ specimens are not ignored but are used to assess the predictive strength of each of the models. Because rpart assigns a single confidence value at the terminal nodes, this type of test is not possible for the rpart models.

After the twelve modern models were constructed, fossil specimens from the Kedung Brubus and Trinil collections were included in each of the models as unclassified cases (habitat unknown) to predict the most likely and second most likely habitat categories. For the discriminant models, the Kedung Brubus and Trinil samples are simply added to the modern samples but are not assigned a habitat category. The SPSS program then assigns a most-likely and second most-likely prediction to each of the ‘unknown’ fossil samples, along with an associated confidence value. These confidence values will then be compared to the cutoff values calculated for the extant species models to aid in the selection of the most acceptable model. The rpart routine creates a classification tree using the extant bovid data. The fossil samples must then be ‘dropped down’ the tree to find their habitat classifications. The likelihood predictions for these specimens are based on the associated confidence values at each of the terminal nodes. Once the fossil astragalai have been tested using each of the constructed models, the results will be compared and an interpretation of the associated paleoenvironments will be presented.

## CHAPTER 4

### RESULTS

The results indicate that all twelve models constructed for the extant sample of bovids were at least two times better than chance for predicting habitat from the measurements taken. The combined models, however, had consistently higher accuracy percentages than any of the other individual models. Each of the models produced differing interpretations of the fossil data although some patterns were evident. All of these models will be examined below in greater detail, as well as the fossil sample results for each model.

#### FOUR-HABITAT MODELS

The summary statistics for the raw and size-corrected measurements are presented for the four-habitat grouping scheme (Tables A.3 and A.4) and for each species (Tables A.5 and A.6). The pattern of increase for the raw measurement variables by habitat is similar to that of DeGusta and Vrba (2003). The order of the variables from least to highest in the majority of cases is Forest, Light Cover, Heavy Cover, and Open. In two cases (WI and WD), Open and Heavy Cover are reversed, with Heavy Cover representing the maximum value. This is the pattern recorded by DeGusta and Vrba (2003). In only one case (LL), the means of the Open and Heavy Cover variables were identical. In all cases, the means of the Open and Heavy Cover categories were quite similar, most-likely

reflecting the large body size of the Southeast Asian bovids inhabiting these environments.

There is little discernable pattern for the size-corrected measurements. The positive values (LM, LI and LL) display a pattern from least to most of Light Cover, Heavy Cover, Open, and Forest. There is no discernable pattern for the WI, WD, TI, or TD measures, represented by negative values.

#### *Raw Measurements – Discriminant Analysis*

The discriminant function produced by SPSS correctly predicted habitat group for 63 of the 81 total extant bovid specimens in the sample, for an overall accuracy of 77.8% (3.1 times that expected by chance (25%) for a four-habitat model; see Table A.7). The analysis calculated three discriminant functions that accounted for 45.1, 34.1, and 20.7% of the variance, respectively (Table A.7). The matrix of the pooled within-group correlations showed that all of the variables were most strongly correlated with function 3. The specific misclassifications are presented by taxon in Table A.8.

The automated cross-validation test accurately predicted 70.4% of the held-out specimens to habitat class. This is better than the results of the jackknife procedure created by eliminating one specimen from each species (62.5%). The 24-specimen generator test correctly assigned 66.7% of the specimens to habitat class. The ten randomized generator tests produced accuracies ranging from 65% - 90%, with an average value of 73.5%. This is comparable to the automated cross-validation results. These validation tests indicate that the 77.8% accuracy of the model is a good



representative estimate. The results of all validation tests for the raw measurement four-habitat models appear in Table A.9.

In addition to the validation tests, an examination of the confidence values associated with each habitat prediction provides insight into the reliability of each prediction. For this model, an ‘indeterminate’ classification would be assigned to those specimens with confidence values less than 66% to produce a model with a 5% misclassification rate (4 misclassifications / 81 total specimens). This value will be taken into consideration when analyzing the fossil specimens.

Specimen misclassifications for this model were concentrated in two regards (Table A.8). Open specimens were misclassified in seven cases. Two of these specimens were the African species *Connochaetes taurinus*, all of which were classified as Open habitat in the work of DeGusta and Vrba (2003) but were classified as Light Cover in this study. Both *Procapra gutturosa* specimens were misclassified as Forest and all three *Pseudois nayaur* specimens were misclassified as Light Cover. These misclassifications may be related to the small body size of both species (30-50 kg). The other concentration of misclassifications occurred in the *Capricornis sumatraensis* specimens. Three of these Heavy Cover specimens were misclassified as Open and one as Light Cover. This may be the result of multiple habitat use within this species. In all other cases, specimens that were misclassified were classified into the next closest habitat category.

#### *Raw Measurements – Recursive Partitioning*

The rpart analysis produced only slightly less classification accuracy (74.1%) than the discriminant model. Rpart was able to correctly classify 60 of the total 81 specimens.

The resulting full classification tree is presented in Figure B.4. A total of five terminal nodes are present. To fully understand how the classification tree and associated splitting rules can be used to assign habitat classifications, however, a brief explanation using the raw measurements of *Bison bison* (UT 4945, Appendix C) is warranted.

The classification tree created by rpart for this model, uses only the LI, LL, TD, and TI metrics (Figure B.4). The first splitting rule, denoted as Node 2 and located at the top of the tree, asks if  $LI < 35.55$  mm.  $LI = 57.8$  mm for UT 4945. Therefore, the answer would be, “false,” and the researcher is directed to the right of the classification tree, or Node 3. The next splitting rule then asks if  $TI < 24.5$  mm. Again, for UT 4945, the answer is, “false,” and therefore leads to the right of the classification tree to the final splitting rule,  $LL \geq 79.95$  mm (Node14). The LL measurement for UT 4945 is 74.3 mm, thus leading to the right and to the terminal node “O,” or Open habitat. The yprob value, or probability that UT 4945 belongs to this habitat classification, is 0.73. These splitting rules are then applied to the measurements of all remaining specimens to obtain their habitat classification. In all subsequent classification tree figures, “true” responses lead to the left branch whereas “false” responses always lead to the right branch.

The results of the validation tests appear in Table A.9. The cross-validation test indicates an accuracy of 59.8%. The constructed jackknife test was able to correctly classify only 12 of the 24 held-out specimens. This is considerably less than the LDA results. The generalized ‘generator’ test was also less accurate, only correctly classifying 50% of the test sample. The randomized generator tests produced a wide range of accuracy percentages (45-80%). This wide range indicates that recursive partitioning is

quite sensitive to sample size and composition. The average of these ten tests (57.5%), however, is quite similar to the cross-validation test.

An examination of the complexity parameter plot (Figure B.5) shows a slight rise in the cross-validated relative error for the five terminal node tree. This indicates that, although trees with three, four, or five terminal nodes fall below the designated 1 SE cut-off value, there is a slight rise in the improvement in fit for a five-node model. It could be argued that this tree be pruned to result in only four terminal nodes, but the resulting prediction accuracy of this pruned tree (69.1%) decreases the overall value of the model. Therefore, the full model was selected for use in this study.

The confidence values assigned by rpart are different from those used in LDA. The confidence values (yprob) in rpart are assigned at each terminal node (Figure B.4). In the case of this model, rpart calculated only a 66.7% confidence value to the Forest classification category. Pruning the model as described above does not increase this confidence value. Therefore, if this value is used as the 'cut-off value' and all of these specimens are labeled as 'indeterminate,' the interpretive power of the model is lost due to the lack of any specimens identified to the Forest category. The second most-likely category for these specimens, according to the confidence values (20%), is the Heavy Cover category. Three of the misclassified Forest specimens were actually Heavy Cover species. Only two of the Forest misclassifications were Open, the third most-likely category according to the confidence values (13.3%).

Overall, most misclassifications in this model occurred in the Open and Heavy Cover categories (Table A.8). This is probably due to the similar means for the measurements in these two habitat categories (Table A.3). As in the LDA model, both of

the *Procapra gutturosa* were misclassified as Forest and all three *Pseudois nayaur* were misclassified as Light Cover. Again, this may be due to their small body size. The misclassifications, however, for *Capricornis sumatraensis* were slightly better in the rpart model. Only two specimens were misclassified. These were classified as Open and Light Cover, rather than Heavy Cover. The other misclassifications were primarily concentrated within the large-bodied species.

#### *Raw Measurements – Combined Model*

The combined model accurately predicted 79.0% of the specimens to habitat class. The rpart model was able to correctly classify 64 of the 81 specimens. Four terminal nodes are present in the full model (Figure B.6). The first two canonical variates generated by the LDA analysis are primary splitter variables at two of the three branches on this classification tree. According to Feldesman (2002), this indicates that LDA is a more appropriate technique for these data and it supports the assertion that LDA is robust to the violations of the required assumptions.

Based on the similarity between the values of the automated cross-validation and the average of the generator tests obtained from the previous independent models, the generator tests have been omitted from the combined model analyses. The cross-validated accuracy for this model is 68.9% (Table A.9). This is slightly better than the rpart analysis alone but is slightly worse than the LDA model. This may indicate that, although the overall accuracy of this combined model is better than the two individual models, the LDA model is still the better choice. The complexity parameter plot for this model (Figure B.7) confirms that pruning is unnecessary.

The confidence values for the terminal nodes of the combined rpart model are all quite high. The lowest confidence value (73.3%) was assigned to the Open habitat terminal node. There were no duplicate terminal nodes constructed by the model. Therefore, based on these confidence values, it would be unreasonable to exclude any predicted classification using this model.

The specific misclassifications for this model were concentrated primarily in the Heavy Cover category (Table A.8). Seven of the ten Heavy Cover misclassifications occurred in the *Capricornis sumatraensis* specimens. Of these seven specimens, five were misclassified as Open, one was misclassified as Forest, and one was misclassified as Light Cover. Taking into account the high confidence values associated with all of the predictions, these misclassifications further support the assertion that this species utilizes multiple habitat types. Both *Capricornis crispus* specimens were also misclassified, one as Forest and one as Light Cover. This specimen was classified as Heavy Cover based on its tendency to inhabit rugged mountains, covered with thick brush or forest (Nowak, 1991). The Forest misclassification here, and in the raw rpart model, may actually reflect this species true habitat. The Light Cover misclassification here, and in the LDA model, however, is less clear. Again, both *Procapra gutturosa* specimens were also misclassified. These Open habitat specimens were both misclassified as Forest. If body size is driving the misclassifications of *Capricornis* and *Procapra*, the size-corrected models should indicate this.

### *Size-Corrected Measurements – Discriminant Analysis*

Like the raw measurement model, the discriminant function produced by SPSS for the size-corrected measurements correctly predicted habitat group for 63 of the 81 bovid specimens (77.8%). The analysis calculated three functions that accounted for 65.1, 25.8 and 9.1% of the variance (Table A.10). The matrix of the pooled within-group correlations showed that the size-corrected variables LM, LL, LI, TD, and WI were most strongly correlated with function 1, WD with function 2, and TI with function 3.

The results of the size-corrected four-habitat validation tests appear in Table A.11. This model performed slightly poorer under cross-validation than the raw measurement model, with only 65.4% accuracy. The jackknife procedure, however, performed slightly better (66.7%). The 24-specimen generator test correctly assigned 75% of the specimens to habitat class. The ten randomized generator tests performed comparably, with accuracies between 60-80% and averaging 70.5%. These results are better than the cross-validation test and support the accuracy of the overall model. The results also indicate that, in this case, eliminating size has little effect on predicting habitat.

Whereas the confidence value cut-off for the raw measurement model was 66%, a 70% confidence value is applicable here. Therefore, any specimen with a confidence value less than 70% could be assigned an ‘indeterminate’ classification for use in determining the weight of the estimated predictions. It should be emphasized, however, that if this was applied to the current model, roughly 50% (41 out of 81) of the specimens would be classified as ‘indeterminate.’”

Specimen misclassifications were quite similar to the raw measurement model, with a few notable exceptions (Table A.12). Nine Open habitat specimens were misclassified. One *Bison bison* specimen was assigned to the Forest category and one *Bos javanicus* was given a Heavy Cover classification. Three *Connochaetes taurinus* specimens were also misclassified. Two were assigned to the Light Cover category, as in the raw measurement model, and one was classified as Heavy Cover. This model was able, however, to correctly classify one specimen each of *Procapra gutturosa* and *Pseudois nayaur*. These results indicate that body size may indeed play some role in predicting habitat class for bovid species but that it has little effect on the overall accuracy of the four-habitat LDA model.

#### *Size-Corrected Measurements – Recursive Partitioning*

The rpart size-corrected model produced a slightly higher accuracy percentage (77.8%) than the raw measurement model, indicating that rpart is sensitive to this type of data manipulation. This accuracy was equal to that of both LDA models. Rpart was able to correctly classify 63 of the 81 specimens. A full classification tree with five terminal nodes is presented in Figure B.8.

The cross-validated accuracy for this model is 67.2% (Table A.11). The jackknife test was able to correctly classify 79.2% of the held-out specimens to habitat class. This was the highest percentage of any of the individual models. The generalized ‘generator test’ was able to correctly classify 16 of the 24 test samples, while the randomized generator tests produced accuracies between 55-80% and averaged 66.0%. Again, this indicates that the cross-validated value is comparably useful for assessing model

accuracy. All of the validation results were equal to or better than the raw-measurement rpart tests.

The complexity parameter plot for the full model indicates that, although there is a slight rise in the cross-validated relative error in the five-terminal node tree, this model could benefit from pruning (Figure B.9). Pruning this model, using a complexity parameter cutoff of 0.08, results in a four terminal node model (Figure B.10). Rpart does not produce a table of the branching statistics for pruned models; therefore, this table is absent in the pruned classification tree figures. The complexity parameter plot shows that the cross-validated error for this pruned model intersects the 1 SE line at a complexity parameter that is only slightly lower than the fourth terminal node (Figure B.11). The resulting accuracy of the model is only slightly affected by pruning (75.3%) with a cross-validated accuracy of 66.7%. The pruned model reduces the accuracy of predicting the Open habitat category, but it increases the accuracy of predicting Light Cover specimens. The accuracies of the Forest and Heavy Cover categories are not affected. The resulting pruned model also eliminates the use of the WI measurement, which could be helpful when testing 'unknown' fossil samples that have been damaged. The pruned model will be used to test the fossil assemblages.

The full model produced two terminal nodes for the Open habitat class. One of these nodes had an associated confidence value of 79.2%, whereas the other had a confidence value of only 50%. The pruned model eliminates the 50% confidence value terminal node. Therefore, the lowest confidence value was then associated with the Light Cover category (60.7%). If this value were accepted as a 'cut-off' value all of the Light



Cover specimens would be deemed ‘indeterminate.’ It would be unreasonable to exclude any predicted classification using this model.

The majority of misclassifications occurred in the Heavy Cover category (Table A.12). Six of these misclassifications were of the species *Capricornis sumatraensis*. Three of these specimens were misclassified as Open, and three were misclassified as Light Cover. One specimen of the Light Cover species *Capra sibirica* was misclassified in this model, unlike the raw measurement model in which all specimens were correctly classified. Two specimens of the Open habitat *Damaliscus lunatus* were also misclassified in this model but all were correctly classified in the raw measurement model. These misclassifications indicate that the inclusion of body-size has a positive influence on the predictive power of the rpart analyses. Conversely, the elimination of body-size in this model permitted the accurate prediction of habitat for both specimens of *Procapra gutturosa*, which were incorrectly classified in both raw measurement models. Therefore, caution must be exercised when interpreting the prediction of unknown samples using either of these models, exclusively.

#### *Size-Corrected Measurements – Combined Model*

Like the combined raw model, the combined size-corrected model was able to correctly classify 64 of the 81 specimens (79.0%). Five terminal nodes are present in the full model (Figure B.12). The first two canonical variates generated by the LDA analysis are primary splitter variables at two of the four branches on this classification tree. Again, this indicates that LDA is most likely the appropriate technique for these data and

it further supports the assertion that LDA is robust to the violations of the required assumptions.

The cross-validated accuracy for the full model is 63.2%. This is worse than both of the individual size-corrected models. After examining the complexity parameter plot for the full model (Figure B.13), a complexity parameter pruning value of 0.07 was applied to refine this classification tree. The resulting ‘pruned’ tree produced a model with only four terminal nodes and an overall prediction accuracy of 76.5% (Figure B.14). The cross-validation value for this refined model (69.1%) is also comparable to the original model. The pruned model also utilized the first two canonical variates of the LDA analysis and will be used to test the fossil assemblages.

The confidence values for the terminal nodes of the pruned rpart model improve the distinction between the Light and Heavy Cover categories but are slightly lower for the Open habitat category. The lowest confidence value (65%) was assigned to the Open habitat terminal node. There were no duplicate terminal nodes constructed by the pruned model. Therefore, as in the previous combined model, it would be unreasonable to exclude any predicted classification using this model.

The majority of misclassifications for the combined model occurred in the Light Cover category (Table A.12). A total of nine Light Cover specimens were misclassified. Five of these misclassifications occurred in the *Capra sibirica* specimens. This is considerably worse than any other four-habitat model. These specimens were also misclassified in the full, ‘non-pruned,’ model previously discussed. There is no explanation as to why this model performed so poorly for this Light Cover species. Heavy Cover specimens were also frequently misclassified. Six *Capricornis*

*sumatraensis* specimens were misclassified in this combined size-corrected model. Again, this demonstrates that the elimination of body-size in the rpart models negatively affects habitat prediction for this species. An alternative explanation, however, is that the constructed habitat designations used in this study are invalid for these species. Both species will be assigned to the Mountain category in the five-habitat model examinations.

## FIVE-HABITAT MODELS

The summary statistics for the raw measurement and size-corrected five-habitat model measurements are presented for each habitat group in Tables A.13 and A14. There are two discernable patterns for the raw measurements in the five-habitat model (Table A.13). The order of the increase from least to most in four of the cases (LM, LI, LL, and WD) is Forest, Light Cover, Mountain, Open, and Heavy Cover. In the three remaining cases (WI, WD, and TD), the pattern of increase is Forest, Mountain, Light Cover, Open, and Heavy Cover. Whereas Heavy Cover and Open were most similar in the four-habitat model, average measurements for Light Cover and Mountain are most similar in this model. There is no discernable pattern for the size-corrected measurements (Table A.14).

### *Raw Measurements – Discriminant Analysis*

The discriminant function produced by SPSS correctly predicted habitat group for 60 of the 81 total extant bovid specimens in the sample, for an overall accuracy of 74.1% (3.7 times than expected by chance (20%) for a five-habitat model). The overall accuracy, therefore, is slightly less than that for the four-habitat model (77.8%). The analysis calculated four discriminant functions, accounting for 57.2, 22.7, 18.1, and 2.0%

of the variance (Table A.15). The matrix of pooled within-group correlations indicated that all of the variables were most strongly correlated with function 2 in this model. The specific misclassifications are presented by taxon in Table A.16.

The automated cross-validation test accurately predicted 65.4% of the held-out specimens to habitat class. This is lower than the results of the jackknife procedure created by eliminating one specimen from each species (75.0%). The jackknife procedure for this model actually produced the best results of the four LDA models. The 24-specimen generator test correctly assigned 62.5% of the specimens to habitat class. The ten randomized generator tests produced accuracies ranging from 60% - 80%, with an average accuracy of 68.5%. These results are similar to the cross-validation test. The range of accuracies for all of the validation tests indicates that the 74.1% accuracy of the model is a good representative estimate. A list of all accuracy values is presented in Table A.17.

For this model, an 'indeterminate' classification would be assigned to those specimens with confidence values less than 61% to produce a model with a 5% misclassification rate. For this model, 42% of the specimens would have to be classified as 'indeterminate,' using this criterion. Although the specimens with confidence values less than 61% are not eliminated from the analysis, the value will be used to assess the reliability of the fossil specimen predictions.

The majority of specimen misclassifications for this model occurred in the Mountain category (n = 11), though seven Open specimens were also misclassified (Table A.16). Of the reclassified Mountain species, all, except *Capricornis swinhoei*, resulted in some misclassifications. Two *Capra sibirica* specimens were misclassified as

Open and one was misclassified as Light Cover. Three *Capricornis sumatraensis* were also misclassified, one as Open and two as Light Cover. The remaining five Mountain category misclassifications occurred in *Capricornis crispus*, *Naemorhedus goral* and *Pseudois nayaur*. These species also had misclassifications in the raw, four-habitat model. With the exception of *Capricornis swinhoei* and *Pseudois nayaur*, the addition of the Mountain category made no noticeable improvement to habitat prediction and actually decreased the number of accurate predictions for *Naemorhedus goral*. Of the misclassified Open specimens, both *Procapra gutturosa* specimens were misclassified as Forest, as in the four-habitat model. Three of the *Connochaetes taurinus* specimens were also misclassified, two as Mountain and one as Light Cover. One *Damaliscus lunatus* specimen was also misclassified as Mountain. The misclassifications associated with *Procapra gutturosa* and *Pseudois nayaur* in both raw-measurement models strengthens the argument that this may be due to small body size. In all remaining misclassifications, specimens that were misclassified were classified into the next closest habitat category.

#### *Raw Measurements – Recursive Partitioning*

The result of the rpart analysis for the raw-measurement five-habitat model was an improvement over both the four-habitat rpart model and the LDA five-habitat model (75.3%). Rpart was able to correctly classify 61 of the 81 specimens. The full classification tree is presented in Figure B.15. A total of nine terminal nodes are present. An attempt was made to prune this classification tree. The resulting five-terminal node model, however, was slightly less accurate than the full model (71.6%; not shown). The full model will be used in this study for reasons described below.

The cross-validation test for the full model indicated an accuracy of 52.1%. The jackknife test was able to correctly classify only 12 of the 24 held-out specimens, as in the four-habitat model. This is still considerably less than the LDA model. The generalized 'generator' test was the least accurate of all models tested. For this model only 37.5% of the test sample was correctly classified. The randomized generator tests again produced a wide range of accuracy percentages (25-60%) with an average accuracy of 55.5%, considerably worse than any other model. The examination of the complexity parameter plot further confirms the inadequacy of this particular model (Figure B.16). The plot indicates that the only suitable tree for this dataset would be one with only two terminal nodes. This is clearly not acceptable for the purpose of constructing a five-habitat prediction model. Therefore, the full model will be used simply for the point of comparison between all constructed models. The validation results strengthen the argument that rpart is sensitive to sample size. These results also indicate that for this small sample, the cross-validation test is a good representation of the validity of the full model.

For the full model, rpart created two terminal nodes for the Open, Light Cover, Heavy Cover, and Mountain categories. Of these, each of the secondary terminal nodes for the Light Cover and Heavy Cover categories had associated confidence values of only 50%. If this value is chosen as the cut-off value, eight of the Light Cover specimens and ten of the Heavy Cover specimens would be assigned an 'indeterminate' classification. The model correctly classified four of these Light Cover specimens, one was originally classified as Forest, and three were originally Mountain. The Heavy Cover predictions were accurate for four specimens, but misclassified two Forest and three Open category

specimens. If these specimens were eliminated from the model, the resulting accuracy would increase to 84.1% (53 correctly classified / 63 total specimens).

Most misclassifications in this model occurred in the Open and Mountain categories (Table A.16). Six of the reclassified *Capricornis sumatraensis* specimens were misclassified. Three specimens were each assigned to the Open and Light Cover categories. The only other Mountain misclassification occurred in one specimen of *Pseudois nayaur*. Overall, this rpart model was better able to predict the reclassified Mountain specimens than any other model. Of the misclassified Open specimens, the two *Bubalus bubalis* specimens and three of the *Connochaetes taurinus* specimens were misclassified as Heavy Cover, whereas the two *Procapra gutturosa* specimens were misclassified as Forest. Again, the misclassified *Procapra gutturosa* specimens suggest that small body size is driving the habitat prediction for this species. It is also interesting to note that this model was unable to correctly classify any of the members of the genus *Bubalus*.

#### *Raw Measurements – Combined Model*

The combined five-habitat, raw measurement model accurately predicted 83.9% (68 of 81) of the specimens to habitat class. This was the highest accuracy of all models examined. Five terminal nodes are present in the full model (Figure B.17). There is no reason to prune this classification tree. The first and third canonical variates generated by the LDA analysis are primary splitter variables at two of the four branches on this classification tree. The remaining two branches utilized the LM measurement twice. The

use of the canonical variates confirms that the LDA model is the better of the two individual models.

The cross-validated accuracy for this model is 66.9%. This is better than both of the individual models for the five-habitat, raw measurements. This may indicate that a combination of the parametric and non-parametric data is the best choice for predicting specimens in a five-habitat model, based on raw measurements, though considerably labor-intensive. It can be seen in the complexity parameter plot that this model will not benefit from pruning (Figure B.18).

The lowest confidence values occurred at the Forest (71.4%) and Light Cover (70.6%) terminal nodes, though these values are still respectable. There were no duplicate terminal nodes constructed by the model. Therefore, based on these confidence values, it would not be reasonable to exclude any predicted classification using this model.

The specific misclassifications for this model were concentrated primarily in the Mountain category (Table A.16). Five of these misclassifications occurred in the *Capricornis sumatraensis* specimens. Three were misclassified as Open and two were misclassified as Light Cover. Taking into account the high confidence values associated with all of the predictions, these misclassifications further support the assertion that this species utilizes multiple habitat types. Two of the *Capra sibirica* specimens were also misclassified as Light Cover. All of the *Capra sibirica* specimens were correctly classified in the raw measurement rpart model, but three of these specimens were misclassified in the LDA model. These three specimens, however, only included one of the two specimens misclassified in this combined model. Both *Procapra gutturosa* specimens were also misclassified. These Open habitat specimens were both



misclassified as Forest. This is not surprising, since these specimens were both misclassified as Forest in all of the raw measurement LDA and rpart models, including the four-habitat models. The size-corrected analyses should indicate if body-size is influencing the misclassifications.

#### *Size-Corrected Measurements – Discriminant Analysis*

The discriminant function produced by SPSS for the five habitat size-corrected measurements correctly predicted habitat group for only 56 of the 81 bovid specimens (69.1%), the worst results of any tested model. The analysis produced four discriminant functions that accounted for 53.0, 36.5, 9.1, and 1.4% of the variance (Table A.18). The pooled within-groups covariance matrix showed that the variables LL, TD, LM, and WI were most strongly correlated with function 1, WD with function 3, TI with function 3, and LI with function 4.

The results of the validation tests appear in Table A.19. Under cross-validation, the model only produced 59.3% accuracy. The jackknife procedure, though, performed slightly better than the automated cross-validation (62.5%). The 24-specimen generator test correctly assigned 62.5% of the specimens to habitat class. The ten randomized generator tests performed comparably, with accuracies between 45-75%. Again, this indicates that the overall model accuracy of 69.1%, while less than the other models, is probably a good estimate. The elimination of size from the five-habitat model, however, may have contributed to this decreased accuracy. The confidence value cut-off for this model is 65%.

Specimen misclassifications, compared to the raw measurement model, increased primarily for those specimens in the Mountain category (Table A.20). More than 50% of the Mountain specimens (13 / 25) were misclassified, indicating that this category may not lend much to habitat prediction. Eight Open habitat specimens were also misclassified. As in the four-habitat model, one *Bison bison* specimen was assigned to the Forest category. Only one of the *Procapra gutturosa* specimens was misclassified in this model, but four *Connochaetes taurinus* specimens and two *Damaliscus lunatus* specimens were misclassified. The misclassified specimens, unfortunately, do not display a discernable pattern of misclassification comparable to the previous models.

#### *Size-Corrected Measurements – Recursive Partitioning*

Rpart was able to correctly classify 63 of the 81 specimens (77.8%) in this model, 3.9 times better than chance for a five-habitat model. This accuracy percentage is equal to that of both four-habitat size-corrected models and the raw measurement four-habitat LDA model. This is considerably better than the size-corrected five-habitat LDA model and only slightly better than either of the raw measurement five-habitat models. It also supports the assertion that rpart responds favorably to size-corrected measurements. A full classification tree with six terminal nodes is presented in Figure B.19.

The cross-validated accuracy for this model is 60.7%, while the jackknife test was able to correctly classify 70.8% of the held-out specimens to habitat class (see Table A.17). The generalized ‘generator test’ was only able to correctly classify 54.1% of the test samples, while the randomized generator tests produced accuracies between 35-80%. The average of these tests (55.5%) was only slightly lower than the cross-validation

value. All of the generator tests applied to this model, with the exception of ‘generator tests five, six, and nine,’ were equal to or better than the raw-measurement rpart tests. The complexity parameter plot (Figure B.20) indicates that addition of a sixth terminal node is a slight improvement to a model with only five terminal nodes. Therefore, this model was not pruned.

Two of the terminal nodes in this model predict the Forest habitat class. One of these nodes has an associated confidence value of 71.4%, whereas the other has a confidence value of only 57.1%. If 57.1% is accepted as a ‘cut-off’ value, seven specimens would be considered ‘indeterminate.’ Of these specimens, four were correctly classified as Forest. The remaining three were all originally classified as Mountain, the second most-likely habitat classification (42.9%). With the elimination of these seven specimens, the overall accuracy of the resulting model would only increase to 79.7% (59 correctly classified / 74 total specimens). Therefore, the use of associated confidence values in this model may contribute little to the interpretation of unknown datasets.

The majority of misclassifications in this model occurred in the Mountain category (Table A.20). Three of these misclassifications occurred in the *Naemorhedus goral* specimens. The specimens were misclassified as Forest, which was the habitat classification of this species in the four-habitat model. It is interesting to note that, in general, the reclassification of species using the Mountain habitat category neither improved nor worsened the predictions of the size-corrected models. Three specimens of the Open habitat species *Connochaetes taurinus* were also misclassified, one each as Heavy, Forest, and Mountain. Only one of the specimens of the Light Cover species *Capra sibirica* was misclassified in this model. As in the four-habitat models, size-

correction did not improve the predictive power of the model for this species. It did, however, accurately predict both specimens of *Procapra gutturosa*, just as it did in the four-habitat model.

#### *Size-Corrected Measurements – Combined Model*

The full, combined size-corrected model was able to correctly classify 66 of the 81 specimens (81.5%), with a cross-validated accuracy of 60.0% (Table A.17). This is greater than all of the models tested. Six terminal nodes, however, are present in the full model (Figure B.21). The complexity parameter plot is unique in that the cross-validated relative error associated with the six-terminal node model actually increases to a value about the 1 SE pruning point after dipping below this value for a four or five terminal node model (Figure B.22). It can therefore be argued that the full model is the preferred choice. The first two canonical variates generated by the LDA analysis are primary splitter variables at two of the five branches on this classification tree.

The model produced two terminal nodes for the Forest category. The confidence values associated with the nodes are 57.1% and 71.4%, as in the individual rpart size-corrected model. If 57.1% is accepted as a ‘cut-off’ value, seven specimens would be considered ‘indeterminate.’ Of these specimens, four were correctly classified as Forest. The remaining three were all originally classified as Mountain, the second most-likely habitat classification (42.9%). With the elimination of these seven specimens, the overall accuracy of the resulting model would be 85.1% (63 correctly classified / 74 total specimens). The use of associated confidence values in this model may contribute to the interpretation of unknown datasets.

As in both of the individual size-corrected measurement models, the majority of misclassifications occurred in the Mountain category (Table A.20). Six of these Mountain specimens were misclassified as Open, whereas the remaining four were misclassified as Forest. Only two *Capricornis sumatraensis* specimens were misclassified, one as Forest and one as Open. As in the individual models, two of the three *Pseudois nayaur* specimens were misclassified, however both were misclassified as Open in this model. Three of the five *Naemorhedus goral* specimens were misclassified as Forest. This is identical to the individual size-corrected rpart model. All of the Heavy Cover and Forest category specimens were correctly classified. This indicates that the addition of the Mountain category may be of no significance to those specimens within that category, but the addition of the category improves the predictive power of the analysis for other categories. It may serve to minimize the ‘noise’ associated with the four-habitat models. The only other concentration of misclassifications occurred in the Forest category. The inconsistencies and patterns observed in all twelve of these models will be taken into account as each is applied to the fossil collection and used to make a final decision regarding the model(s) of choice for use in predicting habitat for fossil bovid specimens from Southeast Asia.

## FOSSIL SAMPLES

The results of the fossil analyses appear in Table A.21. Although the results differ for each of the test models constructed, a common trend is evident. In all cases, the percentage of Open habitat specimens increases from the Trinil to Kedung Brubus faunas. There is also a subsequent decrease in the percentage of Heavy Cover specimens

between the two faunas. These trends, and others, will be examined in greater detail for the results obtained from the fossil analyses.

*Trinil – Four Habitat Model, Raw Measurements*

The habitat classifications for the Trinil specimens and the probabilities of their assignment to that group for each of the models are given in Table A.22. In all three models, Heavy Cover specimens are three times more abundant than Open category specimens. The only model to classify all of the *Duboisia santeng* specimens to one habitat type was the combined raw measurement model. In this model, all of these specimens were classified as Forest.

In addition to the probability of assignment, those confidence values for the LDA model that did not meet the confidence value ‘cut-off’ (66%) are indicated by boldface type. For this model, 17 predictions fell below this value. Of these specimens, seven were classified as Open, as the most likely habitat classification. The second most-likely category predicted for these seven specimens included three Light Cover, one Heavy Cover, and three Forest. The three Forest specimens were all *Duboisia santeng*. Five of the Trinil fossils that failed to meet the 66% cut-off were Heavy Cover specimens. The second most-likely category for four of these specimens was Open. One was also predicted as Light Cover as the second most-likely category. Three Light Cover specimens also had prediction probabilities below the cut-off value. Of these, two were classified as Heavy Cover and one as Forest as the second most-likely group. The Forest specimen was a *Duboisia santeng* specimen. Two of the *Duboisia* specimens, classified

as Forest, also fell below the cut-off value. In both cases, the second most-likely grouping was the Open category.

Only three of the *Duboisia santeng* specimens were identified as Forest in the raw measurement rpart model. Eleven *Duboisia* were predicted to be Light Cover habitat specimens. In the combined model, however, all 14 *Duboisia* specimens were classified as Forest. This consistency would be expected for specimens from one species that occupy a single, well-defined habitat. Although the combined model for the extant species demonstrated that of the individual models the LDA method is preferred, clearly the combined model has refined the results. No specimens were predicted as Light Cover in this model. This, combined with the consistent classification of *Duboisia santeng* into one habitat type is an argument for the use of this combined model for predicting unknown fossil specimens from Southeast Asia.

#### *Kedung Brubus – Four Habitat Model, Raw Measurements*

The predicted habitats for the Kedung Brubus specimens and their associated prediction probabilities for the three raw measurement models appear in Table A.23. The most abundant habitat prediction for this collection was the Open category in all three models. The second most abundant category was Heavy Cover. Open specimens were more than twice as abundant in the LDA model, whereas in the individual and combined rpart models these specimens are more than three times as abundant. All three models classified the single *Duboisia santeng* specimen as Forest. No other specimens were classified as Forest.

Four specimen predictions fell below the 66% cut-off value for the LDA model. Two of these were Open specimens. In both cases, the second most-likely habitat prediction was Heavy Cover. One Heavy Cover specimen and one Light Cover specimen also fell below the cut-off value. The second most-likely classification for each of these specimens was the Open habitat category.

Although both rpart models classified the *Duboisia santeng* specimen as Forest, the prediction for the individual rpart model had an associated confidence value of only 66.7% (see Table A.23). The second most-likely category according to the rpart model was Light Cover. This is not surprising considering that the individual rpart model for the Trinil sample presented above classified 11 of the 14 *Duboisia* specimens as Light Cover. The combined rpart model for this sample did not classify any specimens to the Light Cover category. This was also the case for the Trinil sample. The apparent refinement of the results by the combined model may be a positive feature of this type of analysis.

#### *Trinil – Four-Habitat Model, Size-Corrected Measurements*

The results of the four-habitat size-corrected analysis of the Trinil sample appear in Table A.24. As in the raw-measurement analysis, Heavy Cover specimens dominate all three models. The pruned rpart models, however, only show approximately twice as many Heavy Cover specimens as those classified as Open. The LDA model was more similar to the raw-measurement results described above. No model classified all of the *Duboisia santeng* specimens in a single category, though both rpart models classified all but one specimen as Forest. In both cases, the models classified this individual as Open.



The confidence value cut-off for the four-habitat size-corrected LDA model is 70%. A total of 40 specimens fell below this cut-off value (Table A.24). This is 45% of the entire Trinil sample. The majority of these specimens were those predicted to most likely be Heavy Cover specimens (n = 18). The second most-likely classification for these specimens was most frequently to the next closest group, Light Cover; however, the second most-likely classification of seven specimens was the Open habitat category. Twelve of the Open habitat specimens also fell below the cut-off value. In six cases, the second most-likely classification was Heavy Cover. Five specimens were classified as Forest as the second most-likely category; four of these were *Duboisia santeng* specimens. The remaining specimen had a second most-likely prediction value as Light Cover. All but one of the Light Cover specimens that fell below the cut-off value, were classified as Heavy Cover as the second most-likely habitat grouping. Of the three Forest specimens with prediction probabilities below 70%, the second most-likely predictions for two were Open and one as Heavy Cover. The high number of specimens failing to have prediction probabilities greater than the cut-off value indicates that although the raw measurement and size-corrected measurement models had identical accuracies for the extant samples, the raw measurement model may be the better choice for analysis of unknown samples in a four-habitat model.

The pruned rpart models both predicted fewer Heavy Cover and more Open habitat specimens from the Trinil sample than any of the other four-habitat models (Table A.24). In addition, the pruned individual rpart model classified more specimens as Light Cover than any of the other Trinil sample models (15.7%). While the results of the pruned model for the individual rpart model were quite similar to the ‘un-pruned’ full

model (results not shown), the results of the full combined rpart model were more consistent with the size-corrected LDA model and all of the raw-measurement models than the pruned version. This indicates that, while the pruned combined model produced a classification tree with fewer branches, the slight reduction in accuracy observed in the extant model may be amplified when used to classify unknown samples. Alternatively, these pruned models may actually represent a true classification of the fossil sample that the other models fail to discriminate. There is, unfortunately, no way to know for certain in either case.

*Kedung Brubus – Four-Habitat Model, Size-Corrected Measurements*

The results of the Kedung Brubus sample for this series of models are less dramatic than those for the raw measurement model. Although there is still a relative decrease in Heavy Cover specimens and an increase of Open specimens, compared to the results of the Trinil sample, Open cover specimens do not dominate all three models (Table A.25). Heavy cover specimens were more abundant in the LDA model (44.4%). Open cover specimens, however, were more abundant in both rpart models. The combined, pruned, rpart model results were more consistent with the raw measurement models presented previously. All three models classified the single *Duboisia santeng* specimen as Forest.

Surprisingly, 72% of the specimens tested failed to meet the 70% confidence value cut-off for the LDA model. Four specimens were not classified due to a lack of one or more measurements. Therefore, only five specimens met the cut-off value. Specimens failing to meet the cut-off were not concentrated in any particular habitat category. The

majority, however, were Heavy Cover specimens. In these six cases, the second most-likely category was the Open habitat category. Of the specimens classified as Light Cover, none met the 70% cut-off value. These poor results argue against the use of size-corrected measurements when attempting to predict habitat for unknown specimens.

The individual rpart model predicted a similar percentage of Open habitat specimens as the LDA model, but roughly half as many as the combined rpart model (Table A.25). Additionally, the individual rpart model also predicted more Light Cover specimens than any other model tested. This is undoubtedly due to pruning of the original full model. The full model failed to predict any Light Cover specimens (not shown), but the pruned model replaced five Open habitat specimens with Light Cover predictions. These Light Cover specimens have a prediction probability of only 60.7% and replaced those Open habitat specimens with only a 50.0% prediction probability in the original full model. The combined rpart model produced results similar to the raw measurement models.

#### *Trinil – Five-Habitat Model, Raw Measurements*

The habitat classifications of all fossil specimens and the probabilities for their assignment to that group for each of the models are given in Table A.26. In the LDA and combined rpart models, Heavy Cover specimens are five times more abundant than Open category specimens. The Heavy Cover specimens in the individual rpart model are approximately four times as abundant as the Open habitat specimens. As in the raw measurement four-habitat models, the only model to classify all of the *Duboisia santeng*

specimens to one habitat type was the combined model. In this model, however, all of these specimens were classified as Mountain.

The confidence value cut-off for the LDA model is 61%. Eleven predictions fell below this value. Of these specimens, all but two were *Duboisia santeng* specimens. The *Duboisia* specimens that fell below the cut-off value were comprised of four Mountain, three Forest, and two Open specimens. In all of the Mountain cases, the second most-likely category was Forest. The second most-likely predictions for the Forest specimens were Open in one case and Mountain for the remaining two. This apparent assignment conflict between the Mountain and Forest categories was also apparent in the extant specimens of *Bubalus mindorensis*, *Bubalus depressicornis*, and *Naemorhedus goral*. The two Open specimens were both predicted to be Mountain as the second most-likely category. The two remaining Bovidae samples that did not meet the cut-off value were Open and Light Cover specimens. The second most-likely categories for these specimens were Light Cover and Open, respectively.

Eight of the *Duboisia santeng* specimens were identified as Mountain in the raw measurement rpart model. The remaining six specimens were classified as Light Cover, similar to the raw measurement four-habitat rpart model. All 14 *Duboisia* specimens were classified as Mountain in the combined rpart model. As mentioned in the previous four-habitat model results, this consistency would be expected for specimens from a single species. The classification of these specimens to the Mountain category in this model, however, indicates that this species may have been adapted to both Forest and Mountain habitats. This is comparable to the extant species *Naemorhedus goral* and, to a lesser extent, *Capricornis sumatraensis*. The results of the combined rpart model again

demonstrate its ability to refine the individual results. No specimens were classified as Light Cover or Forest in this model.

*Kedung Brubus – Five-Habitat Model, Raw Measurements*

The predicted habitats for the Kedung Brubus specimens and their associated prediction probabilities for the three raw measurement models appear in Table A.27. The most abundant habitat prediction for this collection was the Open category in all three models. The second most abundant category was Heavy Cover. Open specimens were more than twice as abundant in the LDA and combined rpart model, whereas they are four times more abundant in the individual rpart model. The LDA and individual rpart models classified the single *Duboisia santeng* specimen as Forest. The combined rpart model classified this specimen as Mountain. No other specimens were classified as Forest or Mountain.

Three specimen predictions fell below the 61% cut-off value for the LDA model. Two of these were Light Cover specimens. In both cases, the second most-likely habitat prediction was Open. One Open habitat specimen also fell below the cut-off value. The second most-likely classification for this specimen was Light Cover.

The rpart models produced conflicting results for the *Duboisia santeng* specimen. Although the individual rpart model is consistent with the four-habitat classifications of *Duboisia* as Forest, the combined model is consistent with the Trinil five-habitat model results presented previously. The second most-likely category for this Mountain specimen according to the combined rpart model was Forest. The combined rpart model for this sample did not classify any specimens to the Light Cover or Forest categories.

The results of the LDA and individual rpart models, however, are quite similar to their four-habitat model counterparts.

*Trinil – Five-Habitat Model, Size-Corrected Measurements*

The results of the five-habitat size-corrected analysis of the Trinil sample appear in Table A.28. As in all previous analyses, Heavy Cover specimens dominate all three models, though the relative percentages of these specimens decrease slightly compared to the raw measurement model results. The LDA and individual rpart models also show a slight decrease in Open habitat specimens but an increase in Mountain classifications. The converse is true for the combined rpart model. No model classified all of the *Duboisia santeng* specimens to a single category.

The confidence value cut-off for the five-habitat size-corrected LDA model is 65%. More than 50% of the total specimens failed to reach this value. A total of 45 specimens fell below the 65% cut-off value (Table A.28). These poor results are consistent with the size-corrected models presented previously. Most of the specimens were Mountain specimens (n = 17). The second most-likely classification for the majority of these specimens was Heavy Cover; though five were predicted to be Open and two were predicted to be Light Cover. There appears to be no pattern to the second most-likely categories for the specimens failing to meet the confidence value cut-off. Likewise, there is no consistent pattern to the predictions associated with the *Duboisia santeng* specimens in this model.

The results of the individual rpart model were quite similar to the LDA model results, with the exception of the Heavy Cover and Forest category predictions (Table

A.28). Fewer Heavy Cover specimens were identified in the rpart model, whereas Forest specimens more than doubled. The combined model again appears to be a refinement of the two individual models, but it failed to eliminate the Light Cover category as in previous models. The relative percentages are, however, similar to both of the individual models.

*Kedung Brubus – Five-Habitat Model, Size-Corrected Measurements*

The results of the five-habitat, size-corrected Kedung Brubus sample are similar to those of the four-habitat, size-corrected model. Neither model resulted in an overwhelming dominance of Open habitat specimens. In fact, the percentage of Open and Heavy Cover specimens in the LDA model were identical (Table A.29). Open cover specimens, however, were more abundant in both rpart models. The combined rpart model results were more consistent with the raw measurement models presented previously. All three models classified the single *Duboisia santeng* specimen as Forest.

Although the percentage of specimens failing to meet the 65% confidence value cut-off was not as high as the size-corrected four-habitat Kedung Brubus results, a still remarkable 61% of these specimens failed to meet this value. Specimens failing to meet the cut-off were not concentrated in any particular habitat category. These poor results further argue against the use of size-corrected measurements when attempting to predict habitat for unknown specimens.

The individual rpart model predicted an identical percentage of Open habitat specimens as the LDA model (38.9%). The combined model predicted 50% of the specimens as Open. The two Light Cover specimens in the individual rpart model were

predicted as Open in the combined rpart model. Therefore, if these specimens were removed from the analysis, the results of the two rpart models would be identical.



## CHAPTER 5

### DISCUSSION

Several models were tested in this research for their applicability in interpreting habitat from the astragalus for Southeast Asian bovids. Although all of the models tested favorably, a summary of the results for the extant species reveals that there are strengths and weakness for each of the models. These strengths and weaknesses are also reflected in the interpretation of the fossil specimens. Overall, the combined four and five habitat models provide the most refined, and most accurate results in this study. Also, according to the criterion asserted by Feldesman (2002), the results of the combined models indicate that LDA is robust to the violation of the assumptions of normality and equal covariance. The summaries will be presented and an interpretation of the results in terms of their contribution to the paleoenvironmental reconstructions for the Trinil H.K. and Kedung Brubus faunas will be addressed. The degree to which these results can provide insight into the behavior of *Homo erectus* will also be discussed.

#### EXTANT SPECIES

The results of the extant model constructions indicate that while size-corrected measurements increased the classification accuracy of some species, such as *Procapra gutturosa*, the majority did not. In both cases of the LDA size-corrected models, the predictions were associated with poor confidence values. This indicates that body size contributes to the predictive power of parametric analyses. The non-parametric rpart

models, however, performed better using size-corrected measurements. The combination of the two types of analyses produced the best overall results.

The use of size-corrected measurements aided the interpretation of habitat use for those species whose habitat predictions were neither improved nor worsened, compared to the raw-measurement models. Species such as *Capricornis sumatraensis* were misclassified in similar numbers for both types of testing. Since body size did not appear to be driving the predictions of this species, it can be concluded that this species is adapted to and ranges over a variety of habitat types.

The results also indicate that the addition of a Mountain category to the ecomorphological analysis of Southeast Asian bovids may be unwarranted. Although the combined five-habitat models produced the highest prediction accuracies of all models tested, the prediction probabilities associated with the LDA analyses and the cross-validation values associated with the rpart models indicate that, overall, these model accuracies are suspect. In most cases, the addition of the Mountain category did little to improve the misclassification rate of those species reclassified as Mountain in the models. Instead, the high accuracies most likely reflect the improvement in classification of the species associated with the remaining four habitat types. This is particularly true for the five-habitat size-corrected LDA model.

## FOSSIL PREDICTIONS

The fossil analyses clearly demonstrate a change in the relative abundance of Heavy Cover and Open habitat specimens from the older Trinil sample to the younger Kedung Brubus sample. The percentage of Heavy Cover species decreases as the

percentage of Open habitat species increases. This is consistent with the current environmental reconstructions based on fossil assemblage compositions for the Trinil and Kedung Brubus faunas (de Vos et al., 1992, 1994). A more thorough examination of the paleoenvironmental interpretation is presented below.

An additional feature of the fossil analyses was the ability to test the predictions associated with a known fossil species, *Duboisia santeng*. The inclusion of this species not only allowed for prediction of its most likely habitat type, but it also aided in choosing which of the models constructed for the extant species is most useful. It is reasonable to conclude that those models that accurately predicted all members of this species to one habitat type are most effective. In the case of these models, only the combined raw-measurement models were successful. It is interesting, though, that this species was classified as Forest in the four-habitat model but was classified as Mountain in the five-habitat model. Although it is believed that this endemic fossil species is most closely related to *Boselaphus tragocamelus* (Hooijer, 1958), defined as Heavy Cover in this study, its functional adaptation to both of these environments would suggest a behavioral similarity to *Naemorhedus goral*.

Based on all of the results, it can be argued that the four-habitat combined raw-measurement model is the most applicable model for the ecomorphological analysis of Southeast Asian bovids, though the addition of the Mountain category provided insight into the predicted habitat preference of *Duboisia* that would not have been possible if the four-habitat model was used exclusively. The combined four-habitat model was able to correctly classify 79% of the modern specimens. This is 3.2 times better than chance

(25%) and better than the accuracy results of the ecomorphological model for the astragalus of African species (67%; see DeGusta and Vrba, 2003).

## PALEOENVIRONMENTAL RECONSTRUCTION

The paleoenvironmental reconstructions for the Trinil H.K. and Kedung Brubus faunas, based on faunal composition and limited palynological studies, have been limited to relatively vague interpretation. The Trinil H.K. fauna has been associated with an ‘open woodland’ environment, whereas the environment associated with the Kedung Brubus fauna has been interpreted as a ‘dry, open woodland’ environment (de Vos et al., 1992, 1994). This study has provided an empirical test of these interpretations. The results support the current paleoecological reconstructions; however, by coupling the fossil results of the combined four-habitat model with the previous reconstructions, a more detailed view has been provided for these paleontologically and anthropologically important faunal groups.

### *Trinil H.K.*

The large number of bovids in this fauna was previously interpreted as being indicative of a relatively dry biotope (de Vos et al., 1994) and was corroborated by studies of the avian fauna (Weesie, 1982; de Vos et al., 1994). This study has shown that the generalized view of large-bodied bovids as indicators of open environments needs revision. The large-bodied bovids of Java appear to be adapted not only to open environments but also to environments classified here as Heavy Cover. In fact, Heavy Cover specimens dominate the Trinil H.K. collection from Trinil (70.8%). The

abundance of the endemic *Duboisia santeng* also indicates that forests were most likely an important part of the environmental landscape.

The dominance of grasses in the fossil pollen record of the Bapang (Kabuh) Formation at Sangiran has been used to support the previous interpretation of an open woodland environment (Semah, 1982). The Trinil H.K. fauna are also found within the Grenzbank formation at Sangiran. Therefore, the pollen diagram associated with the Grenzbank and Lower Bapang formations will be reviewed in greater detail in an attempt to reconcile the results of the faunal data (Figure B.23). It must be emphasized, however, that the palynological results may only reflect local phenomena at the Sangiran site and may not reflect the entire environmental setting associated with the Trinil H.K. fauna or the site of Trinil during this time.

The pollen associated with the Grenzbank formation is consistent with an interpreted dry, open environment (Figure B.23). Grasses (Gramineae) and herbs (Compositae) dominate this sample. Some herb and shrub pollen from the Euphorbiaceae is also present. Tropical sedges (Cyperaceae), which inhabit damp or marshy environments (Jones and Luchsinger, 1986), are absent in the Grenzbank sample. There is limited evidence for arboreal pollen from the tropical and subtropical Mimosaceae, Papilionaceae, Caesalpiniaceae, and Moraceae / Urticaceae. A trace amount of pollen from the evergreen conifer, *Podocarpus*, is also present.

Gramineae pollen continues to dominate the pollen sample from the Lower Bapang (Kabuh) formation (Figure B.23). There is a distinct change, however, in this sample. Compositae are absent, whereas ferns (*Pteris* spp.) appear to proliferate. Herbs and shrubs such as Chenopodiaceae increase and Rosaceae appear. There is also a return,

though limited, of the marsh-dwelling Cyperaceae during this period. Papilionaceae and Caesalpiniaceae are still present in this sample. Pollen from the evergreen, *Podocarpus*, is relatively more abundant than the preceding Grenzbank formation. Semah (1982:169) notes that the pollen from the uppermost portion of the diagram (Figure B.23) “cannot be quantitatively interpreted because of the small number of grains counted and because of the nature of the sediment.” These data appear as open bars in the figure. The reported samples, however, are also small (n = 111 and 114), thus making any interpretation of the Sangiran pollen sample preliminary.

A cursory examination of the pollen data, particularly the dominance of Gramineae, does not appear to agree with the bovid results presented here. There are some details of the Lower Bapang (Kabuh) sample, however, that need to be addressed. Primarily, the abundance of ferns suggests that dry, open conditions were not uniform during this period. Many ferns thrive in cool, moist, shady habitats, particularly in areas of high humidity. The assertion of a moist habitat is supported by the presence of Cyperaceae pollen. This presence of marsh-adapted plants implies that the open habitat grasses did not extend to the edges of water sources. Further, tropical Papilionaceae and Caesalpiniaceae shrubs may have also inhabited these areas. *Podocarpus* is probably not associated with these wet environments. Semah (1982) reports that *Podocarpus* pollen is not local but comes from forests at higher altitude.

This reinterpretation of the pollen record from Sangiran, coupled with the results of the ecomorphological analysis, provides evidence of a more detailed view of the paleoenvironment associated with the Trinil H.K. fauna. The environment at this time may be better described as open grasslands, broken by areas of dense vegetation

surrounding fluvio-lacustrine features. There is also evidence that forests were present, perhaps at higher elevations. The presence of macaque (*Macaca fascicularis*) and silver-leafed monkey (*Trachypithecus cristatus*) supports the assertion of forest and/or dense vegetation. The size of these habitats or the level of continuity between these broken environments cannot be ascertained from a single pollen spectrum. The limited pollen evidence for these environments may indicate that these areas were relatively small at Sangiran. The high abundance of Heavy Cover bovids at Trinil, however, suggests the dense habitat around the Solo River was much greater during the Middle Pleistocene.

The bovid record indicates that only three species were present in the Trinil H.K. fauna. This study has shown that the small-bodied, endemic *Duboisia santeng* is most likely adapted to Forest / Mountain habitats. Therefore, it can be inferred that *Duboisia* probably did not inhabit the densely covered marsh, or wet, habitats but was more likely associated with the hypothesized upland forests, dominated by *Podocarpus*.

The habitats of *Bubalus palaeokerabau* and *Bibos palaesondaicus* are more difficult to interpret. The combined four-habitat ecomorphological analysis indicates that the large-bodied bovids were adapted to Open and Heavy Cover habitats, exclusively. There is currently no way to identify the astragalus to either of the species. Therefore, any interpretation of the habitats associated with these Pleistocene species is ultimately speculation.

The behavior of the modern banteng (*Bos javanicus*), however, may provide some insight into the behavior of its putative ancestor, *Bibos palaesondaicus*. *Bos javanicus* was classified as an Open cover specimen in the ecomorphological analysis, but is more specifically an edge or ecotone adapted species. As previously mentioned, Nowak

(1991:1429) states that *Bos javanicus* is “found in drier, more open areas . . . [but] it depends on dense thickets and forest for shelter.” If the ancestral counterpart of this species displayed a similar behavior, *Bibos palaesondaicus* probably depended upon the hypothesized upland forests and dense habitats near water for protective cover but primarily utilized the open grasslands between these habitats.

The connection between the modern species, *Bubalus bubalis*, and its presumed ancestor, *Bubalus palaeokerabau*, is less clear. In this study, *Bubalus bubalis* specimens were also classified as an Open habitat species for reasons described previously. The published habitat for this species, however, is “wet grasslands, swamps, and densely vegetated river valleys” (Nowak, 1991:1420), or Heavy Cover. If the fossil specimens classified as Heavy Cover are in actuality, *Bubalus palaeokerabau*, this habitat description would support the reinterpreted paleoenvironmental reconstruction. The successful reclassification of *Bubalus bubalis* as Open habitat in the modern models suggests there is some degree of plasticity regarding its functional morphology and that the specimens utilized in this study were most likely not wild animals when obtained. Therefore, it is assumed here that the Heavy Cover specimens identified in the fossil analysis do represent *Bubalus palaeokerabau*. This species was most likely associated with the hypothesized densely vegetated river valleys and lakes during the Pleistocene. This interpretation strengthens the argument that the ecomorphology method predicts habitat based on functional morphology, independent of phylogenetic relationships. It must be noted, however, that the relatively high abundance of these Heavy Cover specimens may be the result of the location of the Trinil site along the Solo River.



Ecomorphological studies of other bovid assemblages associated with the Trinil H.K. fauna, or pollen analyses at the Trinil site, would address this possibility.

### *Kedung Brubus*

Based on the composition of the Kedung Brubus fauna, particularly the lack of non-hominid primates, the environment has been interpreted as dry, open woodland with a more mainland character (de Vos et al., 1994). This period coincides with the onset of distinct sea level fluctuations and the emergence of the Sunda Shelf (de Vos et al., 1994; Van den Bergh et al., 2001). Unfortunately, no pollen data associated with the Kedung Brubus fauna yet exist. Therefore, the results of the ecomorphology study will be placed into the context of change to drier conditions from the preceding Trinil H.K. faunal period.

The combined raw-measurement four-habitat study indicates that Open habitat specimens dominate the Kedung Brubus collection (77.8%), whereas Heavy Cover specimens contributed 16.7% to the overall collection. *Duboisia* was represented by one individual and thus contributed only 5.6% to the entire sample. The results confirm the interpretation of drier open woodland conditions at Kedung Brubus during this time. Based on the reinterpretation of the environment associated with the Trinil H.K. fauna, this suggests an expansion of open grasslands and subsequent reduction in the densely vegetated river valley and upland forests. The perceived abundance of Open habitat adapted bovids, however, may be confounded by the arrival of the large-bodied *Epileptobos groenveldtii*.

Post-cranial skeletal identification is limited to the atlas and metacarpus. No astraglai have been positively identified for this species. Additionally, there is no extant counterpart to infer its behavior or locomotor adaptation. If it was adapted to Open habitats, then some of the astragalus elements classified in this category may represent this additional species rather than the expansion of the grassland habitat. Conversely, it may be represented by some of those astraglai identified as Heavy Cover. In this case, the expansion of the grasslands would indeed be more pronounced.

Another confounding effect is the location of the Kedung Brubus site itself. Kedung Brubus is located in the Kendeng Hills of Central Java. It is not located within a river valley, like the site of Trinil. Therefore, the relative lack of Heavy Cover specimens may be the result of local environmental differences. It would be expected that the environment at this site would have been dominated by grassland and upland forest habitats, based on the previous reinterpretation of the Trinil H.K. paleoenvironment. The single specimen of *Duboisia*, however, suggests that any upland forest habitat at this time may have been reduced. This claim is also supported by the absence of non-human primates in this collection. Although, the lack of *Duboisia* specimens could equally represent recovery or preservation biases. If, however, the Kedung Brubus collection is an accurate representation of the environment at this time, the above paleoenvironmental reconstruction is valid. All of these possibilities could be resolved with additional palynological and paleontological research.

## HOMO ERECTUS

As previously mentioned, the presence of *Homo erectus* during these periods has been identified from fossils from the Trinil and Kedung Brubus sites as well as the correlated deposits from Sangiran. These early hominids, consequently, would have experienced the interpreted environmental changes presented above. These changes, however, probably had little negative affect on this hominid. In fact, the adaptations that permitted *Homo erectus* to leave Africa were most likely well suited to the open woodland environments encountered during these two periods. These adaptations include larger body size compared to earlier hominids, bipedality, linear body proportions, and a more sophisticated tool kit (Spencer, 1997).

Specifically, bipedality would have permitted foraging in open environments (Rodman and McHenry, 1980), whereas large body size would have been useful for surviving interactions with large predators also found in these habitats (Walker, 1993). Others (Anton et al., 2002) have suggested that the maintenance of this large body size, as well as increased brain size, may have resulted from greater nutritional dependence on animal fat and protein. This may have necessitated the increase in tool sophistication for acquiring this additional component of the diet. Finally, the long, linear body proportions found in *Homo erectus* might have been an advantage for heat dissipation in tropical, open grasslands, like those found in Java during this time (Ruff, 1994).

The question remains, however, “How do these adaptations explain the presence and subsequent success of *Homo erectus* in Java?” Anton et al. (2002) have proposed a model for the initial hominid dispersal from Africa that may help answer this question. They suggest that ecological change provided an increase in niches within grassland and

wooded grassland environments for terrestrial herbivores. Hominids of relatively larger brain and body size, in turn, took advantage of these animal resources and ultimately increased their own reproductive success (Leonard and Robertson, 1997; Anton et al., 2002). As foraging strategy and the ecosystem structure changed, the home range of these hominids increased leading to greater dispersal capability. Additionally, the dispersing herbivores not only provided a subsistence resource but may have also served as an impetus for hominid dispersal (Anton et al., 2002).

It has been shown that the Middle Pleistocene faunas of Java are closely related to the faunas of India and Burma (de Vos, 1995). Thus, based on the model of Anton et al. (2002), it can be inferred that as these species migrated southward, they began to occupy the open grasslands, densely vegetated river valleys, and upland forests of Java during the Early to Middle Pleistocene (ca. 1.2 – 1.0 Ma). As the hominids followed the migrating herbivores, they too would have taken advantage of the resources afforded by the landscape at this time. The Sunda Shelf then became exposed approximately 800,000 years ago, grasslands expanded, and more species began to enter Java. This increased resource base may have lead to increased reproductive success of *Homo erectus*. Therefore, it can be concluded that the environment associated with the Trinil H.K. fauna was probably ideal at the time *Homo erectus* entered Java, and the subsequent expansion of the grasslands only increased this hominid's success during the period associated with the Kedung Brubus fauna.

## CHAPTER 6

### CONCLUSIONS

The research presented here represents the successful extension of the ecomorphology method to include Southeast Asian bovids. The study demonstrates that the functional morphology of the astragalus can be used to accurately predict the habitat of modern species from this region. The study also demonstrates its applicability for predicting habitat for fossil specimens. The addition of African species in the modern models further suggests that a broader model including the entire dataset of African and Southeast Asian species is possible.

The statistical models generated by this research indicated that although LDA appears to be robust to the violations of normality and equal covariance matrices for this dataset, a combination of this parametric method with the non-parametric rpart method produces better results. The use of size-corrected measurements revealed that body-size does contribute to the prediction of habitat based on skeletal measurements and that the absence of the ‘size’ component produces undesirable results. Therefore, it is concluded that the raw measurement models are the best choice for this type of analysis.

Further, the inclusion of a fifth Mountain category appears unwarranted for this region. The results indicated that although the five-habitat models produced higher overall predictive accuracies for the modern dataset, accurate predictions for those species reclassified as Mountain actually decreased. The fossil results of the five-habitat raw measurement model did, however, reveal information regarding the habitat

adaptations of *Duboisia santeng* that would not have been possible if a four-habitat model was exclusively used. Based on all of the results, the combined four-habitat raw measurement model was chosen as the best overall model.

The bovid fossils of the Trinil and Kedung Brubus assemblages of the Dubois Collection represent the most extensive collection of fossils from the associated Trinil H.K. and Kedung Brubus faunas. Therefore, these collections were chosen for study. The astragalus was chosen based on its abundance in these collections, most likely due to its resistance to post-depositional destruction. The results of the fossil analyses reveal that there was a shift from a dominance of Heavy Cover specimens in the older Trinil H.K. fauna to a dominance of Open habitat specimens in the Kedung Brubus collection. This shift was most clearly represented by the combined four-habitat raw measurement model. The results also indicated that *Duboisia santeng* was most likely adapted to upland forest environments.

The previous interpretation of the paleoenvironment associated with the Trinil H.K. fauna indicated an “open woodland” environment. The combination of the ecomorphology study with the pollen diagram for Sangiran provided evidence for a reevaluation of this paleoenvironmental reconstruction. The paleoenvironment associated with the Trinil H.K. fauna was most likely composed of open grasslands, densely vegetated river valleys, and upland forests. This assertion is supported by the relatively high proportion of bovids from the Trinil site adapted to heavy cover, as well as the presence of the upland forest-adapted *Duboisia santeng*. As conditions became drier and the Sunda Shelf emerged, the open grasslands may have expanded and a greater variety of species immigrated to Java, as observed in the Kedung Brubus fauna. The

dominance of open habitat bovids at the Kedung Brubus site may support this claim, but this perceived dominance may be due to the introduction of *Epileptobos groenveldtii* during this time. An additional consideration is that these fossil collections may simply represent local environmental differences between these two sites.

The physical and cultural adaptations of *Homo erectus* permitted this early hominid to successfully exploit the resources afforded by these environments. As the species associated with the Trinil H.K. fauna migrated to Java from India and Burma during the Early Pleistocene, so too did *Homo erectus*. The subsequent environmental change associated with the Kedung Brubus fauna and the arrival of new species only helped to increase the reproductive success of this early hominid by expanding its resource base.

The study presented here builds upon previous research by expanding the application of ecomorphology to include bovids from Southeast Asia. Although it is largely methodological, its successful application to the fossil record of the Trinil and Kedung Brubus sites provides insight into the paleoenvironment associated with Javanese *Homo erectus*. The resulting paleoenvironmental reconstructions further serve to strengthen the notion that the environment holds the key to understanding the behavioral and morphological adaptations of hominids in this region. This research serves as an additional tool for anthropologists by providing a necessary empirically testable method for use in addressing major theoretical questions regarding the behavioral challenges associated with environmental change.

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## **APPENDICES**

## **APPENDIX A**

### **Tables**

**Table A.1: Current faunal succession for Java (from de Vos, 1984).**

<b>Faunal Unit</b>	<b>Age</b>	<b>Environmental Reconstruction</b>
Satir	1.5 Ma	Island Conditions
Cisaat	1.2 Ma	Drier Conditions?
Trinil H.K.	1.0 Ma	Open Woodland
Kedung Brubus	0.8 Ma	Open Woodland
Ngandong	0.4 Ma	Open Woodland?
Punung	0.08 Ma	Tropical Forest
Wajak	0.01 Ma	Humid Forest

**Table A.2: Intraobserver error.**

<b>Metric</b>	<b>Mean Error</b>	<b>Range</b>
LM	0.1	0.1-0.2
LI	0.5	0.1-1.0
LL	0.2	0.1-0.4
WI	0.2	0-0.6
WD	0.1	0-0.2
TI	0.7	0.2-2.2
TD	0.8	0-2.8



**Table A.3: Raw measurement statistics by four-habitat group<sup>1</sup>.**

<b>MetricHabitat</b>	<b>n</b>	<b>X</b>	<b>SD</b>	<b>OR</b>	<b>CI</b>
LM Open	27	52.8	16.1	25.9-88.5	46.4-59.1
Light Cover	19	35.5	3.9	27.0-41.7	33.6-37.4
Heavy Cover	21	52.3	16.7	28.9-78.3	44.7-59.9
Forest	14	29.3	13.2	14.5-53.6	21.6-36.9
LI Open	27	44.6	13.8	21.3-74.0	39.1-50.0
Light Cover	19	30.1	3.3	22.6-35.1	28.5-31.7
Heavy Cover	21	44.4	14.6	24.4-66.7	37.7-51.0
Forest	14	25.2	11.4	12.5-46.2	18.6-31.8
LL Open	27	56.7	17.8	28.1-97.6	49.7-63.7
Light Cover	19	37.4	4.7	26.1-43.9	35.1-39.7
Heavy Cover	21	56.7	18.9	29.0-87.1	48.1-65.3
Forest	14	31.2	14.4	15.1-57.9	22.9-39.5
WI Open	27	35.6	10.8	16.2-59.6	31.3-39.9
Light Cover	19	25.9	2.6	20.3-30.5	24.7-27.2
Heavy Cover	21	36.9	11.4	20.8-55.0	31.7-42.0
Forest	14	18.7	9.3	8.4-37.7	13.4-24.1
WD Open	27	36.1	11.4	15.9-61.2	31.6-40.6
Light Cover	19	24.7	2.8	19.7-29.8	23.3-26.1
Heavy Cover	21	38.1	13.4	19.9-60.1	32.0-44.2
Forest	14	19.1	9.2	8.7-35.9	13.8-24.4
TI Open	27	29.4	9.4	13.7-52.1	25.7-33.2
Light Cover	19	20.0	2.1	16.3-24.6	19.0-21.0
Heavy Cover	21	29.0	10.0	13.3-44.8	24.5-33.6
Forest	14	15.0	6.9	7.2-27.5	11.0-19.0
TD Open	27	25.1	7.9	11.6-42.2	22.0-28.3
Light Cover	19	18.3	2.5	15.2-24.4	17.1-19.5
Heavy Cover	21	24.8	7.7	11.7-37.5	21.2-28.3
Forest	14	12.5	5.2	6.2-21.8	9.5-15.5

<sup>1</sup>n, Sample size; X, mean; SD, standard deviation; OR, observed range; CI, 95% confidence interval.

**Table A.4: Size-corrected measurement statistics by four-habitat group<sup>1</sup>.**

<b>Metric</b>	<b>Habitat</b>	<b>n</b>	<b>X</b>	<b>SD</b>	<b>OR</b>	<b>CI</b>
LM	Open	27	0.137	0.010	0.118-0.156	0.133-0.141
	Light Cover	19	0.126	0.016	0.101-0.154	0.118-0.134
	Heavy Cover	21	0.131	0.014	0.107-0.165	0.125-0.138
	Forest	14	0.156	0.012	0.128-0.175	0.149-0.163
LI	Open	27	0.063	0.009	0.047-0.079	0.059-0.066
	Light Cover	19	0.054	0.017	0.026-0.085	0.046-0.062
	Heavy Cover	21	0.058	0.027	-0.054-0.084	0.045-0.070
	Forest	14	0.090	0.013	0.070-0.113	0.083-0.098
LL	Open	27	0.167	0.010	0.147-0.191	0.164-0.171
	Light Cover	19	0.148	0.027	0.042-0.169	0.135-0.161
	Heavy Cover	21	0.164	0.012	0.145-0.186	0.158-0.169
	Forest	14	0.182	0.010	0.164-0.198	0.177-0.188
WI	Open	27	-0.343	0.016	-0.060-0.006	-0.040-(-0.028)
	Light Cover	19	-0.010	0.020	-0.052-0.030	-0.020-(-0.001)
	Heavy Cover	21	-0.020	0.018	-0.047-0.019	-0.028-(-0.011)
	Forest	14	-0.048	0.029	-0.079-0.005	-0.065-(-0.031)
WD	Open	27	-0.030	0.011	-0.056-(-0.007)	-0.034-(-0.025)
	Light Cover	19	-0.031	0.013	-0.067-(-0.013)	-0.038-(-0.025)
	Heavy Cover	21	-0.011	0.016	-0.037-0.015	-0.018-(-0.004)
	Forest	14	-0.036	0.018	-0.074-(-0.013)	-0.046-(-0.026)
TI	Open	27	-0.113	0.020	-0.134-(-0.023)	-0.122-(-0.105)
	Light Cover	19	-0.123	0.012	-0.147-(-.0103)	-0.129-(-0.117)
	Heavy Cover	21	-0.129	0.020	-0.179-(-0.010)	-0.138-(-0.119)
	Forest	14	-0.135	0.017	-0.164-(-0.103)	-0.145-(-0.125)
TD	Open	27	-0.186	0.022	-0.235-(-0.134)	-0.194-(-0.177)
	Light Cover	19	-0.163	0.027	-0.200-(-0.110)	-0.176-(-0.150)
	Heavy Cover	21	-0.194	0.023	-0.235-(-0.156)	-0.205-(-0.183)
	Forest	14	-0.210	0.021	-0.260-(-0.181)	-0.222-(-0.197)

<sup>1</sup>n, Sample size; X, mean; SD, standard deviation; OR, observed range; CI, 95% confidence interval.

**Table A.5: Raw measurement statistics by species<sup>1</sup>.**

Genus	Species	n	Habitat	Body mass (kg)	LM (S.D.)	LI (S.D.)	LL (S.D.)	WI (S.D.)	WD (S.D.)	TI (S.D.)	TD (S.D.)
<i>Bison</i>	<i>bison</i>	3	Open	675	70.07 (3.55)	59.10 (2.79)	75.30 (3.22)	45.53 (4.26)	47.67 (2.51)	38.07 (2.06)	31.87 (1.98)
<i>Bos</i>	<i>frontalis</i>	4	Heavy Cover	825	75.55 (2.67)	64.32 (2.78)	82.55 (1.72)	52.00 (2.30)	56.65 (3.40)	42.92 (1.79)	35.02 (2.58)
	<i>gaurus</i>	2	Heavy Cover	825	76.55 (2.47)	65.15 (1.91)	84.65 (3.46)	53.20 (2.55)	56.95 (4.45)	43.30 (2.12)	34.80 (3.53)
	<i>javanicus</i>	3	Open	700	66.73 (2.66)	56.40 (3.24)	71.77 (2.48)	44.70 (2.93)	46.07 (4.70)	37.50 (3.00)	32.73 (3.97)
	<i>sauveli</i>	2	Open	800	60.30 (0.71)	51.85 (0.78)	65.30 (2.26)	40.50 (0.42)	40.90 (0.28)	34.10 (2.26)	28.40 (0.99)
<i>Boselaphus</i>	<i>tragocamelus</i>	1	Heavy Cover	250	49.10	41.80	52.50	34.30	36.30	29.40	24.60
<i>Bubalus</i>	<i>bubalis</i>	2	Open	950	85.30 (4.52)	72.25 (2.47)	94.15 (4.88)	58.35 (1.77)	59.90 (1.84)	50.00 (2.97)	42.15 (0.07)
	<i>depressicornis</i>	2	Forest	225	38.50 (2.55)	33.15 (2.90)	41.70 (3.11)	25.70 (0.14)	25.45 (2.33)	20.25 (1.77)	16.50 (1.13)
	<i>mindorensis</i>	2	Forest	225	52.70 (1.27)	45.05 (1.63)	56.70 (1.70)	34.70 (4.24)	35.15 (1.06)	27.30 (0.28)	20.70 (1.56)
<i>Budorcas</i>	<i>taxicolor</i>	4	Heavy Cover	250	51.07 (3.52)	43.65 (3.73)	55.72 (4.93)	37.65 (3.70)	38.10 (4.07)	27.10 (4.11)	24.55 (4.15)
<i>Capra</i>	<i>siberica</i>	7	Light Cover	85	36.90 (2.73)	31.17 (2.48)	38.96 (2.74)	25.93 (2.01)	25.00 (1.48)	19.90 (1.14)	18.11 (1.43)
<i>Hemitragus</i>	<i>hylocrius</i>	4	Light Cover	75	33.10 (0.56)	28.30 (0.50)	33.05 (4.65)	25.67 (1.00)	23.00 (0.91)	18.90 (0.59)	15.90 (0.71)
<i>Capricornis</i>	<i>crispus</i>	2	Heavy Cover	30	29.80 (1.27)	25.40 (1.41)	30.55 (2.19)	21.70 (0.99)	20.60 (0.99)	15.40 (2.97)	13.20 (2.12)

**Table A.5: Continued<sup>1</sup>.**

<b>Genus</b>	<b>Species</b>	<b>n</b>	<b>Habitat</b>	<b>Body mass (kg)</b>	<b>LM (S.D.)</b>	<b>LI (S.D.)</b>	<b>LL (S.D.)</b>	<b>WI (S.D.)</b>	<b>WD (S.D.)</b>	<b>TI (S.D.)</b>	<b>TD (S.D.)</b>
<i>Capricornis</i>	<i>sumatraensis</i>	7	Heavy Cover	30	42.94 (2.09)	35.79 (5.04)	45.93 (2.09)	30.11 (1.76)	29.94 (1.56)	23.63 (1.04)	20.89 (1.79)
	<i>swinhoei</i>	1	Heavy Cover	30	30.20	26.50	32.80	20.80	20.60	17.00	14.90
					--	--	--	--	--	--	--
<i>Naemorhedus</i>	<i>goral</i>	5	Forest / Mountain	30	30.20 (0.98)	26.24 (1.38)	32.04 (1.30)	19.42 (1.65)	20.02 (1.03)	15.10 (0.25)	13.44 (0.28)
<i>Ovis</i>	<i>ammon</i>	6	Light Cover	180	37.97 (3.08)	32.07 (2.49)	40.72 (2.94)	27.78 (2.14)	27.13 (2.64)	21.93 (2.02)	21.05 (1.96)
	<i>orientalis</i>	2	Light Cover	180	28.30 (1.84)	23.70 (1.56)	30.75 (0.64)	20.80 (0.71)	19.90 (0.28)	16.70 (0.57)	15.65 (0.07)
<i>Procapra</i>	<i>gutturosa</i>	2	Open	30	26.45 (0.78)	21.85 (0.78)	28.55 (0.64)	16.55 (0.49)	16.45 (0.78)	14.50 (1.13)	12.30 (0.99)
<i>Pseudois</i>	<i>nayaur</i>	3	Open	50	33.70 (0.56)	28.73 (0.81)	36.33 (0.93)	24.30 (0.70)	23.43 (0.25)	19.23 (0.99)	17.13 (0.55)
<i>Connochaetes</i>	<i>taurinus</i>	7	Open	180	49.46 (3.64)	42.01 (3.09)	52.30 (4.04)	34.13 (2.54)	33.60 (2.08)	26.94 (2.57)	22.54 (2.46)
<i>Damaliscus</i>	<i>lunatus</i>	5	Open	136	44.66 (0.73)	36.82 (0.89)	47.76 (1.08)	29.48 (1.44)	30.78 (0.81)	24.96 (1.04)	22.02 (2.10)
<i>Cephalophus</i>	<i>monticola</i>	3	Forest	6	15.03 (0.50)	12.87 (0.40)	16.07 (0.76)	8.97 (0.60)	9.50 (0.26)	7.80 (0.66)	6.77 (0.21)
<i>Madoqua</i>	<i>kirki</i>	2	Forest	5	15.55 (1.06)	13.30 (0.85)	16.05 (1.34)	8.80 (0.42)	8.95 (0.35)	8.05 (0.78)	6.40 (0.28)

<sup>1</sup>n, sample size; S.D. standard deviation.

**Table A.6: Size-corrected measurement statistics by species<sup>1</sup>.**

Genus	Species	n	Habitat	Body mass (kg)	LM (S.D.)	LI (S.D.)	LL (S.D.)	WI (S.D.)	WD (S.D.)	TI (S.D.)	TD (S.D.)
<i>Bison</i>	<i>bison</i>	3	Open	675	0.144 (0.004)	0.070 (0.004)	0.175 (0.007)	-0.044 (0.017)	-0.024 (0.005)	-0.121 (0.004)	-0.199 (0.011)
<i>Bos</i>	<i>frontalis</i>	4	Heavy Cover	825	0.128 (0.004)	0.058 (0.002)	0.167 (0.015)	-0.034 (0.009)	0.003 (0.010)	-0.117 (0.003)	-0.206 (0.015)
	<i>gaurus</i>	2	Heavy Cover	825	0.129 (0.009)	0.059 (0.011)	0.173 (0.006)	-0.029 (0.003)	0.000 (0.010)	-0.118 (0.002)	-0.214 (0.021)
	<i>javanicus</i>	3	Open	700	0.129 (0.014)	0.059 (0.008)	0.172 (0.017)	-0.029 (0.008)	0.000 (0.014)	-0.118 (0.004)	-0.214 (0.022)
	<i>sauveli</i>	2	Open	800	0.135 (0.005)	0.061 (0.004)	0.166 (0.005)	-0.040 (0.006)	-0.028 (0.013)	-0.117 (0.018)	-0.177 (0.005)
<i>Boselaphus</i>	<i>tragocamelus</i>	1	Heavy Cover	250	--	--	--	--	--	--	--
<i>Bubalus</i>	<i>bubalis</i>	2	Open	950	0.126 (0.007)	0.054 (0.001)	0.169 (0.006)	-0.038 (0.003)	-0.027 (0.003)	-0.106 (0.010)	-0.179 (0.017)
	<i>depressicornis</i>	2	Forest	225	0.148 (0.001)	0.082 (0.008)	0.182 (0.002)	-0.027 (0.027)	-0.032 (0.010)	-0.132 (0.008)	-0.220 (0.000)
	<i>mindorensis</i>	2	Forest	225	0.155 (0.010)	0.087 (0.005)	0.187 (0.007)	-0.028 (0.033)	-0.021 (0.007)	-0.130 (0.016)	-0.251 (0.012)
<i>Budorcas</i>	<i>taxicolor</i>	4	Heavy Cover	250	0.128 (0.017)	0.059 (0.011)	0.165 (0.006)	-0.006 (0.018)	-0.001 (0.016)	-0.151 (0.020)	-0.194 (0.028)
<i>Capra</i>	<i>siberica</i>	7	Light Cover	85	0.135 (0.012)	0.062 (0.014)	0.159 (0.006)	-0.018 (0.018)	-0.033 (0.016)	-0.132 (0.011)	-0.174 (0.016)
<i>Hemitragus</i>	<i>hylocrius</i>	4	Light Cover	75	0.129 (0.018)	0.061 (0.015)	0.125 (0.056)	0.018 (0.010)	-0.029 (0.012)	-0.114 (0.003)	-0.019 (0.007)
<i>Capricornis</i>	<i>crispus</i>	2	Heavy Cover	30	0.143 (0.020)	0.074 (0.014)	0.154 (0.007)	0.006 (0.019)	-0.170 (0.017)	-0.147 (0.046)	-0.213 (0.032)

**Table A.6: Continued<sup>1</sup>.**

<b>Genus</b>	<b>Species</b>	<b>n</b>	<b>Habitat</b>	<b>Body mass (kg)</b>	<b>LM (S.D.)</b>	<b>LI (S.D.)</b>	<b>LL (S.D.)</b>	<b>WI (S.D.)</b>	<b>WD (S.D.)</b>	<b>TI (S.D.)</b>	<b>TD (S.D.)</b>
<i>Capricornis</i>	<i>sumatraensis</i>	7	Heavy Cover	30	0.134 (0.019)	0.051 (0.046)	0.163 (0.013)	-0.020 (0.018)	-0.023 (0.013)	-0.125 (0.010)	-0.180 (0.021)
	<i>swinhoei</i>	1	Heavy Cover	30	0.129 --	0.073 --	0.165 --	-0.033 --	-0.037 --	-0.120 --	-0.177 --
<i>Naemorhedus</i>	<i>goral</i>	5	Forest / Mountain	30	0.151 (0.015)	0.090 (0.019)	0.177 (0.012)	-0.041 (0.033)	-0.027 (0.013)	-0.149 (0.012)	-0.200 (0.010)
<i>Ovis</i>	<i>ammon</i>	6	Light Cover	180	0.117 (0.016)	0.044 (0.015)	0.148 (0.008)	-0.018 (0.009)	-0.029 (0.011)	-0.121 (0.014)	-0.139 (0.027)
	<i>orientalis</i>	2	Light Cover	180	0.116 (0.015)	0.039 (0.015)	0.152 (0.004)	-0.017 (0.002)	-0.036 (0.019)	-0.113 (0.002)	-0.141 (0.011)
<i>Procapra</i>	<i>gutturosa</i>	2	Open	30	0.151 (0.007)	0.068 (0.004)	0.184 (0.010)	-0.053 (0.007)	-0.056 (0.000)	-0.111 (0.014)	-0.182 (0.015)
<i>Pseudois</i>	<i>nayaur</i>	3	Open	50	0.125 (0.003)	0.056 (0.005)	0.157 (0.004)	-0.017 (0.008)	-0.033 (0.009)	-0.119 (0.015)	-0.169 (0.003)
<i>Connochaetes</i>	<i>taurinus</i>	7	Open	180	0.140 (0.010)	0.069 (0.006)	0.164 (0.004)	-0.021 (0.014)	-0.027 (0.010)	-0.108 (0.038)	-0.202 (0.022)
<i>Damaliscus</i>	<i>lunatus</i>	5	Open	136	0.137 (0.009)	0.053 (0.006)	0.166 (0.009)	-0.044 (0.011)	-0.025 (0.009)	-0.116 (0.007)	-0.172 (0.029)
<i>Cephalophus</i>	<i>monticola</i>	3	Forest	6	0.156 (0.004)	0.089 (0.006)	0.185 (0.011)	-0.068 (0.011)	-0.043 (0.011)	-0.129 (0.018)	-0.190 (0.008)
<i>Madoqua</i>	<i>kirki</i>	2	Forest	5	0.173 (0.002)	0.105 (0.021)	0.187 (0.019)	-0.074 (0.024)	-0.066 (0.017)	-0.113 (0.014)	-0.212 (0.008)

<sup>1</sup>n, sample size; S.D. standard deviation.

**Table A.7: LDA results for the raw-measurement four-habitat model.**

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Pooled within-group correlations between functions and variables. (\*) Indicates largest absolute correlation between variable and function.

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<b>Metric</b>	<b>Function 1</b>	<b>Function 2</b>	<b>Function 3</b>
LL	.356	.175	.885*
LM	.375	.167	.880*
LI	.352	.166	.857*
WD	.375	.271	.852*
TI	.424	.173	.847*
WI	.441	.265	.808*
TD	.500	.193	.787*
% Variance	45.1	34.1	20.7

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Classification results (total correct = 77.8%).

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<b>Actual group</b>	<b>n</b>	<b>Open</b>	<b>Light Cover</b>	<b>Heavy Cover</b>	<b>Forest</b>	<b>% Correct</b>
Open	27	19	5	1	2	70.4
Light Cover	19	2	17	0	0	89.5
Heavy Cover	21	3	2	15	1	71.4
Forest	14	0	0	2	12	85.7

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**Table A.8: Misclassifications by species: Raw-measurement four-habitat models.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Bison bison</i>	Open	3	3		3		3	
<i>Bos frontalis</i>	Heavy Cover	4	4		4		4	
<i>Bos gaurus</i>	Heavy Cover	2	2		2		2	
<i>Bos javanicus</i>	Open	3	3		3		3	
<i>Bos sauveli</i>	Open	2	2		2		2	
<i>Boselaphus tragocamelus</i>	Heavy Cover	1	1		0	1O	0	1O
<i>Bubalus bubalis</i>	Open	2	2		0	2HC	2	
<i>Bubalus depressicornis</i>	Forest	2	2		0	2LC	2	
<i>Bubalus mindorensis</i>	Forest	2	1	1HC	0	2O	0	2O
<i>Budorcas taxicolor</i>	Heavy Cover	4	4		1	3O	4	
<i>Capra sibirica</i>	Light Cover	7	5	2O	7		7	
<i>Hemitragus hylocrius</i>	Light Cover	4	4		4		4	
<i>Capricornis crispus</i>	Heavy Cover	2	1	1LC	0	2F	0	1LC, 1F
<i>Naemorhedus goral</i>	Forest	5	4	1HC	5		5	



**Table A.8: Continued.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Capricornis sumatraensis</i>	Heavy Cover	7	3	3O, 1LC	5	1O, 1LC	1	5O, 1LC
<i>Capricornis swinhoei</i>	Heavy Cover	1	0	1F	0	1F	0	1F
<i>Ovis ammon</i>	Light Cover	6	6		6		6	
<i>Ovis orientalis</i>	Light Cover	2	2		2		2	
<i>Procapra gutturosa</i>	Open	2	0	2F	0	2F	0	2F
<i>Pseudois nayaur</i>	Open	3	0	3LC	0	3LC	0	3LC
<i>Connochaetes taurinus</i>	Open	7	5	2L	6	1H	7	
<i>Damaliscus lunatus</i>	Open	5	5		5		5	
<i>Cephalophus monticola</i>	Forest	3	3		3		3	
<i>Madoqua kirki</i>	Forest	2	2		2		2	

**Table A.9: Validation results for the raw-measurement four-habitat models<sup>1</sup>.**

<b>Test</b>	<b>LDA</b>	<b>rpart</b>	<b>Combined</b>
<b>Full Dataset</b>	77.8%	74.1%	79.0%
<b>Cross-validation</b>	70.4%	59.8%	68.9%
<b>Jackknife (n-1)</b>	62.5%	50.0%	
<b>GT</b>	66.7%	50.0%	
<b>GT1</b>	65.0%	50.0%	
<b>GT2</b>	70.0%	60.0%	
<b>GT3</b>	65.0%	65.0%	
<b>GT4</b>	70.0%	60.0%	
<b>GT5</b>	85.0%	60.0%	
<b>GT6</b>	75.0%	45.0%	
<b>GT7</b>	75.0%	45.0%	
<b>GT8</b>	90.0%	80.0%	
<b>GT9</b>	65.0%	55.0%	
<b>GT10</b>	75.0%	55.0%	

<sup>1</sup>GT, 24-specimen generator test; GT1-10, randomized generator tests.

**Table A.10: LDA results for the size-corrected four-habitat model.**

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Pooled within-group correlations between functions and variables. (\*) Indicates largest absolute correlation between variable and function.

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<b>Metric</b>	<b>Function 1</b>	<b>Function 2</b>	<b>Function 3</b>
LM	-.616*	.263	.124
LL	-.606*	-.061	-.211
LI	-.573*	.287	.357
TD	.538*	.306	-.083
WI	.534*	-.202	.409
WD	.118	-.889*	.068
TI	.146	.133	-.893*
% Variance	65.1	25.8	9.1

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Classification results (total correct = 77.8%).

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<b>Actual group</b>	<b>n</b>	<b>Open</b>	<b>Light Cover</b>	<b>Heavy Cover</b>	<b>Forest</b>	<b>% Correct</b>
Open	27	18	5	2	2	66.7
Light Cover	19	2	17	0	0	89.5
Heavy Cover	21	4	2	15	0	71.4
Forest	14	0	0	1	13	92.9

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**Table A.11: Validation results for the size-corrected four-habitat models<sup>1</sup>.**

<b>Test</b>	<b>LDA</b>	<b>rpart</b>	<b>Combined</b>
<b>Full Dataset</b>	77.8%	77.8%	80.2%
<b>Cross-validation</b>	65.4%	67.2%	63.2%
<b>Jackknife (n-1)</b>	66.7%	79.2%	
<b>GT</b>	75.0%	66.7%	
<b>GT1</b>	60.0%	75.0%	
<b>GT2</b>	80.0%	70.0%	
<b>GT3</b>	60.0%	55.0%	
<b>GT4</b>	70.0%	70.0%	
<b>GT5</b>	80.0%	80.0%	
<b>GT6</b>	75.0%	60.0%	
<b>GT7</b>	60.0%	60.0%	
<b>GT8</b>	70.0%	60.0%	
<b>GT9</b>	70.0%	55.0%	
<b>GT10</b>	80.0%	75.0%	

<sup>1</sup>GT, 24-specimen generator test; GT1-10, randomized generator tests.

**Table A.12: Misclassifications by species: Size-corrected four-habitat models.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Bison bison</i>	Open	3	3		3		3	
<i>Bos frontalis</i>	Heavy Cover	4	4		4		4	
<i>Bos gaurus</i>	Heavy Cover	2	2		2		2	
<i>Bos javanicus</i>	Open	3	3		2	1LC	3	
<i>Bos sauveli</i>	Open	2	2		2		2	
<i>Boselaphus tragocamelus</i>	Heavy Cover	1	0	1O	1		1	
<i>Bubalus bubalis</i>	Open	2	0	2HC	2		2	
<i>Bubalus depressicornis</i>	Forest	2	0	2LC	2		2	
<i>Bubalus mindorensis</i>	Forest	2	0	2O	2		1	1HC
<i>Budorcas taxicolor</i>	Heavy Cover	4	1	3O	4		4	
<i>Capra sibirica</i>	Light Cover	7	7		6	1F	2	4O, 1F
<i>Hemitragus hylocrius</i>	Light Cover	4	4		3	1F	2	1O, 1F
<i>Capricornis crispus</i>	Heavy Cover	2	0	2F	0	1LC, 1F	1	1O
<i>Naemorhedus goral</i>	Forest	5	5		4	1O	4	1O

**Table A.12: Continued.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Capricornis sumatraensis</i>	Heavy Cover	7	5	1O, 1LC	1	3O, 3LC	1	5O, 1LC
<i>Capricornis swinhoei</i>	Heavy Cover	1	0	1F	0	1O	0	1O
<i>Ovis ammon</i>	Light Cover	6	6		6		5	1O
<i>Ovis orientalis</i>	Light Cover	2	2		2		2	
<i>Procapra gutturosa</i>	Open	2	0	2F	2		2	
<i>Pseudois nayaur</i>	Open	3	0	3LC	0	3LC	3	
<i>Connochaetes taurinus</i>	Open	7	6	1HC	5	1LC, 1F	6	1F
<i>Damaliscus lunatus</i>	Open	5	5		3	2LC	5	
<i>Cephalophus monticola</i>	Forest	3	3		3		3	
<i>Madoqua kirki</i>	Forest	2	2		2		2	

**Table A.13: Raw measurement statistics by five-habitat group<sup>1</sup>.**

<b>Metric</b>	<b>Habitat</b>	<b>n</b>	<b>X</b>	<b>SD</b>	<b>OR</b>	<b>CI</b>
LM	Open	24	55.2	15.5	25.9-88.5	48.6-61.7
	Light Cover	12	34.7	4.3	27.0-41.7	32.0-37.5
	Heavy Cover	11	64.4	13.4	47.5-78.3	55.4-73.4
	Forest	9	28.7	16.8	14.5-53.6	15.8-41.6
	Mountain	25	36.0	5.5	28.9-45.6	33.8-38.3
LI	Open	24	46.5	13.3	21.3-74.0	40.9-52.1
	Light Cover	12	29.4	3.6	22.6-34.5	27.1-31.7
	Heavy Cover	11	54.9	11.4	39.9-66.7	47.2-62.6
	Forest	9	24.6	14.4	12.5-46.2	13.5-35.7
	Mountain	25	30.5	4.9	24.4-38.8	28.5-32.5
LL	Open	24	59.2	17.2	28.1-97.6	52.0-66.5
	Light Cover	12	36.5	29.9	26.1-43.9	33.0-40.0
	Heavy Cover	11	70.4	15.1	50.5-87.1	60.3-80.6
	Forest	9	30.8	18.3	15.1-57.9	16.7-44.9
	Mountain	25	38.3	6.0	29.0-48.1	35.8-40.7
WI	Open	24	37.0	10.7	16.2-59.6	32.5-41.5
	Light Cover	12	25.9	3.0	20.3-30.5	24.0-27.8
	Heavy Cover	11	45.4	8.5	34.3-55.0	39.7-51.1
	Forest	9	18.4	11.8	8.4-37.7	9.3-27.4
	Mountain	25	25.1	4.3	17.5-32.8	23.3-26.8
WD	Open	24	37.7	11.2	15.9-61.2	33.0-42.4
	Light Cover	12	24.5	3.4	19.7-29.8	22.4-26.7
	Heavy Cover	11	48.1	10.4	33.7-60.1	41.1-55.1
	Forest	9	18.6	11.6	8.7-35.9	9.7-27.6
	Mountain	25	24.7	4.0	18.4-31.8	23.0-26.3
TI	Open	24	30.7	9.2	13.7-52.1	26.8-34.6
	Light Cover	12	20.0	2.5	16.3-24.6	18.4-21.7
	Heavy Cover	11	36.0	8.5	22.6-44.8	30.3-41.7
	Forest	9	15.0	8.8	7.2-27.5	8.2-21.7
	Mountain	25	19.4	3.4	13.3-24.6	18.0-20.8
TD	Open	24	26.1	7.8	11.6-42.2	22.8-29.4
	Light Cover	12	18.4	3.1	15.2-24.4	16.5-20.4
	Heavy Cover	11	30.2	6.1	20.1-37.5	26.1-34.4
	Forest	9	11.9	6.5	6.2-21.8	6.9-17.0
	Mountain	25	17.3	3.2	11.7-23.1	16.0-18.6

<sup>1</sup>n, Sample size; X, mean; SD, standard deviation; OR, observed range; CI, 95% confidence interval.

**Table A.14: Size-corrected measurement statistics by five-habitat group<sup>1</sup>.**

<b>MetricHabitat</b>	<b>n</b>	<b>X</b>	<b>SD</b>	<b>OR</b>	<b>CI</b>	
LM	Open	24	0.139	0.010	0.118-0.156	0.134-0.143
	Light Cover	12	0.121	0.016	0.101-0.154	0.111-0.131
	Heavy Cover	11	0.128	0.010	0.107-0.147	0.121-0.135
	Forest	9	0.158	0.010	0.147-0.175	0.150-0.166
	Mountain	25	0.137	0.016	0.113-0.165	0.131-0.144
LI	Open	24	0.064	0.009	0.047-0.079	0.060-0.067
	Light Cover	12	0.049	0.017	0.026-0.083	0.038-0.059
	Heavy Cover	11	0.058	0.007	0.048-0.071	0.053-0.063
	Forest	9	0.091	0.010	0.076-0.105	0.083-0.098
	Mountain	25	0.065	0.029	-0.054-0.113	0.053-0.077
LL	Open	24	0.169	0.009	0.147-0.191	0.165-0.173
	Light Cover	12	0.141	0.032	0.042-0.160	0.120-0.161
	Heavy Cover	11	0.166	0.012	0.149-0.186	0.158-0.174
	Forest	9	0.185	0.007	0.176-0.198	0.180-0.191
	Mountain	25	0.163	0.012	0.145-0.190	0.159-0.168
WI	Open	24	-0.036	0.015	-0.060-0.006	-0.043-(-0.030)
	Light Cover	12	-0.006	0.020	-0.035-0.030	-0.018-(-0.007)
	Heavy Cover	11	-0.023	0.017	-0.047-0.014	-0.034-(-0.011)
	Forest	9	-0.051	0.028	-0.079-(-0.004)	-0.073-(-0.030)
	Mountain	25	-0.022	0.023	-0.079-0.019	-0.031-(-0.012)
WD	Open	24	-0.029	0.012	-0.056-(-0.007)	-0.034-(-0.024)
	Light Cover	12	-0.030	0.012	-0.050-(-0.013)	-0.038-(-0.023)
	Heavy Cover	11	0.000	0.008	-0.010-0.015	-0.006-0.005
	Forest	9	-0.041	0.019	-0.074-(-0.015)	-0.055-(-0.026)
	Mountain	25	-0.028	0.014	-0.067-0.001	-0.033-(-0.022)
TI	Open	24	-0.113	0.021	-0.132-(-0.023)	-0.122-(-0.104)
	Light Cover	12	-0.118	0.010	-0.138-(-.0103)	-0.124-(-0.111)
	Heavy Cover	11	-0.128	0.021	-0.176-(-0.101)	-0.143-(-0.114)
	Forest	9	-0.126	0.014	-0.143-(-0.103)	-0.137-(-0.115)
	Mountain	25	-0.133	0.018	-0.179-(-0.104)	-0.14-(-0.126)
TD	Open	24	-0.188	0.022	-0.235-(-0.138)	-0.197-(-0.178)
	Light Cover	12	-0.156	0.031	-0.200-(-0.110)	-0.176-(-0.137)
	Heavy Cover	11	-0.201	0.021	-0.229-(-0.167)	-0.215-(-0.186)
	Forest	9	-0.215	0.025	-0.260-(-0.181)	-0.234-(-0.196)
	Mountain	25	-0.183	0.020	-0.235-(-0.15)	-0.192-(-0.175)

<sup>1</sup>n, Sample size; X, mean; SD, standard deviation; OR, observed range; CI, 95% confidence interval.



**Table A.15: LDA results for the raw-measurement five-habitat model.**

Pooled within-group correlations between functions and variables. (\*) Indicates largest absolute correlation between variable and function.

Metric	Function 1	Function 2	Function 3	Function 4
LM	.473	.836*	.174	.077
LL	.485	.823*	.152	.085
TI	.458	.811*	.244	.197
LI	.473	.809*	.163	.088
TD	.437	.789*	.364	.074
WD	.553	.777*	.234	.098
WI	.501	.751*	.305	.083
% Variance	57.2	22.7	18.1	2.0

Classification results (total correct = 74.1%).

Actual group	n	Open	Light Cover	Heavy Cover	Forest	Mountain	% Correct
Open	24	18	1	0	2	3	75.0
Light Cover	12	0	11	0	0	1	91.7
Heavy Cover	11	0	1	10	0	0	90.9
Forest	9	0	0	0	7	2	92.9
Mountain	25	3	6	0	2	14	56.0

**Table A.16: Misclassifications by species: Raw-measurement five-habitat models.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Bison bison</i>	Open	3	3		2	1F	3	
<i>Bos frontalis</i>	Heavy Cover	4	4		4		4	
<i>Bos gaurus</i>	Heavy Cover	2	2		2		2	
<i>Bos javanicus</i>	Open	3	3		3		3	
<i>Bos sauveli</i>	Open	2	2		2		2	
<i>Boselaphus tragocamelus</i>	Heavy Cover	1	0	1LC	1		0	1O
<i>Bubalus bubalis</i>	Open	2	2		2		2	
<i>Bubalus depressicornis</i>	Forest	2	1	1M	1	1M	0	2M
<i>Bubalus mindorensis</i>	Forest	2	1	1M	2		2	
<i>Budorcas taxicolor</i>	Heavy Cover	4	4		3	1M	4	
<i>Capra sibirica</i>	Mountain	7	4	2O, 2LC	4	1O, 2LC	5	2LC
<i>Hemitragus hylocrius</i>	Light Cover	4	4		3	1M	4	
<i>Capricornis crispus</i>	Mountain	2	1	1LC	1	1LC	2	
<i>Naemorhedus goral</i>	Mountain	5	3	2F	3	2F	5	

**Table A.16: Continued.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Capricornis sumatraensis</i>	Mountain	7	4	1O, 2LC	3	3O, 1LC	2	3O, 2LC
<i>Capricornis swinhoei</i>	Mountain	1	1		0	1O	1	
<i>Ovis ammon</i>	Light Cover	6	6		5	1M	6	
<i>Ovis orientalis</i>	Light Cover	2	2		2		2	
<i>Procapra gutturosa</i>	Open	2	0	2F	1	1F	0	2F
<i>Pseudois nayaur</i>	Mountain	3	1	2LC	1	1O, 1LC	2	1LC
<i>Connochaetes taurinus</i>	Open	7	4	1LC, 2M	3	4M	7	
<i>Damaliscus lunatus</i>	Open	5	4	1M	3	1LC, 1M	5	
<i>Cephalophus monticola</i>	Forest	3	3		3		3	
<i>Madoqua kirki</i>	Forest	2	2		2		2	

**Table A.17: Validation results for the raw-measurement five-habitat models<sup>1</sup>.**

<b>Test</b>	<b>LDA</b>	<b>rpart</b>	<b>Combined</b>
<b>Full Dataset</b>	74.1%	75.3%	83.9%
<b>Cross-validation</b>	65.4%	52.1%	66.9%
<b>Jackknife (n-1)</b>	75.0%	50.0%	
<b>GT</b>	62.5%	37.5%	
<b>GT1</b>	70.0%	55.0%	
<b>GT2</b>	65.0%	50.0%	
<b>GT3</b>	80.0%	45.0%	
<b>GT4</b>	60.0%	25.0%	
<b>GT5</b>	75.0%	55.0%	
<b>GT6</b>	65.0%	40.0%	
<b>GT7</b>	75.0%	40.0%	
<b>GT8</b>	75.0%	35.0%	
<b>GT9</b>	60.0%	55.0%	
<b>GT10</b>	60.0%	50.0%	

<sup>1</sup>GT, 24-specimen generator test; GT1-10, randomized generator tests.

**Table A.18: LDA results for the raw-measurement five-habitat model.**

Pooled within-group correlations between functions and variables. (\*) Indicates largest absolute correlation between variable and function.

Metric	Function 1	Function 2	Function 3	Function 4
LL	-.627*	.131	.158	.416
TD	.576*	.075	-.231	.272
LM	-.524*	.442	.300	.085
WI	.505*	-.230	.247	-.203
WD	-.020	-.883*	.074	.245
TI	.021	.082	-.936*	.086
LI	-.404	.286	.344	-.455*
% Variance	53.0	36.5	9.1	1.4

Classification results (total correct = 74.1%).

Actual group	n	Open	Light Cover	Heavy Cover	Forest	Mountain	% Correct
Open	24	16	1	0	2	5	66.7
Light Cover	12	0	10	0	0	2	83.3
Heavy Cover	11	0	0	10	0	1	90.9
Forest	9	0	0	0	8	1	88.9
Mountain	25	6	5	0	2	12	48.0

**Table A.19: Validation results for the size-corrected five-habitat models<sup>1</sup>.**

<b>Test</b>	<b>LDA</b>	<b>rpart</b>	<b>Combined</b>
<b>Full Dataset</b>	69.1%	77.8%	82.7%
<b>Cross-validation</b>	59.3%	60.7%	60.0%
<b>Jackknife (n-1)</b>	62.5%	70.8%	
<b>GT</b>	62.5%	54.1%	
<b>GT1</b>	55.0%	55.0%	
<b>GT2</b>	75.0%	80.0%	
<b>GT3</b>	60.0%	70.0%	
<b>GT4</b>	70.0%	60.0%	
<b>GT5</b>	75.0%	35.0%	
<b>GT6</b>	55.0%	35.0%	
<b>GT7</b>	65.0%	40.0%	
<b>GT8</b>	60.0%	70.0%	
<b>GT9</b>	45.0%	40.0%	
<b>GT10</b>	65.0%	70.0%	

<sup>1</sup>GT, 24-specimen generator test; GT1-10, randomized generator tests.

**Table A.20: Misclassifications by species: Size-corrected five-habitat models.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Bison bison</i>	Open	3	3		3		3	
<i>Bos frontalis</i>	Heavy Cover	4	4		4		4	
<i>Bos gaurus</i>	Heavy Cover	2	2		2		2	
<i>Bos javanicus</i>	Open	3	3		2	1LC	3	
<i>Bos sauveli</i>	Open	2	2		2		2	
<i>Boselaphus tragocamelus</i>	Heavy Cover	1	1		1		1	
<i>Bubalus bubalis</i>	Open	2	0	2HC	2		2	
<i>Bubalus depressicornis</i>	Forest	2	0	1LC, 1M	2		2	
<i>Bubalus mindorensis</i>	Forest	2	0	1HC	2		2	
<i>Budorcas taxicolor</i>	Heavy Cover	4	4		4		4	
<i>Capra sibirica</i>	Mountain	7	7		6	1LC	6	1O
<i>Hemitragus hylocrius</i>	Light Cover	4	3	1M	3	1O	3	1O
<i>Capricornis crispus</i>	Mountain	2	2		0	1LC, 1HC	1	1O
<i>Naemorhedus goral</i>	Mountain	5	5		2	3F	2	3F

**Table A.20: Continued.**

Species	Habitat	n	LDA		rpart		Combined	
			#Correct	Misclassifications	# Correct	Misclassifications	# Correct	Misclassifications
<i>Capricornis sumatraensis</i>	Mountain	7	1	3O, 3LC	5	1HC, 1F	5	1O, 1F
<i>Capricornis swinhoei</i>	Mountain	1	1		0	1O	0	1O
<i>Ovis ammon</i>	Light Cover	6	5	1M	4	2M	4	2M
<i>Ovis orientalis</i>	Light Cover	2	2		2		2	
<i>Procapra gutturosa</i>	Open	2	0	2F	2		2	
<i>Pseudois nayaur</i>	Mountain	3	2	1LC	1	1O, 1LC	1	2O
<i>Connochaetes taurinus</i>	Open	7	4	3HC	4	1HC, 1F, 1M	5	1F, 1M
<i>Damaliscus lunatus</i>	Open	5	5		5		5	
<i>Cephalophus monticola</i>	Forest	3	3		3		3	
<i>Madoqua kirki</i>	Forest	2	2		2		2	



**Table A.21: Fossil results<sup>1</sup>.**

		Raw Measurements			Size-Corrected		
		LDA	rpart	Combined	LDA	rpart	Combined
<b>4 Habitats:</b>							
<b>Trinil</b>							
	<b>Open</b>	16.9%	16.5%	13.5%	16.9%	22.5%	25.8%
	<b>Light</b>	6.7%	12.1%	0.0%	7.9%	15.7%	5.6%
	<b>Heavy</b>	65.2%	68.1%	70.8%	66.3%	41.6%	48.3%
	<b>Forest</b>	11.2%	3.3%	15.7%	9.0%	20.2%	20.2%
<b>Kedung Brubus</b>							
	<b>Open</b>	61.1%	75.0%	77.8%	33.3%	33.0%	61.1%
	<b>Light</b>	11.1%	0.0%	0.0%	16.7%	27.8%	0.0%
	<b>Heavy</b>	22.2%	20.0%	16.7%	44.4%	16.7%	27.8%
	<b>Forest</b>	5.6%	5.0%	5.6%	5.6%	22.2%	11.1%
<b>5 Habitats:</b>							
<b>Trinil</b>							
	<b>Open</b>	13.5%	16.0%	13.5%	12.4%	14.6%	15.7%
	<b>Light</b>	2.2%	6.4%	0.0%	7.9%	7.9%	1.1%
	<b>Heavy</b>	69.7%	69.1%	70.8%	50.6%	40.4%	55.1%
	<b>Forest</b>	10.1%	0.0%	0.0%	6.7%	14.6%	13.5%
	<b>Mountain</b>	4.5%	8.5%	15.7%	22.5%	22.5%	14.6%
<b>Kedung Brubus</b>							
	<b>Open</b>	55.6%	76.2%	66.7%	38.9%	38.9%	50.0%
	<b>Light</b>	11.1%	0.0%	0.0%	0.0%	11.1%	0.0%
	<b>Heavy</b>	27.8%	19.0%	27.8%	38.9%	22.2%	22.2%
	<b>Forest</b>	5.6%	5.8%	0.0%	5.6%	11.1%	11.1%
	<b>Mountain</b>	0.0%	0.0%	5.6%	16.7%	16.7%	16.7%

<sup>1</sup>Italicized values represent pruned classification tree results.

**Table A.22: Trinil results: Raw-measurement four-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	5820	Heavy Cover	0.966	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	7126	Heavy Cover	0.977	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8419	Heavy Cover	0.708	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8428	Heavy Cover	0.981	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8493	Heavy Cover	0.999	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8494	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8496	Heavy Cover	0.863	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8623	Heavy Cover	0.999	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8629	Heavy Cover	0.802	Open	0.731	Heavy Cover	1.000
Bovidae	8718	Light Cover	<b>0.504<sup>2</sup></b>	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8719	Heavy Cover	0.879	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8720	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8747	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8749	Heavy Cover	0.989	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8750	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8751	Light Cover	0.723	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8756	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8757	Heavy Cover	0.722	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8758	Heavy Cover	0.997	Open	0.731	Heavy Cover	1.000
Bovidae	8760	Heavy Cover	0.991	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8768	Heavy Cover	0.902	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8769	Heavy Cover	0.989	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8771	Heavy Cover	0.873	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8782	Heavy Cover	1.000	Open	0.731	Heavy Cover	1.000
Bovidae	8880	Heavy Cover	0.986	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8913	Heavy Cover	<b>0.647</b>	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9154	Heavy Cover	0.965	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9193	Open	0.676	Heavy Cover	0.750	Open	0.733
Bovidae	9195	Open	<b>0.455</b>	Open	0.731	Open	0.733
Bovidae	9197	Open	<b>0.467</b>	Heavy Cover	0.750	Open	0.733
Bovidae	9228	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9236	Open	0.796	Open	0.731	Open	0.733
Bovidae	9237	Open	0.981	Open	0.731	Open	0.733
Bovidae	9364	Heavy Cover	0.988	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	10235	Open	0.959	Open	0.731	Open	0.733
Bovidae	5823	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8497	Heavy Cover	0.988	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8627	Heavy Cover	0.993	Heavy Cover	0.750	Heavy Cover	1.000

**Table A.22: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8745	Heavy Cover	0.865	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8754	Open	0.841	Heavy Cover	0.750	Open	0.733
Bovidae	8755	Heavy Cover	0.981	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8759	Heavy Cover	<b>0.645</b>	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8761	Heavy Cover	0.767	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8881	Heavy Cover	0.691	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8911	Heavy Cover	0.898	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9153	Heavy Cover	0.985	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9365	Light Cover	0.783	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9414	Heavy Cover	0.954	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	5822	Light Cover	0.806	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	5824	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8427	Heavy Cover	0.783	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8763	Heavy Cover	0.948	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8882	Heavy Cover	0.900	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9151	Heavy Cover	0.784	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9194	Open	0.746	Heavy Cover	0.750	Open	0.733
Bovidae	10324	Heavy Cover	0.933	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	10644	Heavy Cover	0.979	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	5825	Heavy Cover	0.820	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8418	Heavy Cover	0.926	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8498	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8572	Heavy Cover	0.963	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8626	Heavy Cover	<b>0.626</b>	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8753	Light Cover	<b>0.587</b>	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8765	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8767	Heavy Cover	0.998	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8891	Heavy Cover	0.998	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9152	Heavy Cover	0.991	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9229	Heavy Cover	0.807	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9271	Heavy Cover	0.966	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9272	Heavy Cover	0.913	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9366	Heavy Cover	0.917	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	4486	Heavy Cover	<b>0.602</b>	Open	0.731	Heavy Cover	1.000
Bovidae	7830	Open	0.997	Open	0.731	Open	0.733
Bovidae	8624	Heavy Cover	0.996	Open	0.731	Heavy Cover	1.000
Bovidae	8766	Heavy Cover	0.930	Heavy Cover	0.750	Heavy Cover	1.000

**Table A.22: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8773	Open	0.933	Open	0.731	Open	0.733
Bovidae	8780	Heavy Cover	<b>0.610</b>	Open	0.731	Heavy Cover	1.000
Bovidae	8883	Open	<b>0.543</b>	Open	0.731	Open	0.733
Bovidae	8914	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8946	Heavy Cover	0.998	Open	0.731	Heavy Cover	1.000
Bovidae	10310	Open	<b>0.626</b>	Open	0.731	Open	0.733
<i>Duboisia santeng</i>	3238b	Open	<b>0.498</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	2178a	Forest	0.907	Forest	0.667	Forest	0.750
<i>Duboisia santeng</i>	2178b	Forest	0.668	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	264a	Forest	0.655	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	264b	Open	<b>0.491</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797a	Forest	<b>0.517</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797b	Light Cover	<b>0.353</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797c	Forest	0.803	Forest	0.667	Forest	0.750
<i>Duboisia santeng</i>	5797d	Forest	0.891	Forest	0.667	Forest	0.750
<i>Duboisia santeng</i>	5797e	Forest	0.980	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797f	Open	<b>0.570</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797g	Forest	<b>0.561</b>	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797h	Forest	0.926	Light cover	0.760	Forest	0.750
<i>Duboisia santeng</i>	5797i	Forest	0.928	Light cover	0.760	Forest	0.750

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

**Table A.23: Kedung Brubus results: Raw-measurement four-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>P(G/X)</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8684	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9099	Light Cover	0.691	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9100	Open	<b>0.581<sup>2</sup></b>	Open	0.731	Open	0.733
Bovidae	9102	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9105	Open	0.996	Open	0.731	Open	0.733
Bovidae	9106	Heavy Cover	0.991	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9255	Open	0.994	Open	0.731	Open	0.733
Bovidae	9103	Heavy Cover	0.930	Open	0.731	Heavy Cover	1.000
Bovidae	9123	n/a	n/a	Open	0.731	n/a	n/a
Bovidae	8846	Heavy Cover	<b>0.508</b>	Heavy Cover	0.750	Open	0.733
Bovidae	9089	Open	0.941	Heavy Cover	0.750	Open	0.733
Bovidae	9184	Open	0.998	Open	0.731	Open	0.733
Bovidae	9091	Open	0.868	Open	0.731	Open	0.733
Bovidae	9092	Open	0.687	Open	0.731	Open	0.733
Bovidae	9093	Open	0.696	Open	0.731	Open	0.733
Bovidae	9094	n/a	n/a	Open	0.731	n/a	n/a
Bovidae	9095	Light Cover	<b>0.412</b>	Open	0.731	Open	0.733
Bovidae	10875	Open	0.966	Open	0.731	Open	0.733
Bovidae	9087	Heavy Cover	0.666	Open	0.731	Open	0.733
Bovidae	9088	Open	0.986	Open	0.731	Open	0.733
Bovidae	9089	Open	<b>0.519</b>	Open	0.731	Open	0.733
<i>Duboisia santeng</i>	6925a	Forest	0.707	Forest	0.667	Forest	0.750

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

**Table A.24: Trinil results: Size-corrected four-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart<sup>2</sup> Most likely group</b>	<b>(P(G/X))</b>	<b>Combined<sup>2</sup> Most likely group</b>	<b>P(G/X)</b>
Bovidae	5820	Heavy Cover	0.817	Open	0.792	Heavy Cover	0.929
Bovidae	7126	Heavy Cover	0.880	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8419	Heavy Cover	<b>0.592<sup>3</sup></b>	Light Cover	0.778	<b>Open</b>	<b>0.650</b>
Bovidae	8428	Heavy Cover	0.845	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8493	Heavy Cover	0.940	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8494	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8496	Heavy Cover	<b>0.674</b>	Light Cover	0.778	<b>Open</b>	<b>0.650</b>
Bovidae	8623	Heavy Cover	0.961	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8629	Heavy Cover	0.717	Light Cover	0.778	<b>Open</b>	<b>0.650</b>
Bovidae	8718	Light Cover	<b>0.583</b>	Heavy Cover	1.000	Light Cover	0.917
Bovidae	8719	Heavy Cover	0.737	Open	0.792	Heavy Cover	0.929
Bovidae	8720	Heavy Cover	0.970	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8747	Heavy Cover	0.973	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8749	Heavy Cover	0.856	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8750	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8751	Light Cover	<b>0.606</b>	Light Cover	0.778	Light Cover	0.917
Bovidae	8756	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8757	Heavy Cover	<b>0.619</b>	Light Cover	0.778	<b>Open</b>	<b>0.650</b>
Bovidae	8758	Heavy Cover	0.960	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8760	Heavy Cover	0.851	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8768	Heavy Cover	0.702	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8769	Heavy Cover	0.864	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8771	Heavy Cover	<b>0.691</b>	Open	0.792	<b>Open</b>	<b>0.650</b>
Bovidae	8782	Heavy Cover	0.989	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8880	Heavy Cover	0.842	Open	0.792	Heavy Cover	0.929
Bovidae	8913	Heavy Cover	<b>0.618</b>	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9154	Heavy Cover	0.738	Open	0.792	<b>Open</b>	<b>0.650</b>
Bovidae	9193	Open	0.855	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9195	Heavy Cover	<b>0.482</b>	Open	0.792	<b>Open</b>	<b>0.650</b>
Bovidae	9197	Open	<b>0.404</b>	Light Cover	0.778	Open	0.650
Bovidae	9228	Heavy Cover	0.969	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9236	Open	<b>0.379</b>	Forest	0.731	Forest	0.800
Bovidae	9237	Open	<b>0.665</b>	Forest	0.731	Forest	0.800
Bovidae	9364	Heavy Cover	0.874	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	10235	Open	<b>0.608</b>	Open	0.792	Open	0.650
Bovidae	5823	Heavy Cover	0.950	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8497	Heavy Cover	0.861	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8627	Heavy Cover	0.920	Heavy Cover	1.000	Heavy Cover	0.929

**Table A.24: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart<sup>2</sup> Most likely group</b>	<b>(P(G/X))</b>	<b>Combined<sup>2</sup> Most likely group</b>	<b>P(G/X)</b>
Bovidae	8745	Heavy Cover	0.758	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8754	Open	<b>0.584</b>	Open	0.792	Open	0.650
Bovidae	8755	Heavy Cover	0.891	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8759	Heavy Cover	<b>0.613</b>	Light Cover	0.778	Open	0.650
Bovidae	8761	Heavy Cover	<b>0.483</b>	Light Cover	0.778	Light Cover	0.917
Bovidae	8881	Heavy Cover	<b>0.647</b>	Light Cover	0.778	Heavy Cover	0.929
Bovidae	8911	Heavy Cover	<b>0.698</b>	Open	0.792	Heavy Cover	0.929
Bovidae	9153	Heavy Cover	0.847	Open	0.792	Heavy Cover	0.929
Bovidae	9365	Light Cover	<b>0.582</b>	Light Cover	0.778	Light Cover	0.917
Bovidae	9414	Heavy Cover	0.834	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	5822	Light Cover	<b>0.549</b>	Light Cover	0.778	Light Cover	0.917
Bovidae	5824	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8427	Heavy Cover	0.722	Open	0.792	<b>Open</b>	<b>0.650</b>
Bovidae	8763	Heavy Cover	0.762	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8882	Heavy Cover	0.792	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9151	Heavy Cover	<b>0.691</b>	Open	0.792	Open	0.650
Bovidae	9194	Heavy Cover	<b>0.520</b>	Open	0.792	Open	0.650
Bovidae	10324	Heavy Cover	0.793	Open	0.792	Heavy Cover	0.929
Bovidae	10644	Heavy Cover	0.894	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	5825	Heavy Cover	<b>0.630</b>	Forest	0.765	Forest	0.800
Bovidae	8418	Heavy Cover	0.707	Light Cover	0.778	Heavy Cover	0.929
Bovidae	8498	Heavy Cover	0.975	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8572	Heavy Cover	0.884	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8626	Light Cover	<b>0.590</b>	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8753	Light Cover	<b>0.615</b>	Light Cover	0.778	<b>Open</b>	0.650
Bovidae	8765	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8767	Heavy Cover	0.946	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8891	Heavy Cover	0.916	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9152	Heavy Cover	0.924	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9229	Heavy Cover	<b>0.631</b>	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9271	Heavy Cover	0.803	Heavy Cover	1.000	<b>Open</b>	0.650
Bovidae	9272	Heavy Cover	<b>0.638</b>	Forest	0.765	Forest	0.800
Bovidae	9366	Heavy Cover	<b>0.629</b>	Open	0.792	<b>Open</b>	0.650
Bovidae	4486	Heavy Cover	<b>0.569</b>	Open	0.792	Open	0.650
Bovidae	7830	Open	0.877	Open	0.792	Open	0.650
Bovidae	8624	Heavy Cover	0.935	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	8766	Heavy Cover	0.778	Heavy Cover	1.000	Heavy Cover	0.929

**Table A.24: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart<sup>2</sup> Most likely group</b>	<b>(P(G/X))</b>	<b>Combined<sup>2</sup> Most likely group</b>	<b>P(G/X)</b>
Bovidae	8773	Open	<b>0.555</b>	Open	0.792	Open	0.650
Bovidae	8780	Heavy Cover	<b>0.564</b>	Open	0.792	<b>Open</b>	0.650
Bovidae	8883	Open	<b>0.390</b>	Forest	0.765	Forest	0.800
Bovidae	8914	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8946	Heavy Cover	0.950	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	10310	Light Cover	<b>0.428</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
<i>Duboisia santeng</i>	3238b	Open	<b>0.516</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	2178a	Forest	0.982	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	2178b	Open	0.871	Open	0.792	Open	0.650
<i>Duboisia santeng</i>	264a	Forest	<b>0.502</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	264b	Open	<b>0.598</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797a	Forest	<b>0.384</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797b	Open	<b>0.615</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797c	Open	<b>0.494</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797d	Forest	0.706	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797e	Forest	0.980	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797f	Forest	0.753	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797g	Open	<b>0.459</b>	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797h	Forest	0.748	Forest	0.765	Forest	0.800
<i>Duboisia santeng</i>	5797i	Forest	<b>0.467</b>	Forest	0.765	Forest	0.800

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Pruned classification tree results.

<sup>3</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 70%).



**Table A.25: Kedung Brubus results: Size-corrected four-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart<sup>2</sup> Most likely group</b>	<b>(P(G/X))</b>	<b>Combined<sup>2</sup> Most likely group</b>	<b>P(G/X)</b>
Bovidae	8684	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9099	Light Cover	<b>0.584<sup>3</sup></b>	Open	0.792	<b>Open</b>	<b>0.650</b>
Bovidae	9100	Heavy Cover	<b>0.497</b>	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9102	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9105	Open	0.865	Open	0.792	Open	0.650
Bovidae	9106	Heavy Cover	0.886	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9255	Open	<b>0.614</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
Bovidae	9103	Heavy Cover	0.800	Forest	0.765	Heavy Cover	0.929
Bovidae	9123	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8846	Heavy Cover	<b>0.631</b>	Forest	0.765	Heavy Cover	0.929
Bovidae	9089	Light Cover	<b>0.512</b>	Open	0.792	Open	0.650
Bovidae	9184	Open	0.866	Open	0.792	Open	0.650
Bovidae	9091	Open	<b>0.566</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
Bovidae	9092	Light Cover	<b>0.398</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
Bovidae	9093	Heavy Cover	<b>0.477</b>	Open	0.792	Open	0.650
Bovidae	9094	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9095	Heavy Cover	<b>0.412</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
Bovidae	10875	Open	<b>0.423</b>	Forest	0.765	Forest	0.800
Bovidae	9087	Heavy Cover	<b>0.674</b>	Heavy Cover	1.000	Heavy Cover	0.929
Bovidae	9088	Open	0.834	Open	0.792	Open	0.650
Bovidae	9089	Heavy Cover	<b>0.490</b>	<b>Light Cover</b>	<b>0.607</b>	Open	0.650
<i>Duboisia santeng</i>	6925a	Forest	<b>0.516</b>	Forest	0.765	Forest	0.800

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Pruned classification tree results.

<sup>3</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 70%).

**Table A.26: Trinil results: Raw-measurement five-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>P(G/X)</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	5820	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	7126	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8419	Heavy Cover	0.992	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8428	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8493	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8494	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8496	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8623	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8629	Heavy Cover	0.969	Open	1.000	Heavy Cover	1.000
Bovidae	8718	Heavy Cover	0.989	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8719	Heavy Cover	0.995	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8720	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8747	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8749	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8750	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8751	Heavy Cover	0.858	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8756	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8757	Heavy Cover	0.986	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8758	Heavy Cover	1.000	Open	1.000	Heavy Cover	1.000
Bovidae	8760	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8768	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8769	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8771	Heavy Cover	0.914	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8782	Heavy Cover	1.000	Open	1.000	Heavy Cover	1.000
Bovidae	8880	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8913	Heavy Cover	0.998	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9154	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9193	Forest	0.996	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9195	Open	0.682	Open	1.000	Open	0.790
Bovidae	9197	Light Cover	<b>0.552<sup>2</sup></b>	Heavy Cover	0.750	Open	0.790
Bovidae	9228	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9236	Open	0.958	Open	1.000	Open	0.790
Bovidae	9237	Open	0.987	Open	1.000	Open	0.790
Bovidae	9364	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	10235	Open	0.971	Open	1.000	Open	0.790
Bovidae	5823	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8497	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8627	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000

**Table A.26: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8745	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8754	Open	0.860	Heavy Cover	0.750	Open	0.790
Bovidae	8755	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8759	Heavy Cover	0.991	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8761	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8881	Heavy Cover	0.997	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8911	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9153	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9365	Heavy Cover	0.819	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9414	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	5822	Light Cover	0.873	Heavy Cover	0.750	Open	0.790
Bovidae	5824	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8427	Heavy Cover	0.928	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8763	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8882	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9151	Heavy Cover	0.989	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9194	Open	0.901	Heavy Cover	0.750	Open	0.790
Bovidae	10324	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	10644	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	5825	Heavy Cover	0.989	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8418	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8498	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8572	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8626	Heavy Cover	0.999	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8753	Heavy Cover	0.750	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8765	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8767	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	8891	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9152	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9229	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9271	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9272	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9366	Heavy Cover	0.990	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	4486	Heavy Cover	0.747	Open	1.000	Heavy Cover	1.000
Bovidae	7830	Open	0.998	Open	1.000	Open	0.790
Bovidae	8624	Heavy Cover	1.000	Open	1.000	Heavy Cover	1.000
Bovidae	8766	Heavy Cover	0.999	Heavy Cover	0.750	Heavy Cover	1.000

**Table A.26: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8773	Open	0.979	Open	1.000	Open	0.790
Bovidae	8780	Heavy Cover	0.612	Open	1.000	Heavy Cover	1.000
Bovidae	8883	Open	<b>0.605</b>	Open	1.000	Open	0.790
Bovidae	8914	n/a	n/a	Heavy Cover	0.750	n/a	n/a
Bovidae	8946	Heavy Cover	1.000	Open	1.000	Heavy Cover	1.000
Bovidae	10310	Open	0.709	Open	1.000	Open	0.790
<i>Duboisia santeng</i>	3238b	Forest	<b>0.401</b>	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	2178a	Forest	0.670	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	2178b	Forest	0.616	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	264a	Mountain	<b>0.437</b>	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	264b	Open	<b>0.347</b>	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	5797a	Mountain	<b>0.505</b>	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	5797b	Mountain	<b>0.403</b>	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	5797c	Forest	<b>0.511</b>	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	5797d	Forest	0.865	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	5797e	Forest	<b>0.586</b>	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	5797f	Open	<b>0.568</b>	Mountain	0.770	Mountain	0.890
<i>Duboisia santeng</i>	5797g	Mountain	<b>0.476</b>	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	5797h	Forest	0.769	Light cover	0.860	Mountain	0.890
<i>Duboisia santeng</i>	5797i	Forest	0.728	Mountain	0.770	Mountain	0.890

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 61%).

**Table A.27: Kedung Brubus results: Raw-measurement five-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>P(G/X)</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8684	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9099	Light Cover	<b>0.550</b> <sup>2</sup>	Heavy Cover	0.750	Open	0.790
Bovidae	9100	Heavy Cover	0.795	Open	1.000	Heavy Cover	1.000
Bovidae	9102	n/a	n/a	Open	1.000	n/a	n/a
Bovidae	9105	Open	0.998	Open	1.000	Open	0.790
Bovidae	9106	Heavy Cover	1.000	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9255	Open	0.998	Open	1.000	Open	0.790
Bovidae	9103	Heavy Cover	0.934	Open	1.000	Heavy Cover	1.000
Bovidae	9123	n/a	n/a	Open	1.000	n/a	n/a
Bovidae	8846	Heavy Cover	0.936	Heavy Cover	0.750	Heavy Cover	1.000
Bovidae	9089	Open	0.984	Heavy Cover	0.750	Open	0.790
Bovidae	9184	Open	0.999	Open	1.000	Open	0.790
Bovidae	9091	Open	0.944	Open	1.000	Open	0.790
Bovidae	9092	Open	0.829	Open	1.000	Open	0.790
Bovidae	9093	Open	0.834	Open	1.000	Open	0.790
Bovidae	9094	n/a	n/a	Open	1.000	n/a	n/a
Bovidae	9095	Light Cover	<b>0.435</b>	Open	1.000	Open	0.790
Bovidae	10875	Open	0.985	Open	1.000	Open	0.790
Bovidae	9087	Heavy Cover	0.931	Open	1.000	Heavy Cover	1.000
Bovidae	9088	Open	0.988	Open	1.000	Open	0.790
Bovidae	9089	Open	<b>0.562</b>	Open	1.000	Open	0.790
<i>Duboisia santeng</i>	6925a	Forest	0.633	Forest	0.710	Mountain	0.890

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 61%).

**Table A.28: Trinil results: Size-corrected five-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	5820	Heavy Cover	0.850	Open	0.870	Heavy Cover	1.000
Bovidae	7126	Heavy Cover	0.901	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8419	Mountain	<b>0.592<sup>2</sup></b>	Mountain	0.820	Mountain	0.720
Bovidae	8428	Heavy Cover	0.918	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8493	Heavy Cover	0.917	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8494	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8496	Mountain	<b>0.409</b>	Mountain	0.820	Heavy Cover	1.000
Bovidae	8623	Heavy Cover	0.987	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8629	Heavy Cover	<b>0.530</b>	Mountain	0.820	Heavy Cover	1.000
Bovidae	8718	Light Cover	<b>0.608</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8719	Heavy Cover	0.783	Open	0.870	Heavy Cover	1.000
Bovidae	8720	Heavy Cover	0.988	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8747	Heavy Cover	0.976	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8749	Heavy Cover	<b>0.544</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8750	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8751	Light Cover	<b>0.596</b>	Mountain	0.820	Mountain	0.720
Bovidae	8756	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8757	Mountain	<b>0.494</b>	Mountain	0.820	Mountain	0.720
Bovidae	8758	Heavy Cover	0.981	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8760	Mountain	<b>0.594</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8768	Mountain	<b>0.468</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8769	Heavy Cover	0.880	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8771	Mountain	0.878	Forest	0.570	Mountain	0.720
Bovidae	8782	Heavy Cover	0.999	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8880	Mountain	<b>0.500</b>	Mountain	0.820	Heavy Cover	1.000
Bovidae	8913	Heavy Cover	<b>0.581</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9154	Mountain	0.738	Mountain	0.820	Mountain	0.720
Bovidae	9193	Heavy Cover	0.997	Heavy Cover	0.790	Open	0.759
Bovidae	9195	Mountain	<b>0.475</b>	Open	0.870	Open	0.759
Bovidae	9197	Open	<b>0.419</b>	Light Cover	0.690	Open	0.759
Bovidae	9228	Heavy Cover	0.990	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9236	Heavy Cover	<b>0.443</b>	Forest	0.710	Forest	0.714
Bovidae	9237	Open	<b>0.624</b>	Forest	0.710	Forest	0.714
Bovidae	9364	Heavy Cover	0.845	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	10235	Open	<b>0.602</b>	Forest	0.710	Open	0.759
Bovidae	5823	Heavy Cover	0.975	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8497	Heavy Cover	0.942	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8627	Heavy Cover	0.970	Heavy Cover	0.790	Heavy Cover	1.000

**Table A.28: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8745	Heavy Cover	0.832	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8754	Open	0.665	Open	0.870	Open	0.759
Bovidae	8755	Heavy Cover	0.965	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8759	Heavy Cover	<b>0.532</b>	Light Cover	0.690	Heavy Cover	1.000
Bovidae	8761	Light Cover	<b>0.434</b>	Mountain	0.820	Heavy Cover	1.000
Bovidae	8881	Heavy Cover	<b>0.610</b>	Open	0.870	Heavy Cover	1.000
Bovidae	8911	Heavy Cover	0.828	Open	0.870	Heavy Cover	1.000
Bovidae	9153	Heavy Cover	0.738	Mountain	0.820	Heavy Cover	1.000
Bovidae	9365	Light Cover	0.663	Light Cover	0.690	Light Cover	1.000
Bovidae	9414	Heavy Cover	0.842	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	5822	Light Cover	<b>0.522</b>	Light Cover	0.690	Open	0.759
Bovidae	5824	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8427	Mountain	<b>0.406</b>	Mountain	0.820	Mountain	0.720
Bovidae	8763	Heavy Cover	0.807	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8882	Heavy Cover	0.898	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9151	Heavy Cover	<b>0.553</b>	Open	0.870	Open	0.759
Bovidae	9194	Open	<b>0.511</b>	Open	0.870	Open	0.759
Bovidae	10324	Heavy Cover	0.805	Open	0.870	Heavy Cover	1.000
Bovidae	10644	Heavy Cover	0.924	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	5825	Mountain	<b>0.517</b>	Mountain	0.820	Mountain	0.720
Bovidae	8418	Heavy Cover	0.716	Mountain	0.820	Heavy Cover	1.000
Bovidae	8498	Heavy Cover	0.936	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8572	Heavy Cover	0.929	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8626	Light Cover	<b>0.644</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8753	Mountain	<b>0.501</b>	Mountain	0.820	Mountain	0.720
Bovidae	8765	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8767	Heavy Cover	0.980	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8891	Heavy Cover	0.692	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9152	Heavy Cover	0.977	Light Cover	0.690	Heavy Cover	1.000
Bovidae	9229	Heavy Cover	<b>0.410</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9271	Mountain	<b>0.495</b>	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9272	Mountain	<b>0.553</b>	Mountain	0.820	Heavy Cover	1.000
Bovidae	9366	Mountain	0.689	Mountain	0.820	Mountain	0.720
Bovidae	4486	Heavy Cover	<b>0.419</b>	Open	0.870	Open	0.759
Bovidae	7830	Open	0.844	Open	0.870	Open	0.759
Bovidae	8624	Heavy Cover	0.975	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	8766	Heavy Cover	0.878	Heavy Cover	0.790	Heavy Cover	1.000

**Table A.28: Continued.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8773	Open	<b>0.594</b>	Open	0.870	Open	0.759
Bovidae	8780	Mountain	<b>0.552</b>	Mountain	0.820	Mountain	0.720
Bovidae	8883	Open	<b>0.325</b>	Light Cover	0.690	Open	0.759
Bovidae	8914	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8946	Heavy Cover	0.971	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	10310	Light Cover	<b>0.371</b>	Light cover	0.690	Open	0.759
<i>Duboisia santeng</i>	3238b	Forest	<b>0.561</b>	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	2178a	Forest	0.946	Forest	0.570	Mountain	0.720
<i>Duboisia santeng</i>	2178b	Open	0.856	Open	0.870	Open	0.759
<i>Duboisia santeng</i>	264a	Mountain	<b>0.380</b>	Mountain	0.820	Mountain	0.720
<i>Duboisia santeng</i>	264b	Open	<b>0.515</b>	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	5797a	Mountain	<b>0.565</b>	Mountain	0.820	Mountain	0.720
<i>Duboisia santeng</i>	5797b	Open	<b>0.495</b>	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	5797c	Mountain	<b>0.495</b>	Mountain	0.820	Mountain	0.720
<i>Duboisia santeng</i>	5797d	Forest	0.851	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	5797e	Forest	<b>0.491</b>	Forest	0.570	Mountain	0.720
<i>Duboisia santeng</i>	5797f	Forest	<b>0.539</b>	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	5797g	Mountain	<b>0.453</b>	Mountain	0.820	Mountain	0.720
<i>Duboisia santeng</i>	5797h	Forest	<b>0.646</b>	Forest	0.710	Forest	0.714
<i>Duboisia santeng</i>	5797i	Heavy Cover	<b>0.516</b>	Forest	0.570	Mountain	0.720

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).



**Table A.29: Kedung Brubus results: Size-corrected five-habitat models.**

<b>Taxon</b>	<b>Dubois Collection number</b>	<b>LDA Most likely group</b>	<b>P(G/X)<sup>1</sup></b>	<b>rpart Most likely group</b>	<b>(P(G/X))</b>	<b>Combined Most likely group</b>	<b>P(G/X)</b>
Bovidae	8684	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9099	Mountain	<b>0.509<sup>2</sup></b>	Mountain	0.820	Mountain	0.720
Bovidae	9100	Heavy Cover	0.944	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9102	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9105	Open	0.834	Open	0.870	Open	0.759
Bovidae	9106	Heavy Cover	0.907	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9255	Open	<b>0.578</b>	Open	0.870	Open	0.759
Bovidae	9103	Heavy Cover	<b>0.610</b>	Mountain	0.820	Mountain	0.720
Bovidae	9123	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	8846	Heavy Cover	0.845	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9089	Open	<b>0.343</b>	Open	0.870	Open	0.759
Bovidae	9184	Open	0.841	Open	0.870	Open	0.759
Bovidae	9091	Open	<b>0.609</b>	Open	0.870	Open	0.759
Bovidae	9092	Mountain	<b>0.416</b>	Open	0.870	Open	0.759
Bovidae	9093	Heavy Cover	<b>0.557</b>	Forest	0.792	Forest	0.714
Bovidae	9094	n/a	n/a	n/a	n/a	n/a	n/a
Bovidae	9095	Open	<b>0.335</b>	Light Cover	0.690	Open	0.759
Bovidae	10875	Mountain	<b>0.518</b>	Mountain	0.820	Mountain	0.720
Bovidae	9087	Heavy Cover	0.869	Heavy Cover	0.790	Heavy Cover	1.000
Bovidae	9088	Open	0.817	Open	0.870	Open	0.759
Bovidae	9089	Heavy Cover	<b>0.552</b>	Light Cover	0.690	Open	0.759
<i>Duboisia santeng</i>	6925a	Forest	<b>0.606</b>	Forest	0.710	Forest	0.714

<sup>1</sup>P(G/X) is the probability of an individual belonging to the assigned group.

<sup>2</sup>Bold-face probabilities are those less than the calculated confidence value for the LDA analysis (c.v. = 65%).

## **APPENDIX B**

### **Figures**

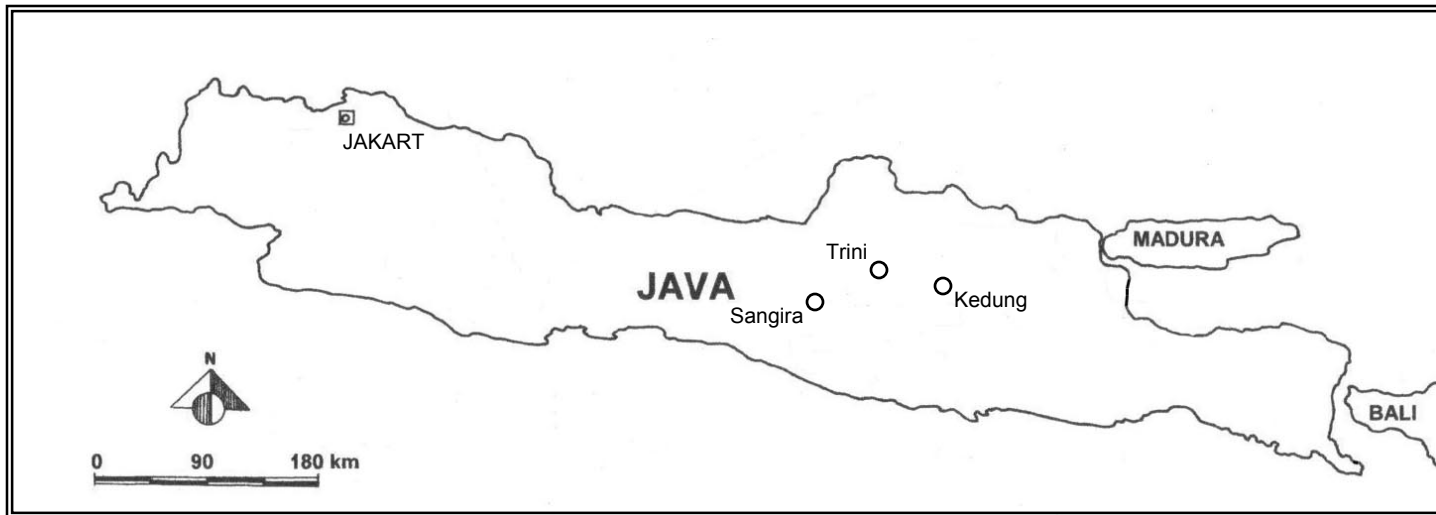


Figure B.1. Site localities in Java.

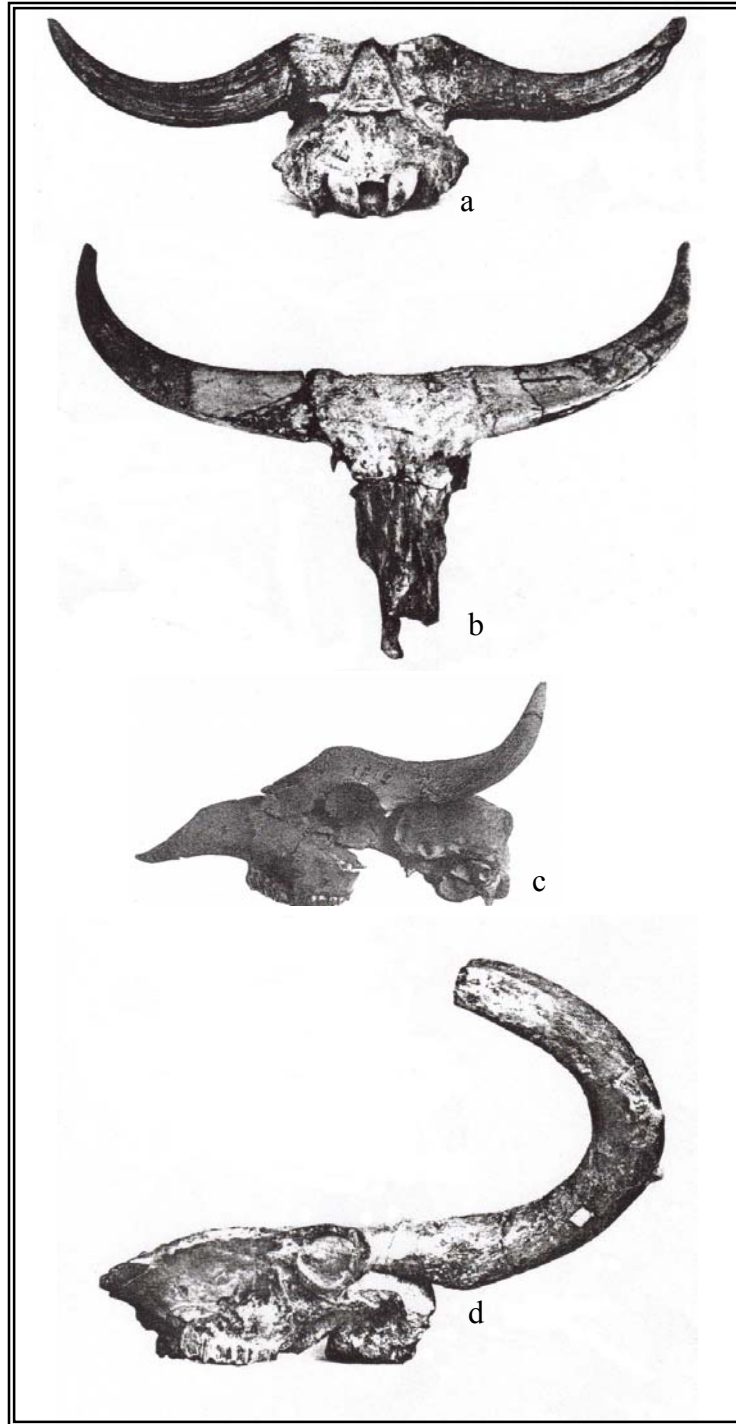


Figure B.2. Fossil Bovidae from Java (from Hooijer, 1958). a) *Bibos palaeosondaicus*; b) *Bubalus palaeokerabau*; c) *Duboisia santeng*; d) *Epileptobos groenveldtii*. Images are not to scale.

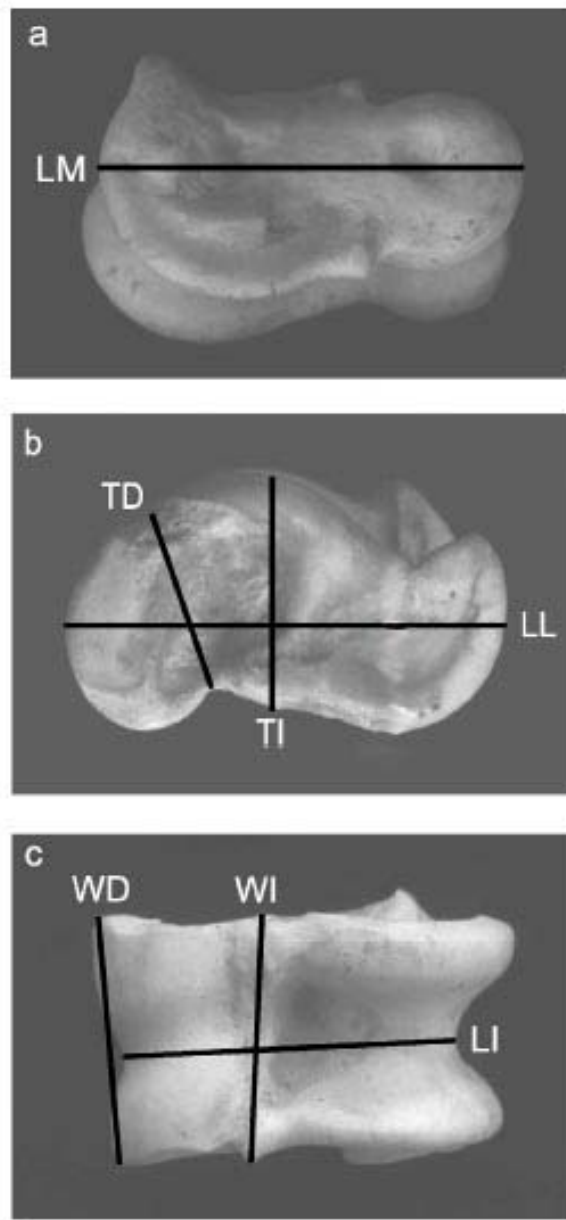


Figure B.3. Astragalus metrics. (a) Medial view of bovid right astragalus with medial length (LM) measurement indicated. (b) Lateral view of bovid right astragalus with distal thickness (TD), intermediate thickness (TI), and lateral length (LL) indicated. (c) Anterior view of bovid right astragalus with distal width (WD), intermediate width (WI), and intermediate length indicated. Adapted from Degusta and Vrba (2003).

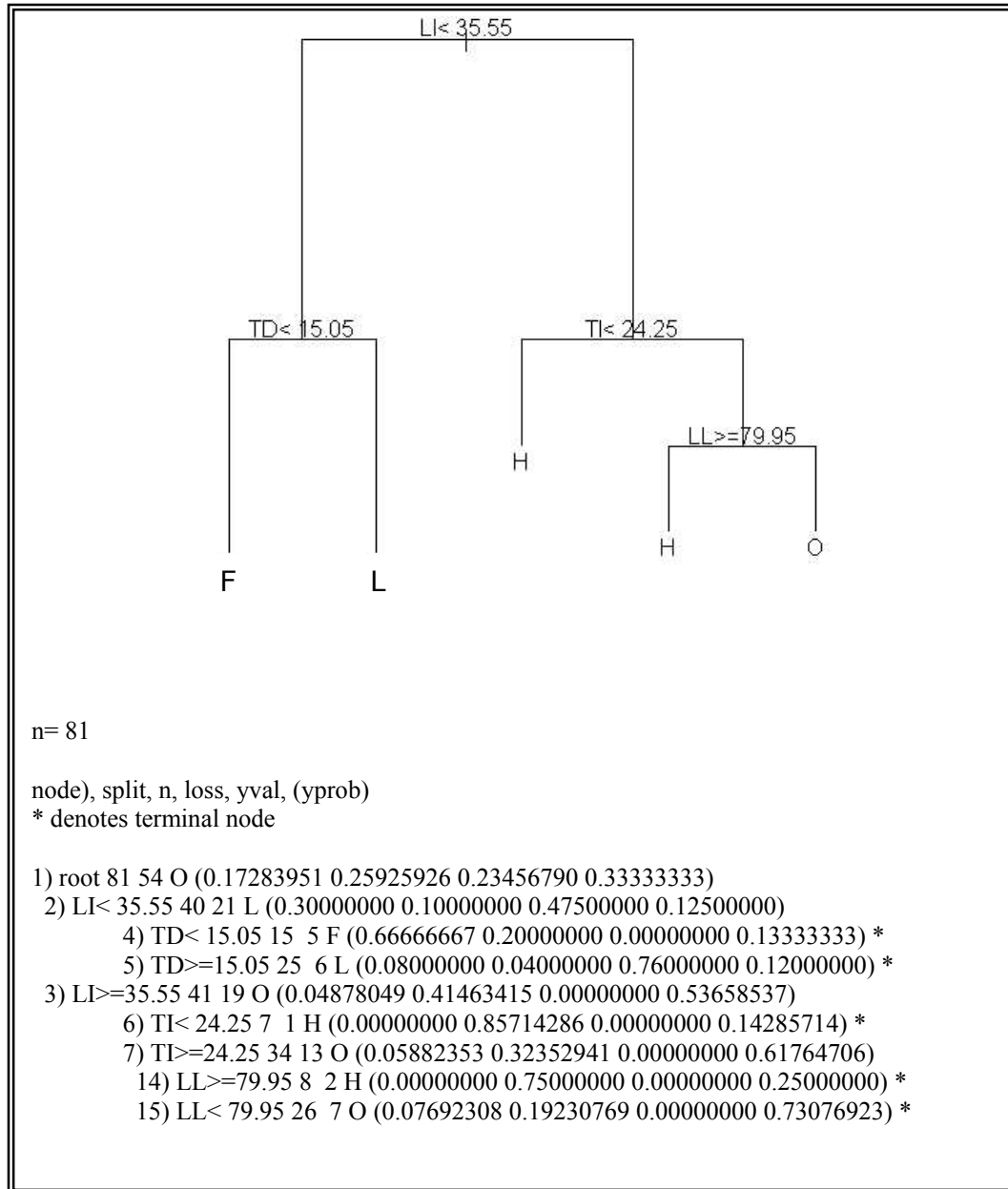


Figure B.4. Full classification tree results: Raw-measurement four-habitat model. “F, L, H, and O” refer to Forest, Heavy Cover, Light Cover, and Open, respectively. “Node” is the branch number, “split” defines the criterion for branching, “n” represents number of cases assigned to node, “loss” represents number of misclassified cases adjusted for prior information, “yval” is classification given to node if it were terminal, and “yprob” represents Bayesian probabilities (Forest, Heavy Cover, Light Cover, Open).

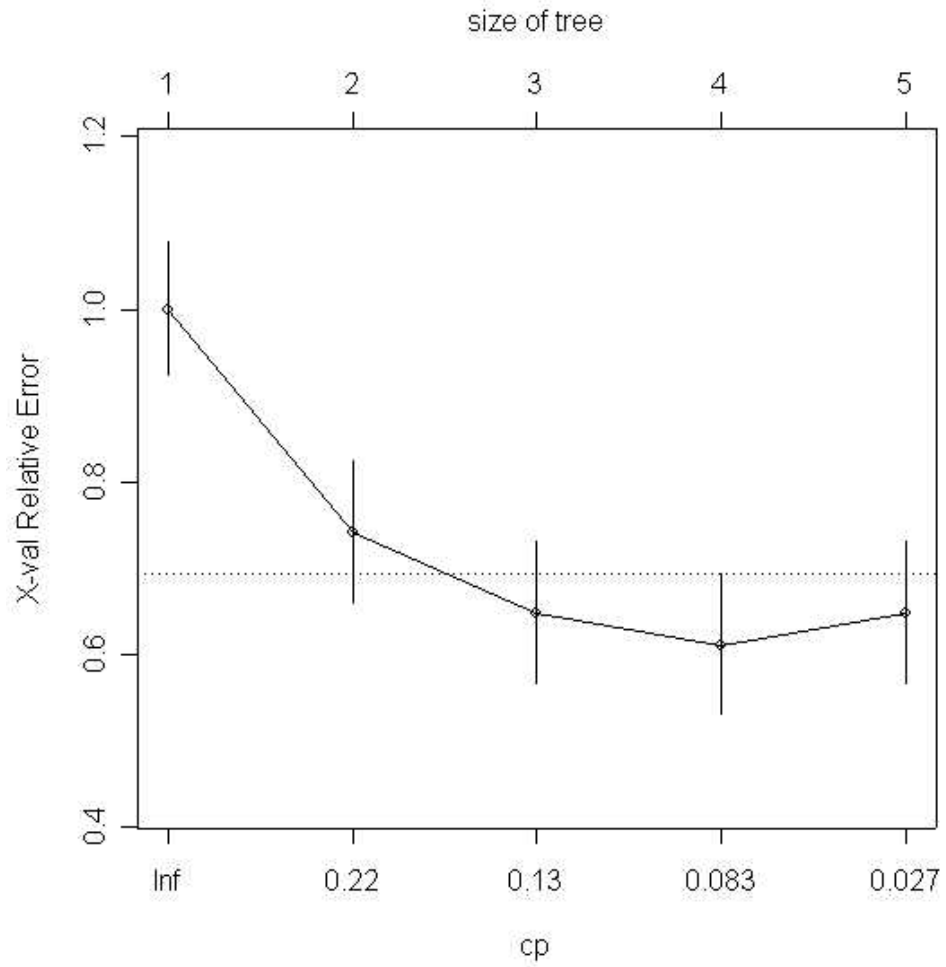


Figure B.5. Complexity parameter plot: Raw-measurement four-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

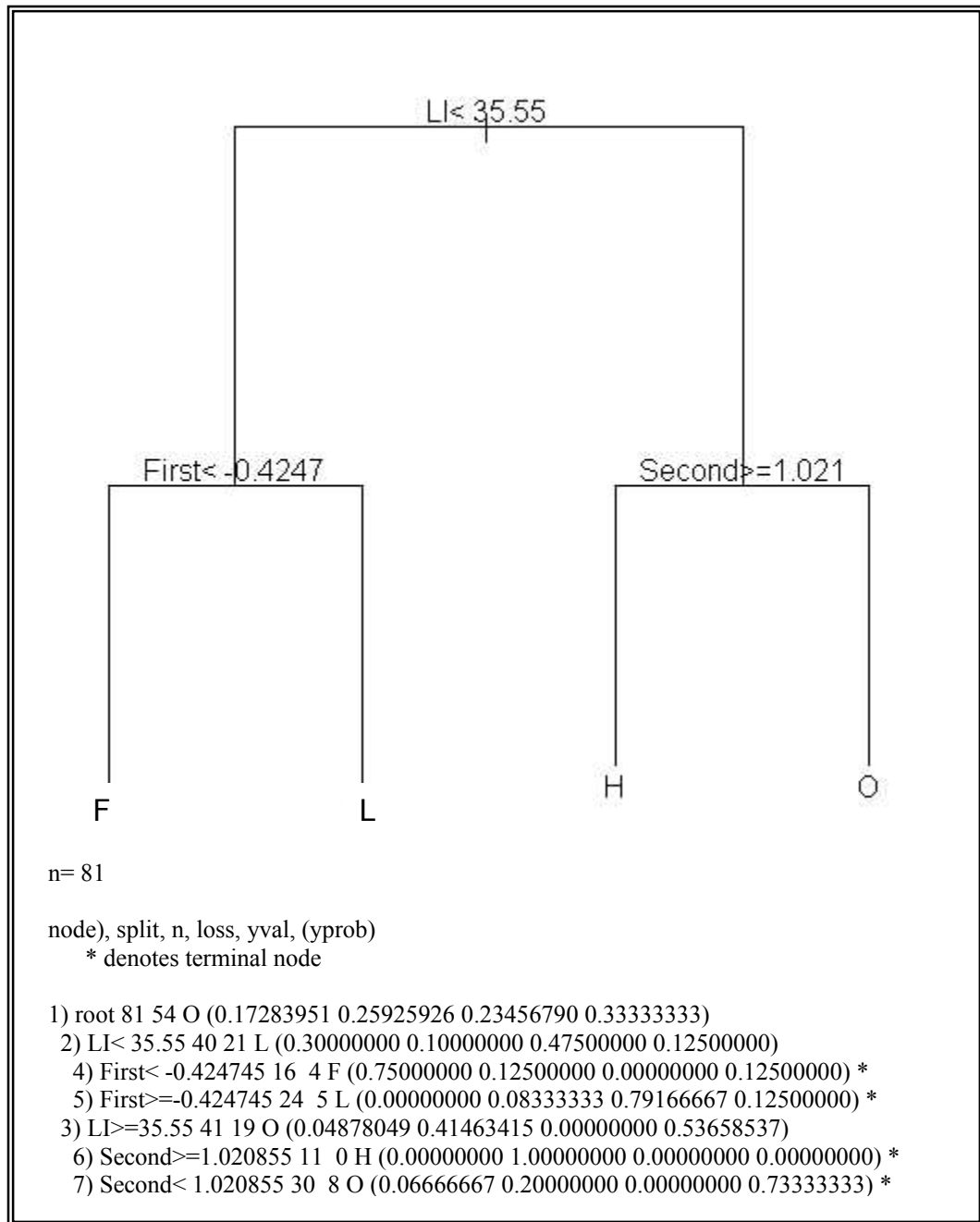


Figure B.6. Full classification tree results: Combined raw-measurement four-habitat model.



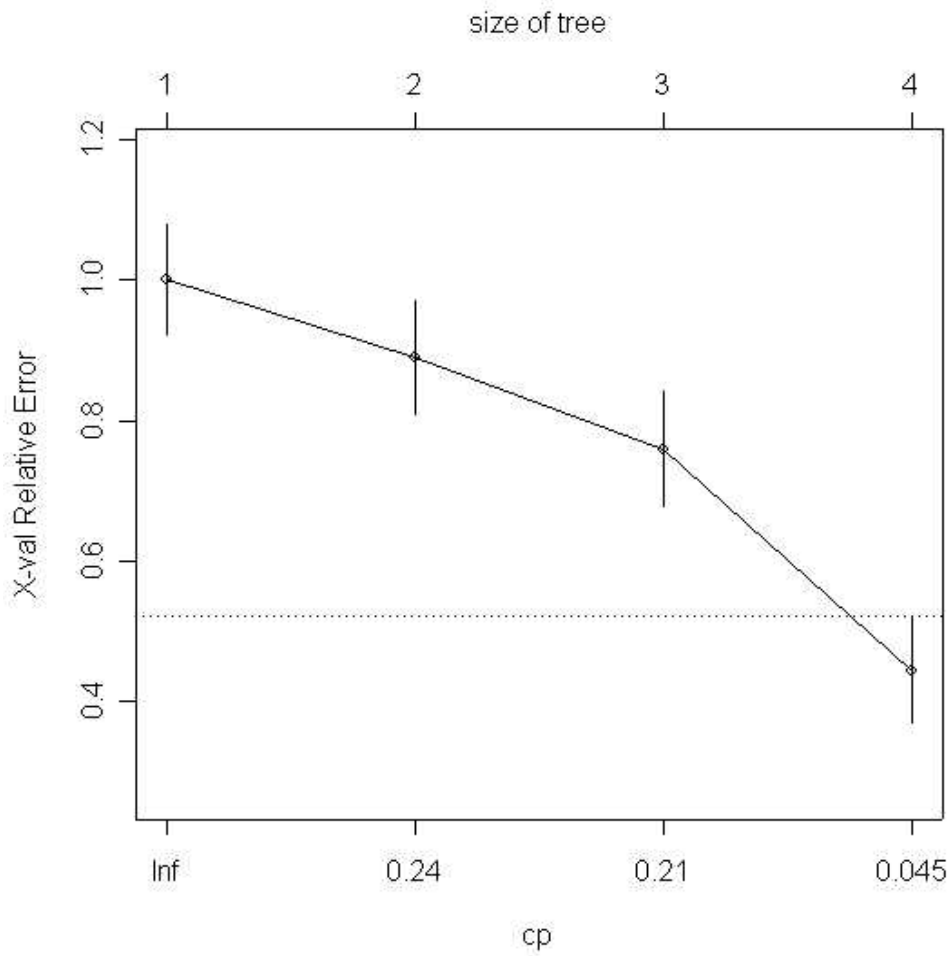


Figure B.7. Complexity parameter plot: Combined raw-measurement four-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

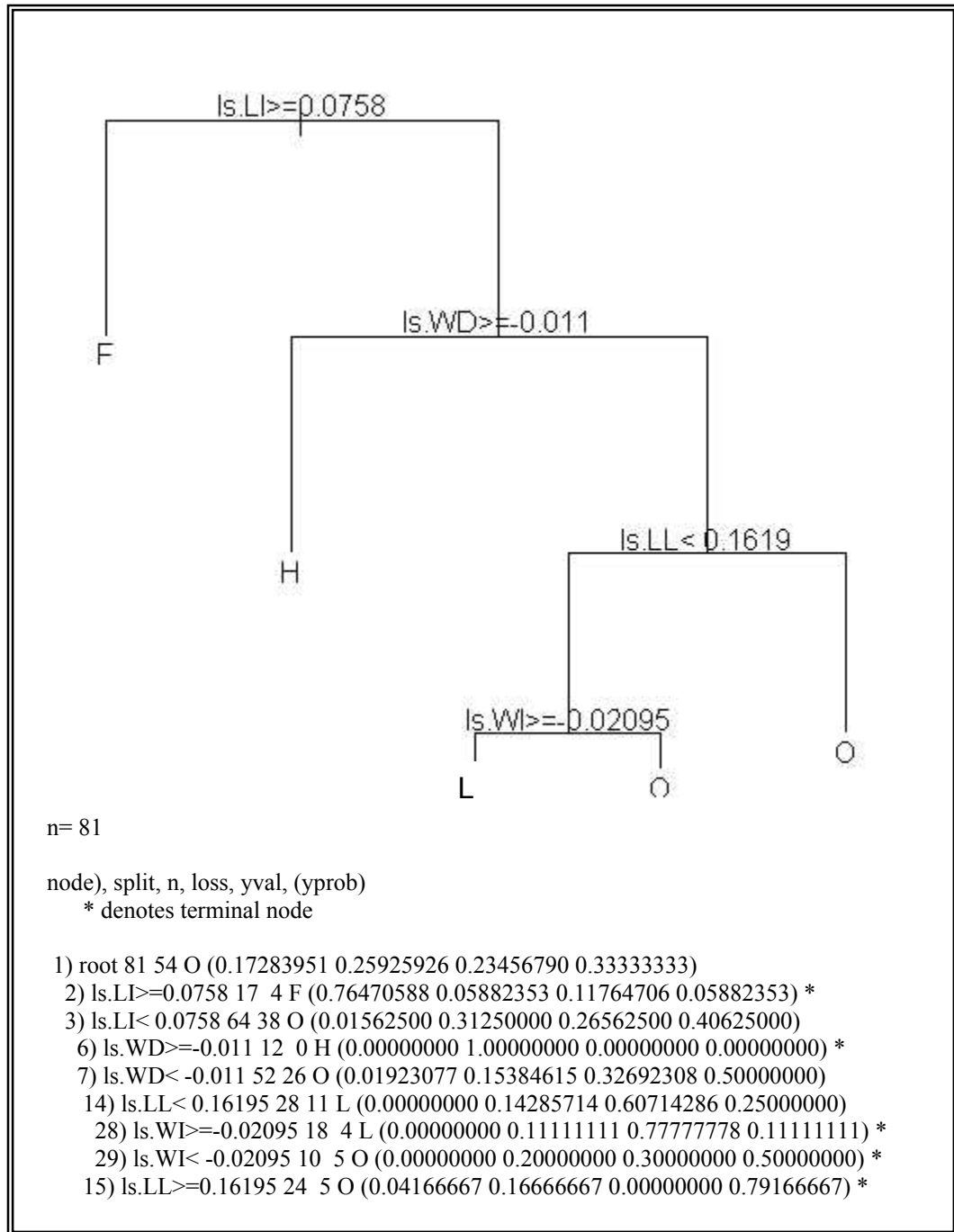


Figure B.8. Full classification tree results: Size-corrected four-habitat model.

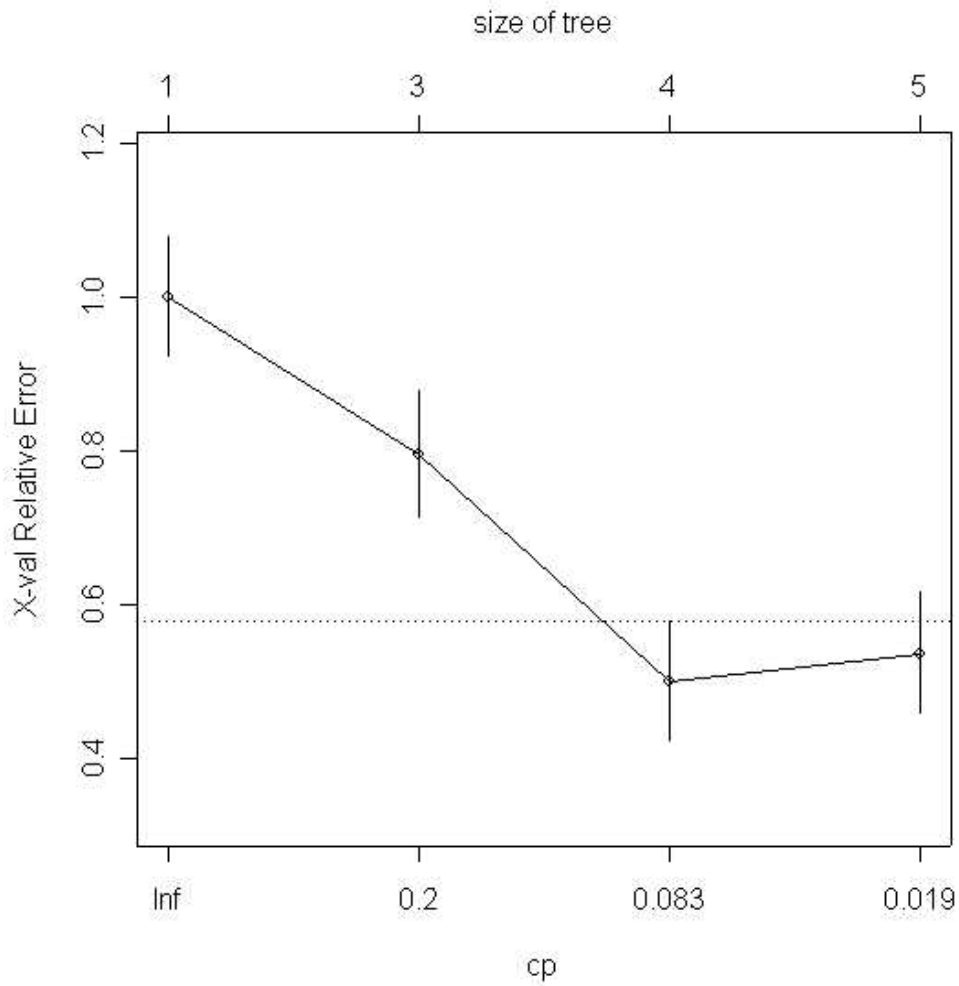


Figure B.9. Complexity parameter plot: Size-corrected four-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

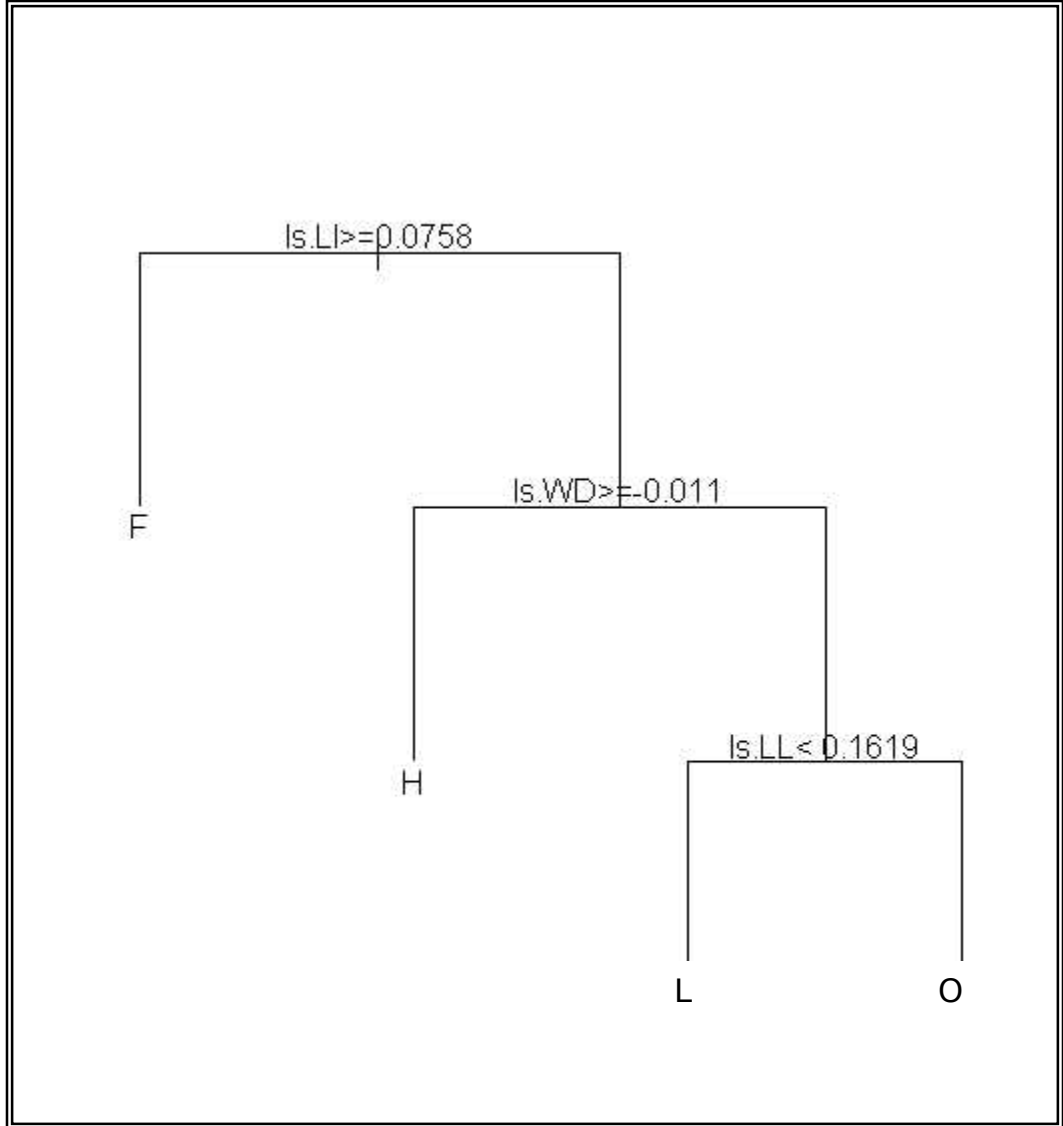


Figure B.10. Pruned classification tree: Size-corrected four-habitat model.

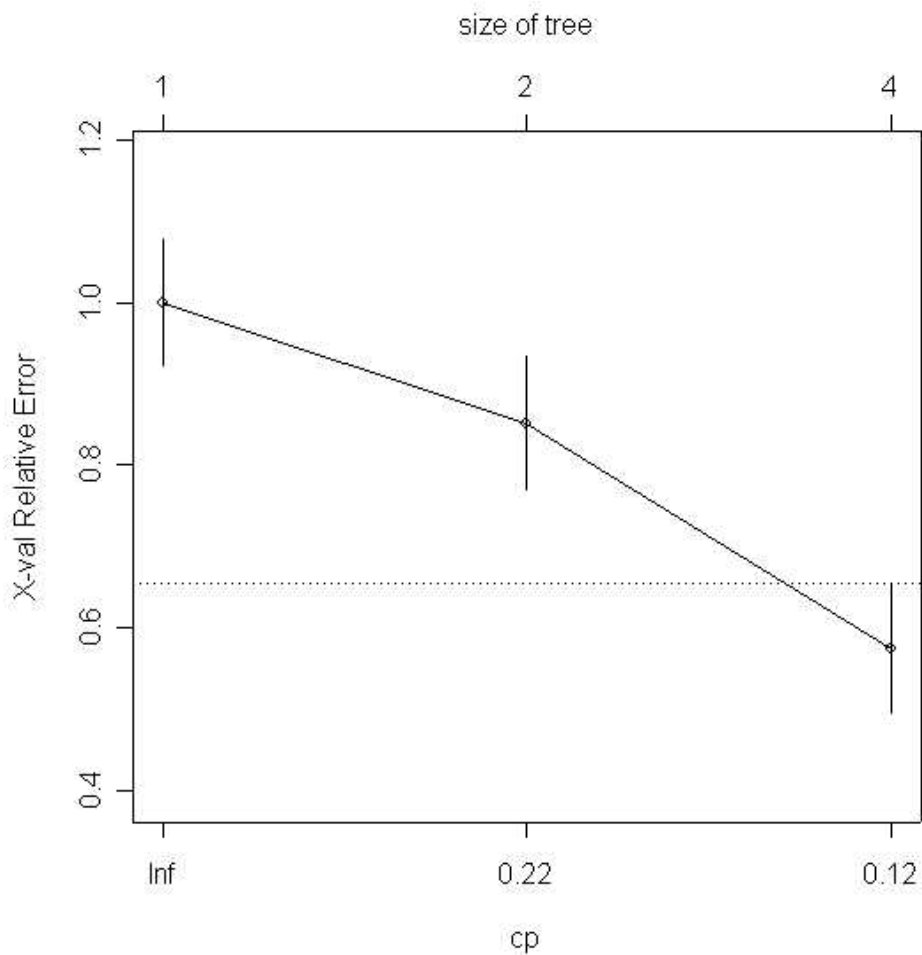


Figure B.11. Complexity parameter plot: Pruned size-corrected four-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

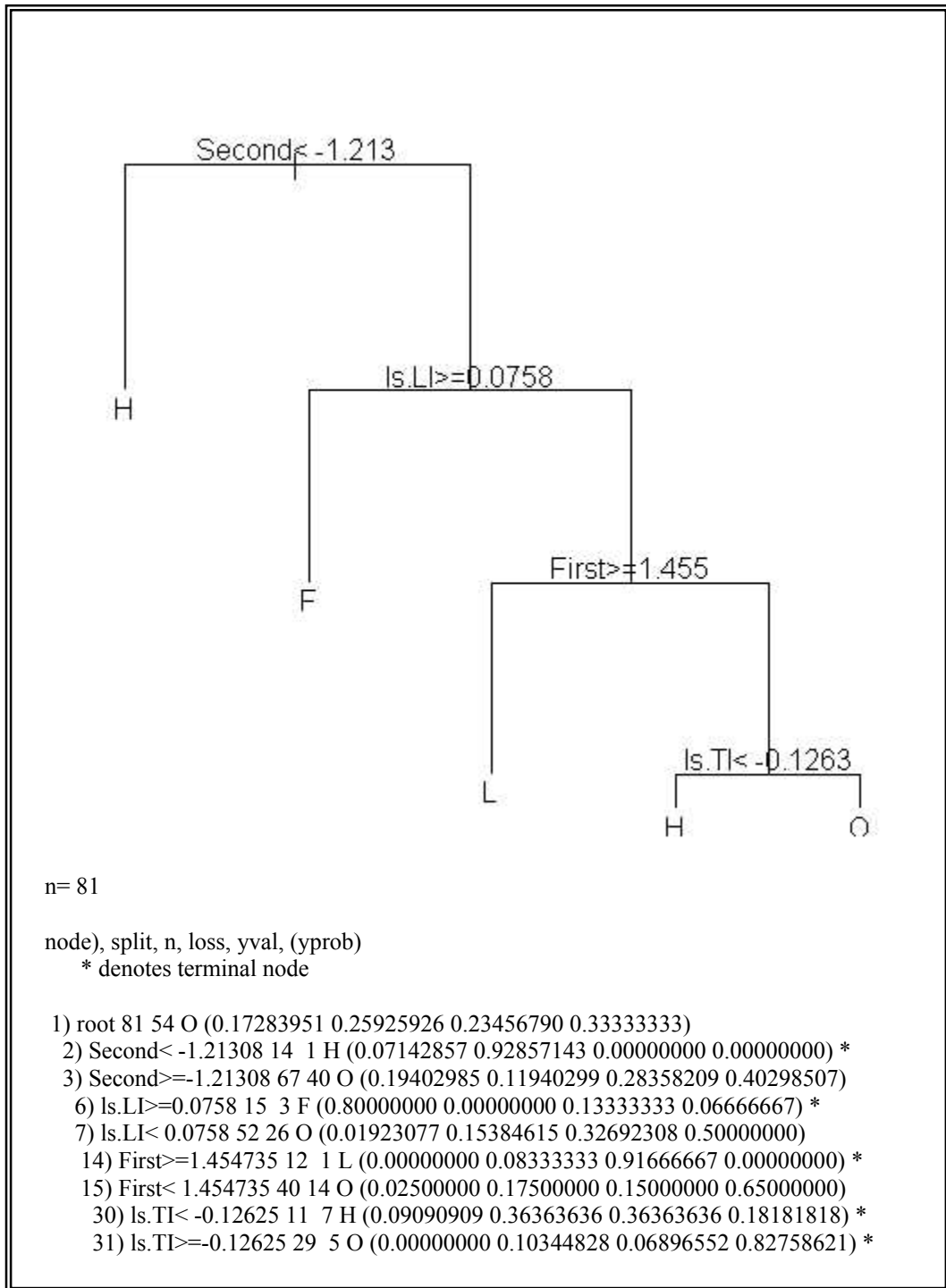


Figure B.12. Full classification tree results: Combined size-corrected four-habitat model.

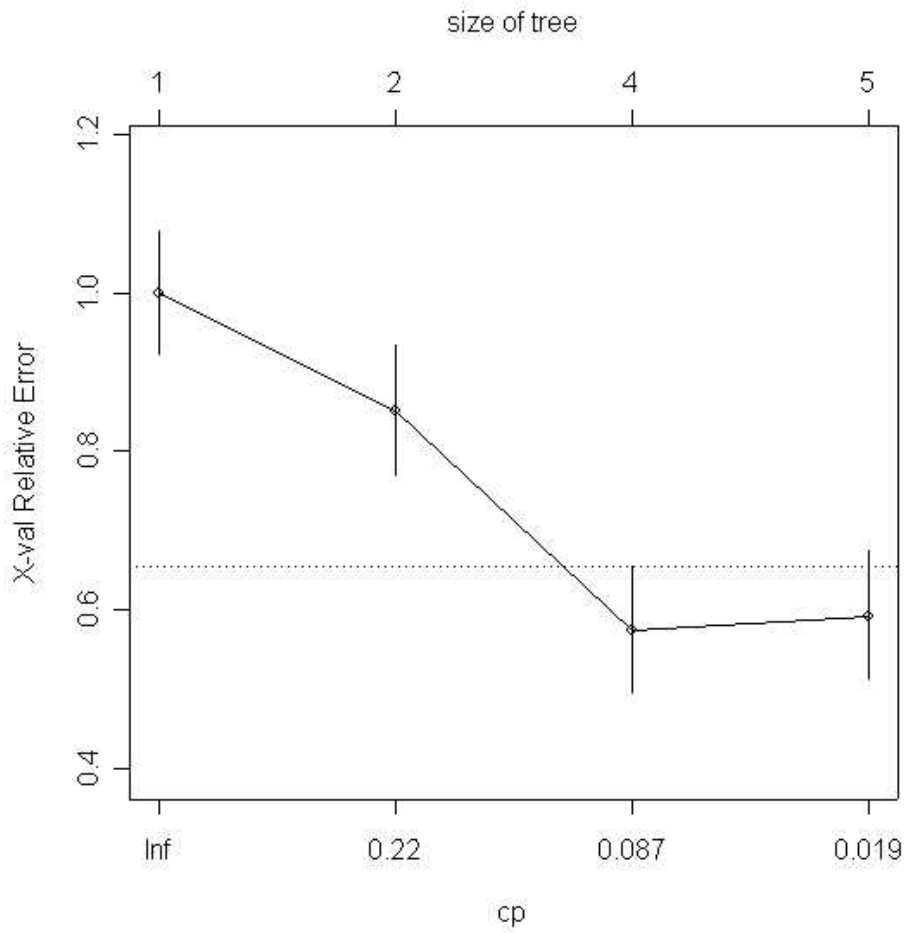


Figure B.13. Complexity parameter plot: Combined size-corrected four-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

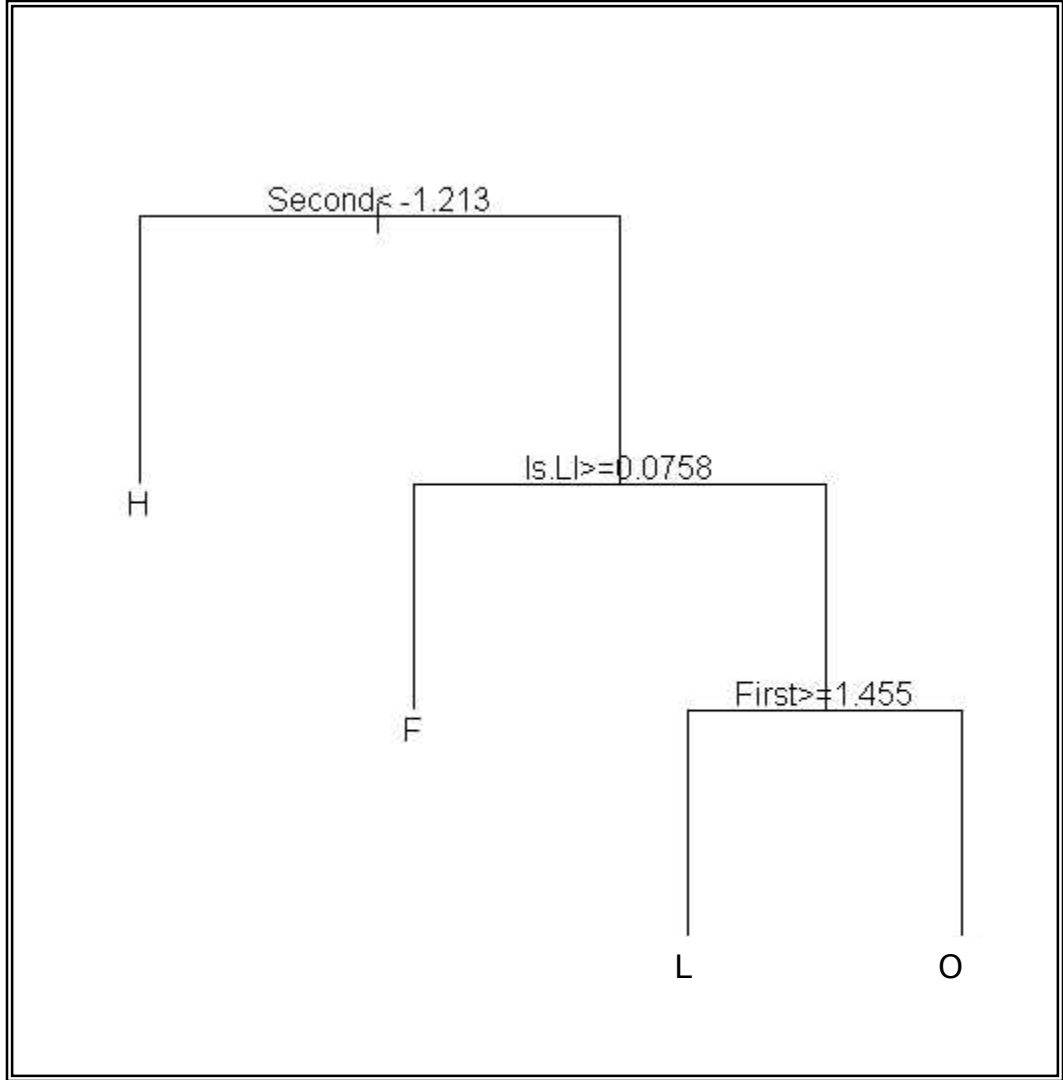


Figure B.14. Pruned classification tree: Combined size-corrected four-habitat model.



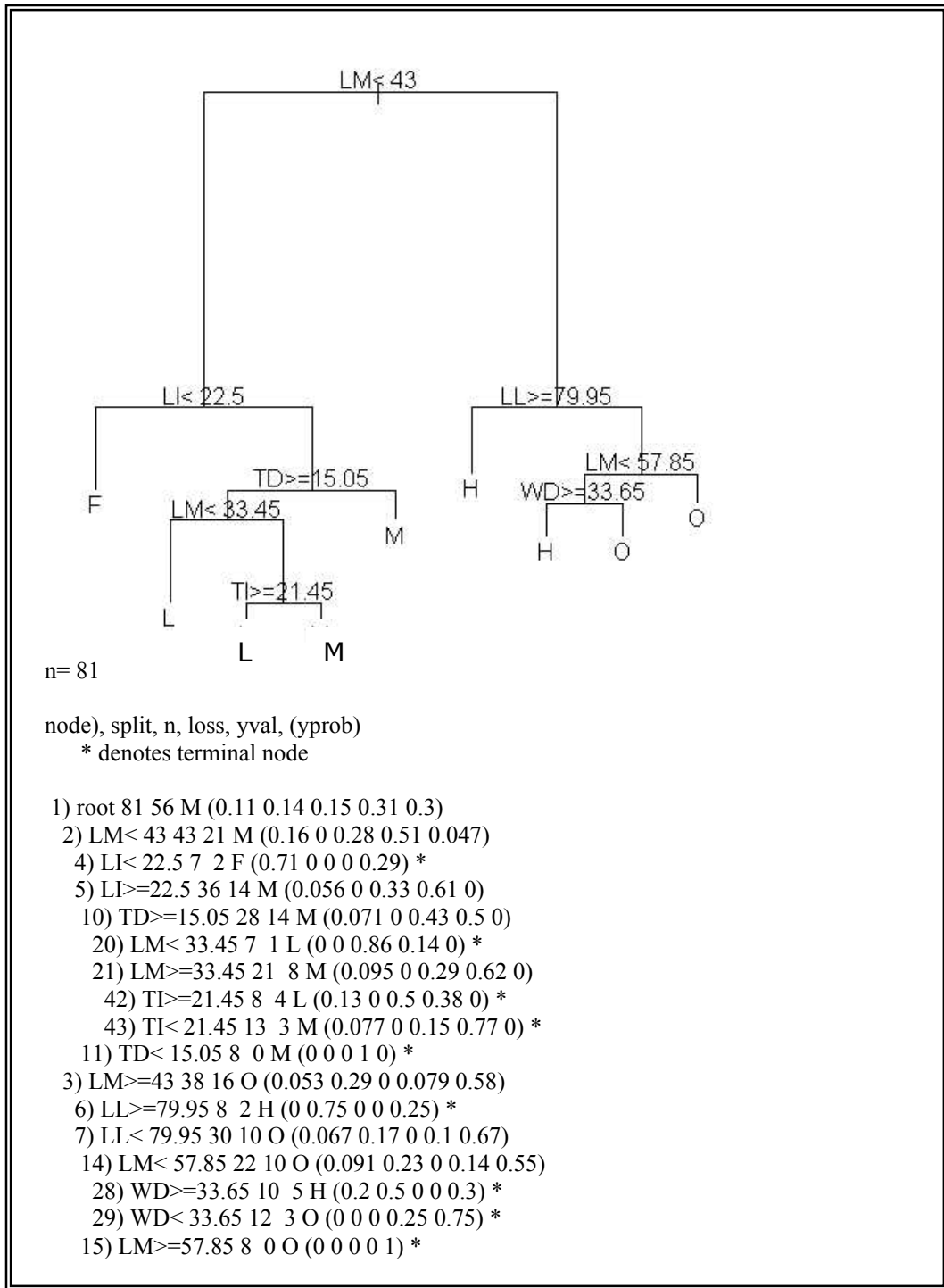


Figure B.15. Full classification tree results: Raw-measurement five-habitat model. “M, F, L, H, and O” refer to Mountain, Forest, Heavy Cover, Light Cover, and Open, respectively. “Yprob” represents Bayesian probabilities (Forest, Heavy Cover, Light Cover, Mountain, Open).

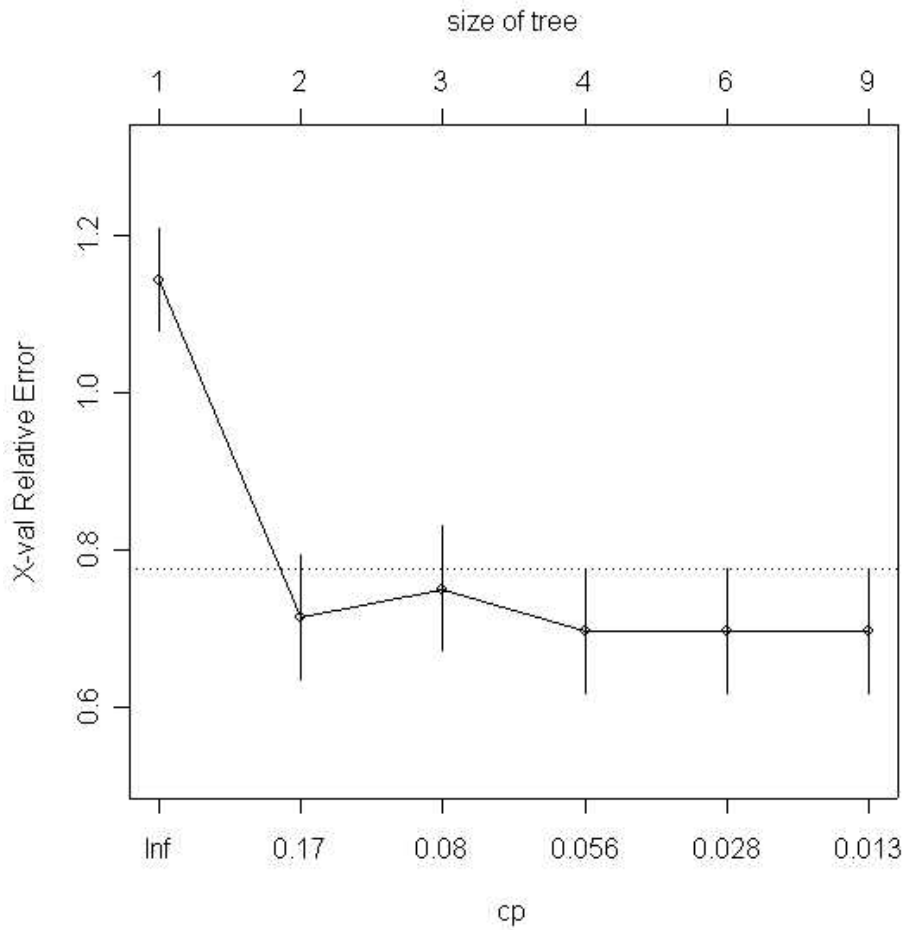


Figure B.16. Complexity parameter plot: Raw-measurement five-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

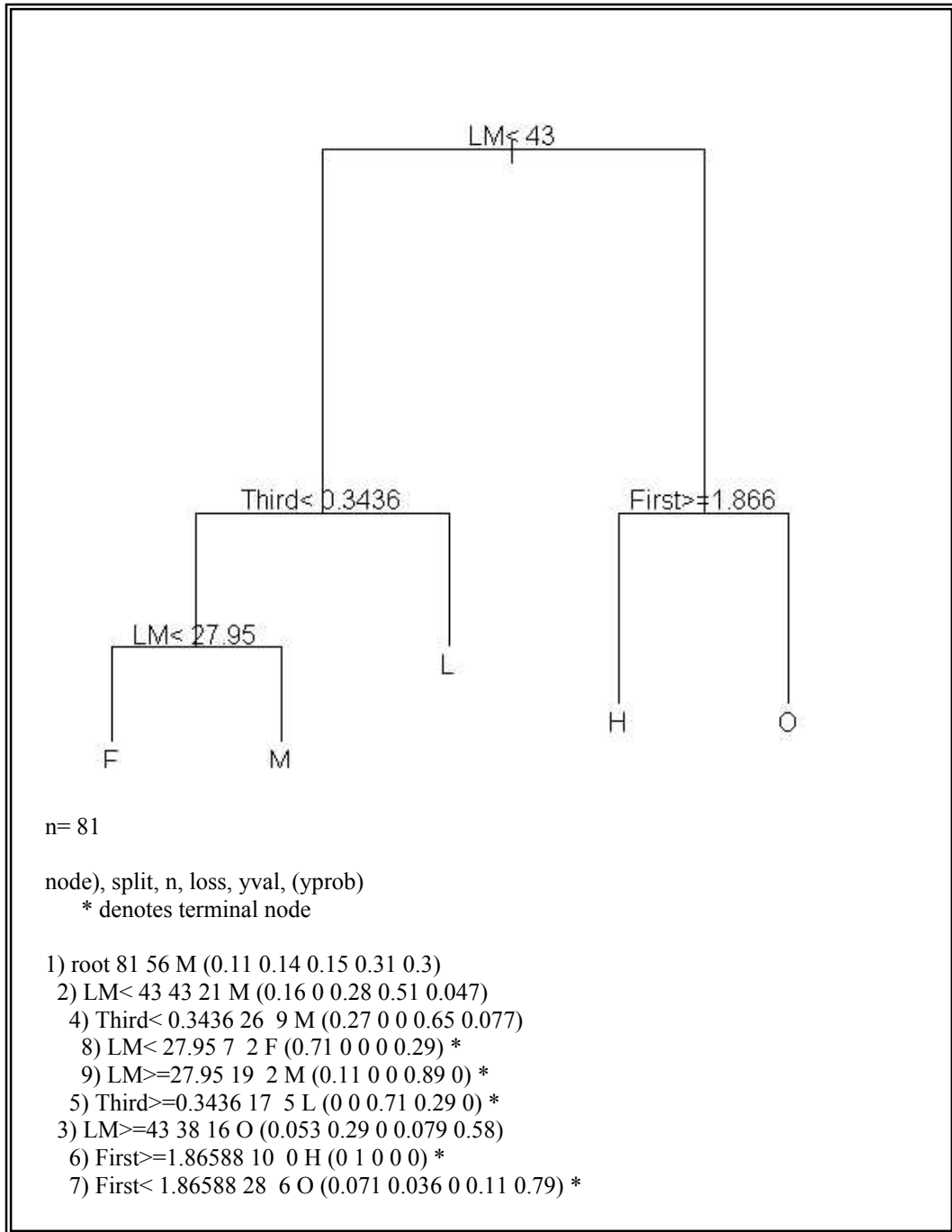


Figure B.17. Full classification tree results: Combined raw-measurement five-habitat model.

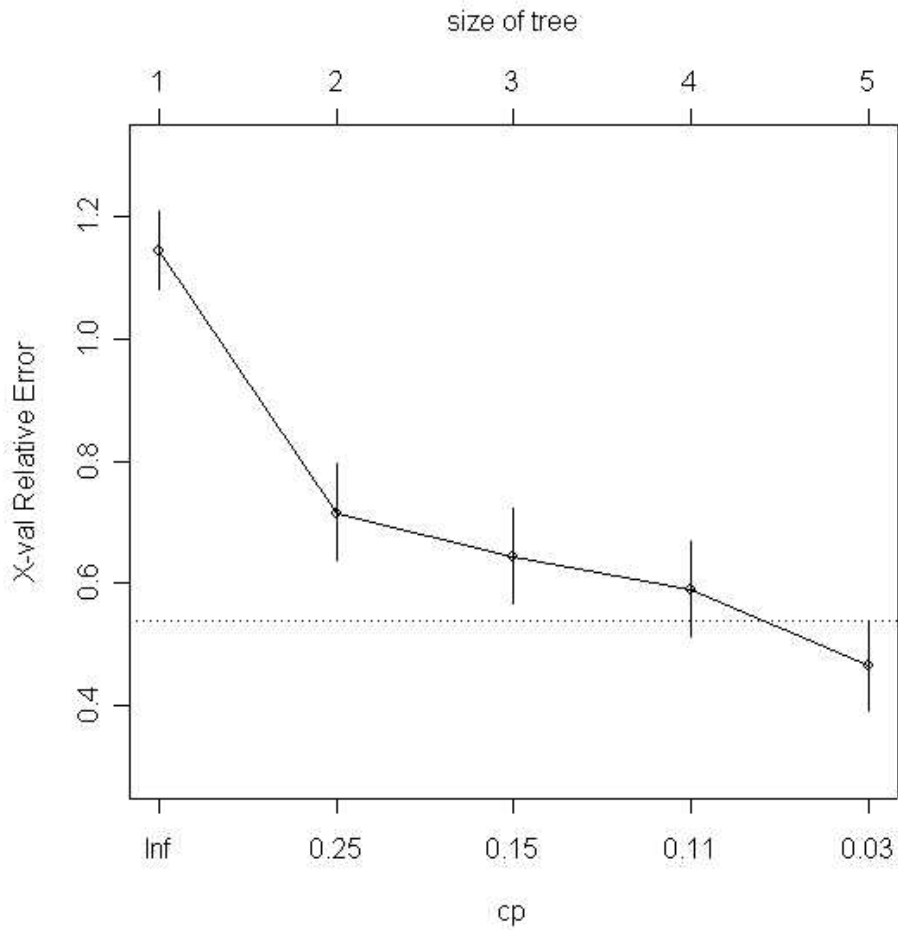


Figure B.18. Complexity parameter plot: Combined raw-measurement five-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

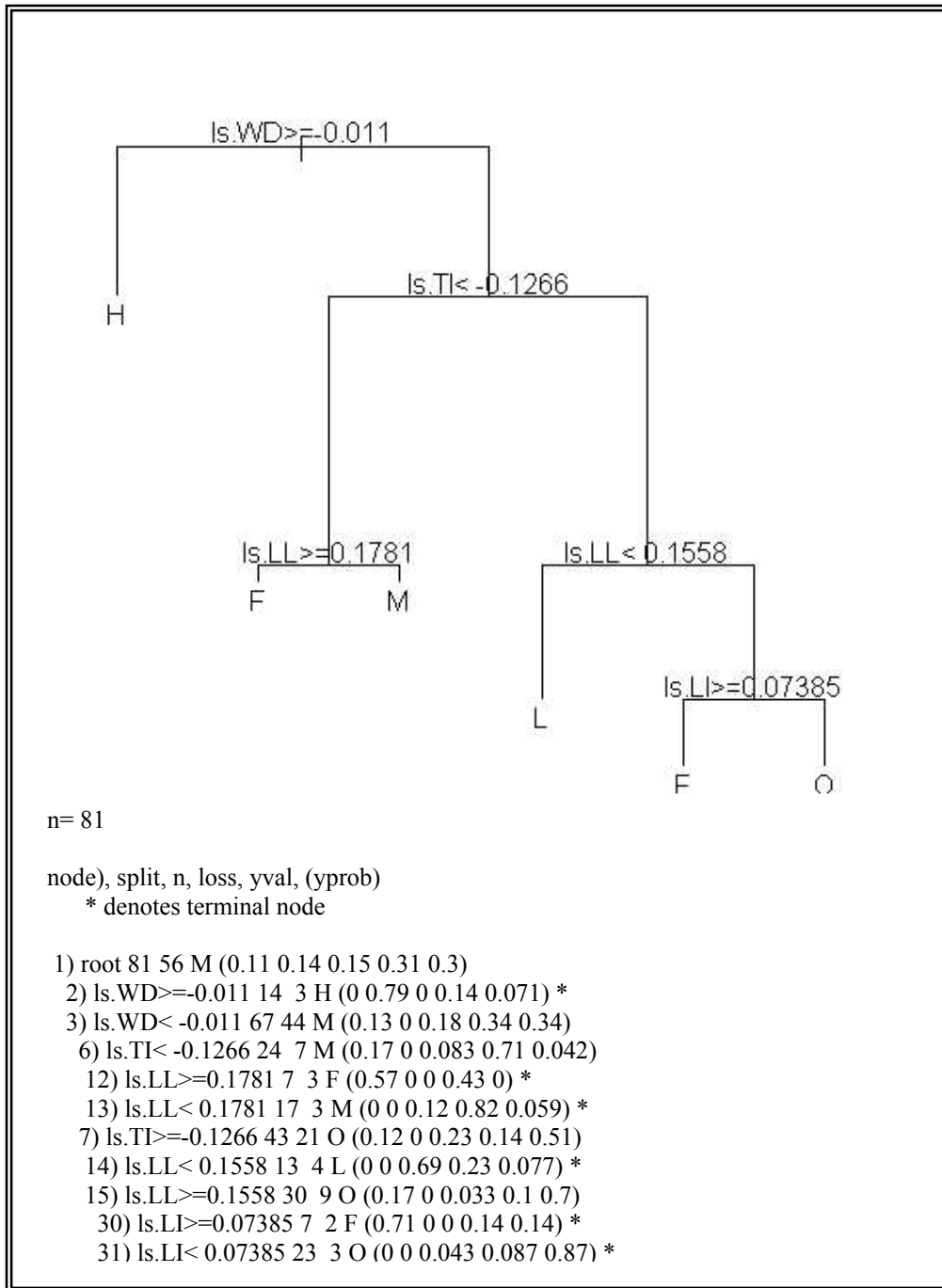


Figure B.19. Full classification tree results: Size-corrected five-habitat model.

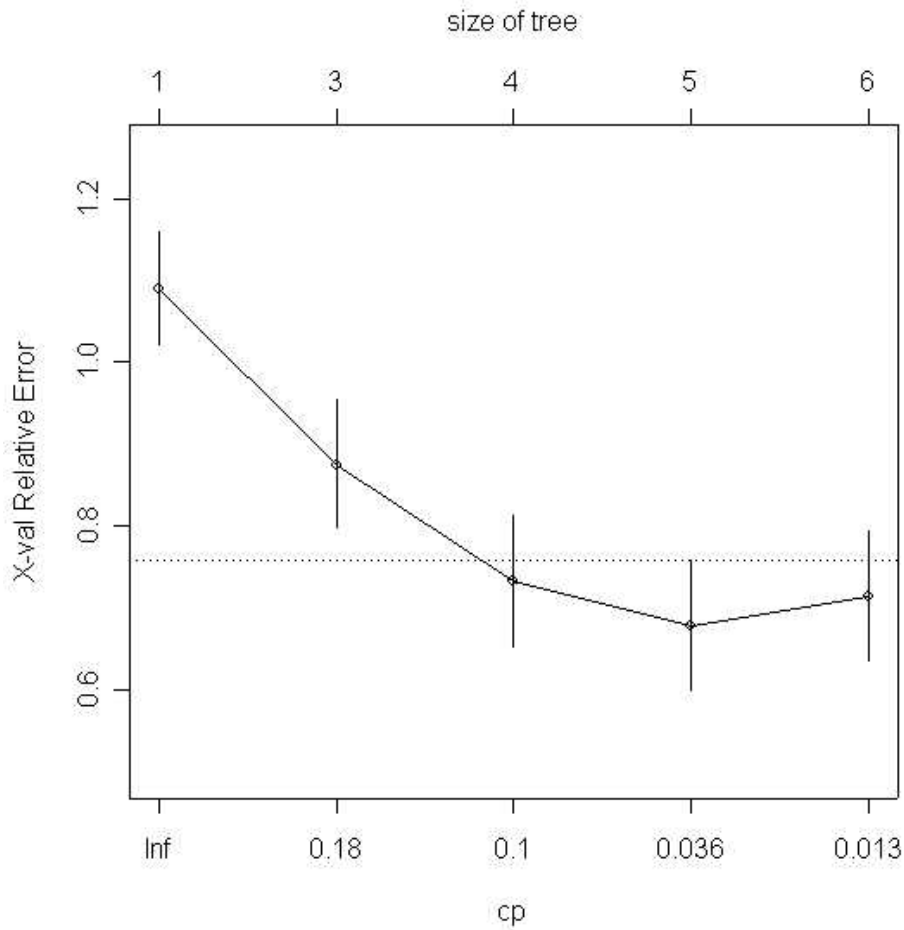


Figure B.20. Complexity parameter plot: Size-corrected five-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.

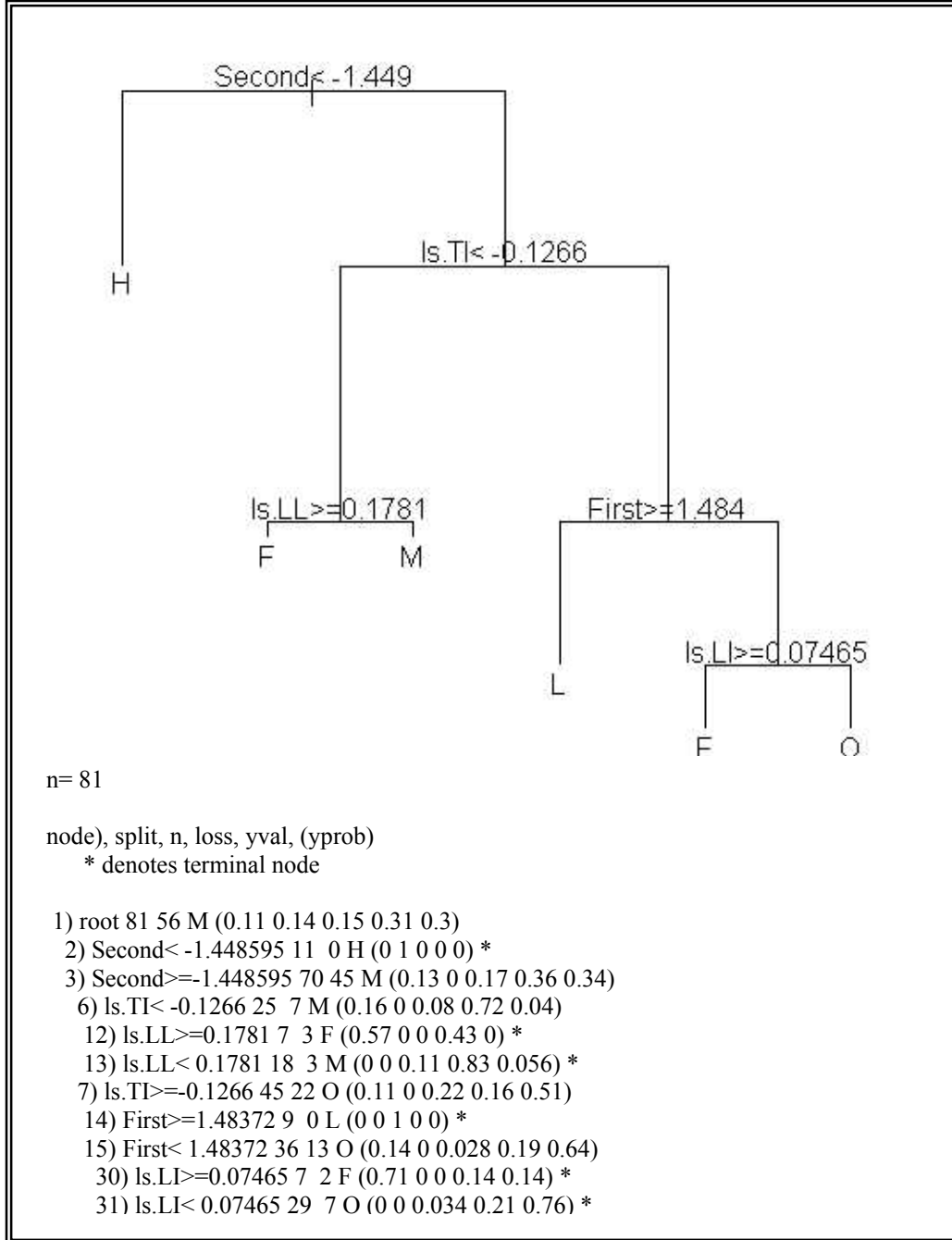


Figure B.21. Full classification tree results: Combined size-corrected five-habitat model.

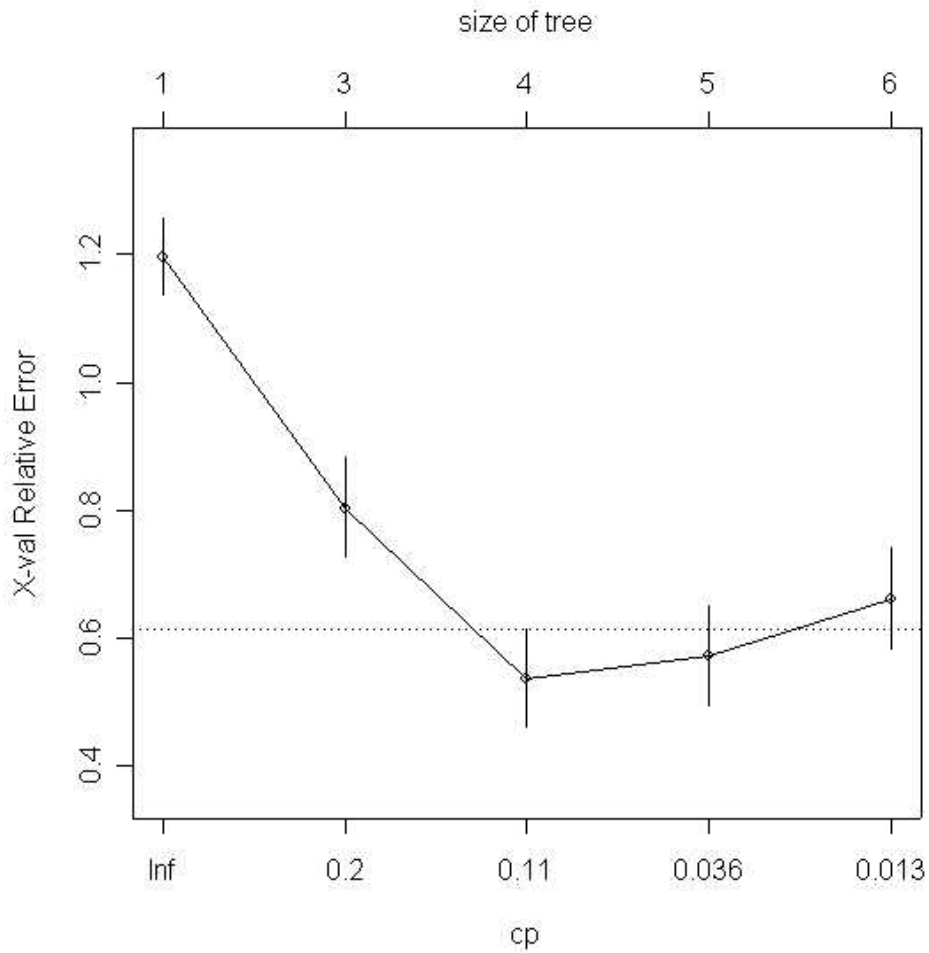


Figure B.22. Complexity parameter plot: Combined size-corrected five-habitat model. Horizontal dotted line represents the 1 SE pruning point recommended by Breiman et al. (1984). “Size of Tree” refers to the number of terminal nodes.



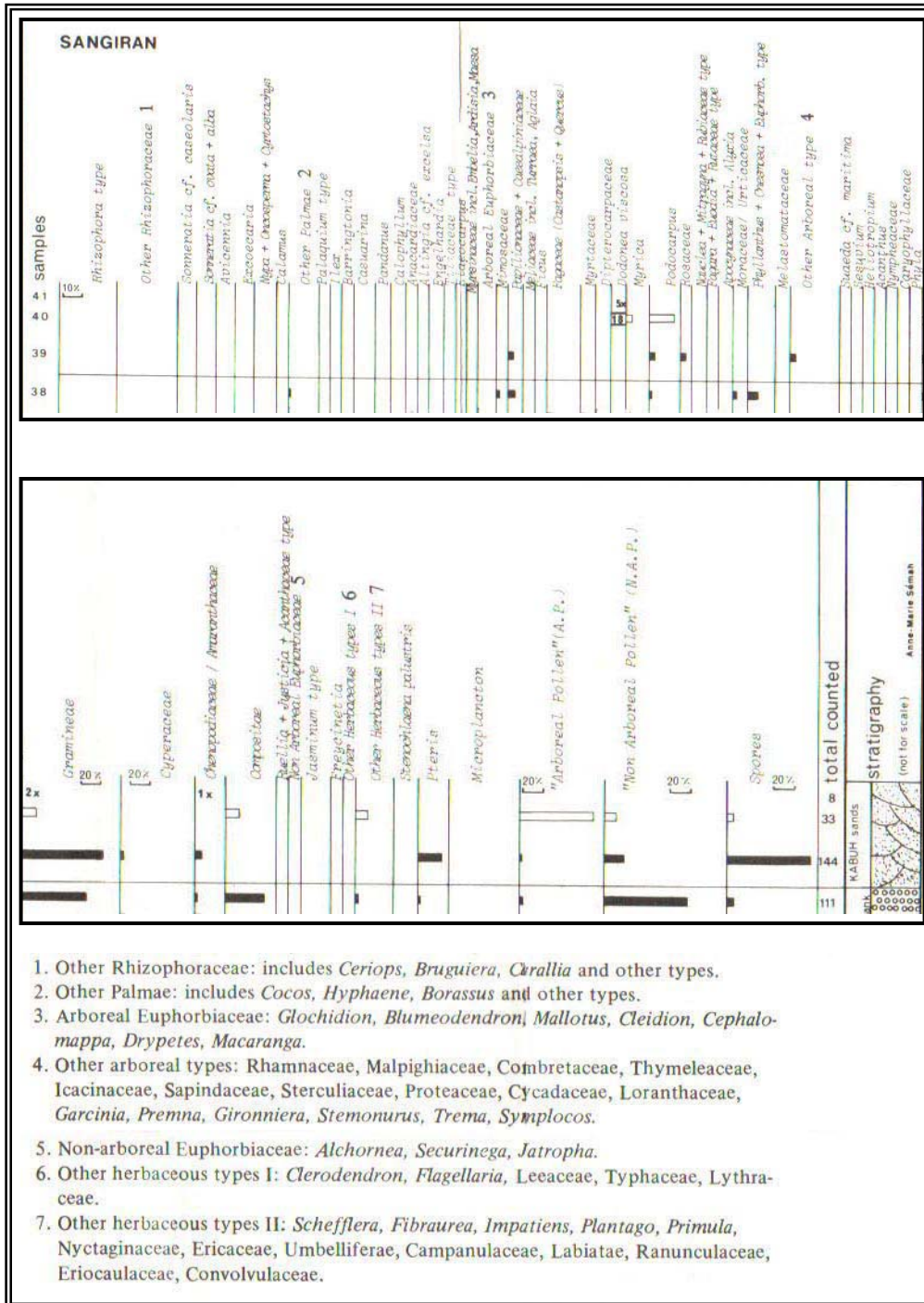


Figure B.23. Sangiran fossil pollen record: Trinil H.K. section (from Semah, 1982)

## **APPENDIX C**

### **Modern Astragali Measurements**

**Appendix C: Modern Astragali Measurements.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
		raw			s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
		s.c.									
<i>Bison</i> (Bison)	<i>bison</i>	UT 4945		O	68.7 0.149	57.8 0.074	74.3 0.183	42.5 -0.060	46.8 -0.018	37.3 -0.117	30.1 -0.210
<i>Bison</i>	<i>bison</i>	UT 9679a		O	67.4 0.142	57.2 0.070	72.7 0.175	43.7 -0.046	45.7 -0.027	36.5 -0.125	31.5 -0.189
<i>Bison</i>	<i>bison</i>	UT 9679b		O	74.1 0.141	62.3 0.065	78.9 0.168	50.4 -0.027	50.5 -0.026	40.4 -0.123	34 -0.198
<i>Bos</i> (Domestic?)	<i>frontalis</i> Gaur)	AMNH 54469		H	71.6 0.133	60.3 0.058	81 0.186	49.5 -0.027	51.6 -0.009	40.4 -0.116	31.4 -0.225
<i>Bos</i>	<i>frontalis</i>	AMNH 54470		H	76.3 0.130	65 0.060	82.2 0.162	50.7 -0.048	58.5 0.015	42.9 -0.120	35.7 -0.200
<i>Bos</i>	<i>frontalis</i>	AMNH 113746		H	77.4 0.124	66.7 0.060	82 0.149	54.5 -0.028	58.8 0.005	44.2 -0.119	37.5 -0.191
<i>Bos</i>	<i>frontalis</i>	AMNH 113747		H	76.9 0.127	65.3 0.056	85 0.170	53.3 -0.032	57.7 0.002	44.2 -0.114	35.5 -0.209
<i>Bos</i> (Gaur)	<i>gaurus</i>	AMNH 112979		H	74.8 0.136	63.8 0.067	82.2 0.177	51.4 -0.027	53.8 -0.007	41.8 -0.117	32.3 -0.229
<i>Bos</i>	<i>gaurus</i>	FMNH 31704	M	H	78.3 0.123	66.5 0.052	87.1 0.169	55 -0.031	60.1 0.008	44.8 -0.120	37.3 -0.200
<i>Bos</i> (Banteng)	<i>javanicus</i>	AMNH 54551		O	69 0.118	59.3 0.052	73.8 0.147	48 -0.039	51.1 -0.012	40.6 -0.112	36.9 -0.154
<i>Bos</i>	<i>javanicus</i>	USNM 154385	F	O	63.8 0.145	52.9 0.064	69 0.179	42.4 -0.032	41.8 -0.038	34.6 -0.121	29 -0.197
<i>Bos</i>	<i>javanicus</i>	USNM 198317	M	O	67.4 0.140	57 0.067	72.5 0.171	43.7 -0.048	45.3 -0.033	37.3 -0.117	32.3 -0.180
<i>Bos</i> (Kouprey)	<i>sauveli</i>	USNM 361392	F	O	60.8 0.132	52.4 0.067	66.9 0.173	40.8 -0.042	40.7 -0.043	35.7 -0.100	29.1 -0.188
<i>Bos</i>	<i>sauveli</i>	USNM 399379	F	O	59.8 0.139	51.3 0.072	63.7 0.167	40.2 -0.033	41.1 -0.024	32.5 -0.126	27.7 -0.195

**Appendix C: Continued.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
		raw			s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
		s.c.									
<i>Boselaphus</i> (Nilgai)	<i>tragocamelus</i>	USNM 269127	M	H	49.1 0.122	41.8 0.052	52.5 0.151	34.3 -0.034	36.3 -0.010	29.4 -0.101	24.6 -0.179
<i>Bubalus</i> (Water Buffalo)	<i>bubalis</i>	AMNH 54765		O	88.5 0.131	74 0.054	97.6 0.174	59.6 -0.040	61.2 -0.029	52.1 -0.099	42.1 -0.191
<i>Bubalus</i>	<i>bubalis</i>	AMNH 54766		O	82.1 0.121	70.5 0.055	90.7 0.165	57.1 -0.036	58.6 -0.025	47.9 -0.113	42.2 -0.168
<i>Bubalus</i> (Lowland)	<i>depressicornis</i> (Anoa)	AMNH 150050		F	40.3 0.147	35.2 0.088	43.9 0.184	25.8 -0.047	27.1 -0.026	21.5 -0.126	17.3 -0.220
<i>Bubalus</i>	<i>depressicornis</i>	AMNH 214382	F	F	36.7 0.148	31.1 0.077	39.5 0.180	25.6 -0.008	23.8 -0.040	19 -0.137	15.7 -0.220
<i>Bubalus</i> (Tamaraw)	<i>mindorensis</i>	AMNH 31660		F	51.8 0.162	43.9 0.090	55.5 0.192	31.7 -0.051	34.4 -0.015	27.1 -0.119	19.6 -0.260
<i>Bubalus</i>	<i>mindorensis</i>	USNM 219049		F	53.6 0.148	46.2 0.084	57.9 0.182	37.7 -0.004	35.9 -0.026	27.5 -0.141	21.8 -0.242
<i>Budorcas</i> (Takin)	<i>taxicolor</i>	AMNH 57014	F	H	50.1 0.137	42.6 0.066	54.9 0.176	35.8 -0.009	36.2 -0.004	25.5 -0.157	22.6 -0.209
<i>Budorcas</i>	<i>taxicolor</i>	AMNH 57016		H	47.5 0.147	39.9 0.071	50.5 0.173	35 0.014	33.7 -0.002	22.6 -0.176	20.1 -0.227
<i>Budorcas</i>	<i>taxicolor</i>	FMNH 39509	F	H	50.8 0.120	43.3 0.050	55.1 0.155	36.7 -0.021	39.4 0.009	28 -0.139	25.8 -0.174
<i>Budorcas</i>	<i>taxicolor</i>	USNM 259079	M	H	55.9 0.107	48.8 0.048	62.4 0.155	43.1 -0.006	43.1 -0.006	32.3 -0.131	29.7 -0.168
<i>Capra</i> (Markhor)	<i>sibirica</i>	AMNH 54902	F	L/M	34.2 0.117	28.8 0.043	37.8 0.161	26 -0.002	24.9 -0.021	19.2 -0.134	17.9 -0.164
<i>Capra</i>	<i>sibirica</i>	AMNH 54905	M	L/M	37.6 0.122	32 0.052	40.6 0.155	28 -0.006	26.4 -0.032	21.1 -0.129	19.6 -0.161
<i>Capra</i>	<i>sibirica</i>	USNM 020409	M	L/M	39.7 0.145	32.9 0.064	40.9 0.158	25.2 -0.052	26.7 -0.027	20.7 -0.138	20.1 -0.150

**Appendix C: Continued.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
					s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
					raw						
					s.c.						
<i>Capra</i>	<i>sibirica</i>	USNM 062091	M	L/M	33.7 0.141	27.9 0.059	35.3 0.161	23.4 -0.018	22.5 -0.035	18 -0.131	16.2 -0.177
<i>Capra</i>	<i>sibirica</i>	USNM 062089	M	L/M	37.7 0.139	31.5 0.061	39.7 0.162	26.7 -0.010	25.9 -0.024	19.5 -0.147	18 -0.182
<i>Capra</i>	<i>sibirica</i>	USNM 062092	F	L/M	34.8 0.136	30 0.072	35.8 0.148	23.6 -0.033	23.9 -0.027	19.7 -0.111	16.6 -0.185
<i>Capra</i>	<i>sibirica</i>	USNM 021846	M	L/M	40.6 0.148	35.1 0.085	42.6 0.169	28.6 -0.004	24.7 -0.068	21.1 -0.136	18.4 -0.195
<i>Hemitragus</i> (Tahr)	<i>hylocrius</i>	AMNH 54755		L	33.3 0.113	28.6 0.047	35.9 0.146	26.7 0.017	24.2 -0.025	19.7 -0.115	16.8 -0.184
<i>Hemitragus</i>	<i>hylocrius</i>	AMNH 54757	M	L	33.8 0.154	28.7 0.083	26.1 0.042	25.4 0.030	23 -0.013	18.4 -0.110	15.5 -0.185
<i>Hemitragus</i>	<i>hylocrius</i>	AMNH 54758	F	L	32.6 0.131	27.6 0.059	34.8 0.160	24.4 0.005	22 -0.040	18.5 -0.115	15.2 -0.200
<i>Hemitragus</i>	<i>hylocrius</i>	AMNH 54857		L	32.7 0.118	28.3 0.055	35.4 0.152	26.2 0.022	22.8 -0.039	19 -0.118	16.1 -0.190
<i>Capricornis</i> (Japanese Serow)	<i>crispus</i>	AMNH 165685		H/M	28.9 0.157	24.4 0.084	29 0.159	21 0.019	19.9 -0.005	13.3 -0.180	11.7 -0.235
<i>Capricornis</i>	<i>crispus</i>	USNM 013829	M	H/M	30.7 0.129	26.4 0.064	32.1 0.149	22.4 -0.007	21.3 -0.029	17.5 -0.115	14.7 -0.190
<i>Naemorhedus</i> (Goral)	<i>goral</i>	AMNH 43004	M	F/M	29.7 0.158	24.6 0.077	30.1 0.164	19.4 -0.027	18.4 -0.049	15.3 -0.130	13.2 -0.194
<i>Naemorhedus</i>	<i>goral</i>	AMNH 110481	M	F/M	29.8 0.143	26 0.084	32.4 0.180	19.5 -0.041	20.2 -0.026	15.1 -0.152	13.9 -0.188
<i>Naemorhedus</i>	<i>goral</i>	USNM 259023	F	F/M	31.7 0.164	28.2 0.113	33.7 0.190	18.7 -0.066	20.6 -0.024	14.9 -0.164	13.3 -0.214
<i>Naemorhedus</i>	<i>goral</i>	USNM 259398	M	F/M	30.6 0.163	26.9 0.107	32.2 0.185	17.5 -0.079	19.8 -0.026	14.8 -0.152	13.3 -0.199

**Appendix C: Continued.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
					s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
<i>Naemorhedus</i>	<i>goral</i>	USNM 259399	F	F/M	29.2 0.128	25.5 0.070	31.8 0.165	22 0.005	21.1 -0.013	15.4 -0.149	13.5 -0.207
<i>Capricornis</i> (Sumatran)	<i>sumatraensis</i> Serow)	USNM 152165	F	H/M	42.6 0.113	38.2 0.066	46.2 0.149	30.9 -0.026	31.8 -0.014	24.2 -0.132	22.9 -0.156
<i>Capricornis</i>	<i>sumatraensis</i>	AMNH 115578	M	H/M	40.6 0.165	24.5 -0.054	42 0.180	28.3 0.009	27.8 0.001	21.4 -0.113	18 -0.188
<i>Capricornis</i>	<i>sumatraensis</i>	FMNH 36783	F	H/M	45.6 0.141	38.8 0.071	47.8 0.162	30.9 -0.028	30.9 -0.028	24.6 -0.127	21.2 -0.191
<i>Capricornis</i>	<i>sumatraensis</i>	USNM 258670	M	H/M	44.9 0.147	37.6 0.070	48.1 0.177	30 -0.028	29.5 -0.036	23.8 -0.129	20.2 -0.200
<i>Capricornis</i>	<i>sumatraensis</i>	USNM 259025	F	H/M	44 0.122	37.9 0.057	46.4 0.145	32.8 -0.005	31.5 -0.023	24.1 -0.139	23.1 -0.158
<i>Capricornis</i>	<i>sumatraensis</i>	USNM 259404	M	H/M	42.9 0.133	37.1 0.070	46.5 0.168	30.4 -0.016	29.9 -0.023	23.5 -0.128	19.7 -0.205
<i>Capricornis</i>	<i>sumatraensis</i>	AMNH 43037	M	H/M	40 0.116	36.4 0.075	44.5 0.162	27.5 -0.047	28.2 -0.036	23.8 -0.109	21.1 -0.162
<i>Capricornis</i> (Formosan)	<i>swinhoei</i> Serow)	USNM 311229	F	H/M	30.2 0.129	26.5 0.073	32.8 0.165	20.8 -0.033	20.6 -0.037	17 -0.120	14.9 -0.177
<i>Ovis</i> (Argali)	<i>ammon</i>	USNM 240688	F	L	32.8 0.111	27.9 0.041	36.2 0.154	24.4 -0.017	22.9 -0.045	19 -0.126	19.4 -0.117
<i>Ovis</i>	<i>ammon</i>	FMNH 25684	M	L	39.7 0.101	34 0.034	43.3 0.139	29 -0.035	29.8 -0.023	24.6 -0.106	24.4 -0.110
<i>Ovis</i>	<i>ammon</i>	AMNH 54871	M	L	36.3 0.103	30.4 0.026	39.1 0.135	27.6 -0.016	27 -0.026	22.6 -0.103	21.8 -0.119
<i>Ovis</i>	<i>ammon</i>	AMNH 54875		L	38.5 0.142	32.7 0.071	39.6 0.154	26.5 -0.020	25.3 -0.041	20.2 -0.138	18.9 -0.167
<i>Ovis</i>	<i>ammon</i>	AMNH 54888		L	38.8 0.116	32.9 0.044	42.2 0.153	28.7 -0.015	28.7 -0.015	22.2 -0.126	20.7 -0.157

**Appendix C: Continued.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
		raw			s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
		s.c.									
<i>Ovis</i>	<i>ammon</i>	USNM 062096	M	L	41.7 0.129	34.5 0.047	43.9 0.152	30.5 -0.006	29.1 -0.027	23 -0.129	21.1 -0.166
<i>Ovis</i> (Asiatic)	<i>orientalis</i> Mouflon)	AMNH 54615	F	L	29.6 0.127	24.8 0.050	31.2 0.150	21.3 -0.016	19.7 -0.050	17.1 -0.112	15.7 -0.149
<i>Ovis</i>	<i>orientalis</i>	AMNH 54616	M	L	27 0.105	22.6 0.028	30.3 0.155	20.3 -0.019	20.1 -0.023	16.3 -0.114	15.6 -0.133
<i>Procapra</i> (Zeren)	<i>gutturosa</i>	AMNH 46444	F	O	27 0.146	22.4 0.064	29 0.177	16.9 -0.058	17 -0.055	15.3 -0.101	13 -0.172
<i>Procapra</i>	<i>gutturosa</i>	AMNH 46453	F	O	25.9 0.156	21.3 0.071	28.1 0.191	16.2 -0.048	15.9 -0.056	13.7 -0.121	11.6 -0.193
<i>Pseudois</i> (Bharal)	<i>nayaur</i>	USNM 259712	M	O/M	33.6 0.124	29.1 0.061	35.9 0.152	23.8 -0.026	23.2 -0.037	19.9 -0.104	17.1 -0.170
<i>Pseudois</i>	<i>nayaur</i>	USNM 084082	M	O/M	34.3 0.122	29.3 0.054	37.4 0.160	25.1 -0.013	23.7 -0.038	19.7 -0.119	17.7 -0.165
<i>Pseudois</i>	<i>nayaur</i>	FMNH 31134	M	O/M	33.2 0.129	27.8 0.052	35.7 0.161	24 -0.012	23.4 -0.023	18.1 -0.134	16.6 -0.172
<i>Connochaetes taurinus</i> (Wildebeest)		AMNH 81716		O	43.1 0.151	36.5 0.079	44.6 0.166	29.2 -0.018	29.9 -0.007	22.2 -0.023	17.7 -0.235
<i>Connochaetes taurinus</i>		AMNH 27824		O	50.6 0.137	43 0.067	53.2 0.159	35.1 -0.021	33.6 -0.040	27.7 -0.124	24.5 -0.178
<i>Connochaetes taurinus</i>		AMNH 54133		O	53.7 0.143	45.8 0.074	56.2 0.163	36.3 -0.027	36.2 -0.028	30.1 -0.108	23.4 -0.217
<i>Connochaetes taurinus</i>		AMNH 54137		O	47.9 0.128	41.6 0.067	51.8 0.162	36.2 0.006	33.6 -0.026	27 -0.121	21.7 -0.216
<i>Connochaetes taurinus</i>		AMNH 82026		O	48.6 0.126	41.8 0.061	52.9 0.163	34.8 -0.019	33.9 -0.030	27.2 -0.126	24.2 -0.176
<i>Connochaetes taurinus</i>		AMNH 82029		O	48.8 0.151	40.4 0.069	50.7 0.168	32.3 -0.028	32.4 -0.027	25.4 -0.132	21.7 -0.201

**Appendix C: Continued.**

Genus	species TD	Specimen #	Sex	Habitat	LM	LI	LL	WI	WD	TI	
					raw <sup>1</sup>	raw	raw	raw	raw	raw	
					s.c. <sup>2</sup>	s.c.	s.c.	s.c.	s.c.	s.c.	
<i>Connochaetes</i>	<i>taurinus</i>	AMNH 80493	O		53.5 0.145	45 0.070	56.7 0.170	35 -0.039	35.6 -0.032	29 -0.121	24.6 -0.192
<i>Damaliscus</i>	<i>lunatus</i> (Topi)	AMNH 83526	O		44.4 0.131	36.6 0.047	47.1 0.157	28.6 -0.060	31.7 -0.015	24.7 -0.123	23.9 -0.138
<i>Damaliscus</i>	<i>lunatus</i>	AMNH 34729	O		45.1 0.145	36.5 0.053	48.5 0.177	30 -0.032	30.8 -0.020	24.3 -0.123	20.4 -0.199
<i>Damaliscus</i>	<i>lunatus</i>	AMNH 82034	O		43.9 0.143	35.9 0.056	46.9 0.172	28.4 -0.046	29.7 -0.027	24.4 -0.112	20.6 -0.186
<i>Damaliscus</i>	<i>lunatus</i>	AMNH 82035	O		44.2 0.142	36.8 0.062	47 0.169	28.6 -0.047	30.3 -0.022	24.6 -0.112	20.5 -0.192
<i>Damaliscus</i>	<i>lunatus</i>	AMNH 113781	O		45.7 0.123	38.3 0.047	49.3 0.156	31.8 -0.034	31.4 -0.040	26.8 -0.108	24.7 -0.144
<i>Cephalophus</i>	<i>monticola</i> (Duiker)	AMNH 269894	F		15.1 0.157	12.8 0.085	16.6 0.198	8.9 -0.073	9.7 -0.035	7.7 -0.136	6.7 -0.196
<i>Cephalophus</i>	<i>monticola</i>	AMNH 269923	F		14.5 0.161	12.5 0.096	15.2 0.181	8.4 -0.076	9.2 -0.037	7.2 -0.143	6.6 -0.181
<i>Cephalophus</i>	<i>monticola</i>	AMNH 34736	F		15.5 0.152	13.3 0.086	16.4 0.177	9.6 -0.056	9.6 -0.056	8.5 -0.109	7 -0.193
<i>Madoqua</i>	<i>kirki</i> (Dik-dik)	AMNH 36352	F		16.3 0.175	13.9 0.106	17 0.193	9.1 -0.078	9.2 -0.074	8.6 -0.103	6.6 -0.218
<i>Madoqua</i>	<i>kirki</i>	AMNH 187819	F		14.8 0.172	12.7 0.105	15.1 0.180	8.5 -0.069	8.7 -0.059	7.5 -0.123	6.2 -0.206

<sup>1</sup>Raw measurements in mm.

<sup>2</sup>Size-Corrected values.



## **APPENDIX D**

### **Fossil Astragali Measurements**

**Appendix D: Fossil Astragali Measurements.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM</b> raw <sup>1</sup> s.c. <sup>2</sup>	<b>LI</b> raw s.c.	<b>LL</b> raw s.c.	<b>WI</b> raw s.c.	<b>WD</b> raw s.c.	<b>TI</b> raw s.c.	<b>TD</b> raw s.c.
Bovidae	Trinil	5820	77.7 0.117	68.9 0.064	87.3 0.167	58.4 -0.007	57.6 -0.013	44.7 -0.124	37.2 -0.203
Bovidae	Trinil	7126	85.5 0.117	73.7 0.052	94.5 0.160	67.7 0.015	64.1 -0.008	49.3 -0.122	40 -0.213
Bovidae	Trinil	8419	81.1 0.124	69.6 0.057	87.9 0.159	63 0.014	58.7 -0.017	44.2 -0.140	38.7 -0.198
Bovidae	Trinil	8428	71.5 0.116	63.7 0.066	80.9 0.170	52.1 -0.021	53.6 -0.009	40.8 -0.128	35 -0.194
Bovidae	Trinil	8493	82.8 0.119	74.3 0.072	93.2 0.170	64.3 0.009	61.9 -0.007	45 -0.146	38.2 -0.217
Bovidae	Trinil	8494	84.5 --	74.1 --	93.1 --	66.8 --	66 --	48.8 --	-- --
Bovidae	Trinil	8496	84.6 0.117	73.8 0.058	93.3 0.160	64.8 0.001	62.6 -0.014	47.4 -0.135	42 -0.187
Bovidae	Trinil	8623	84.2 0.111	75.4 0.063	93.2 0.155	68.1 0.019	65.5 0.002	47.9 -0.134	39.8 -0.215
Bovidae	Trinil	8629	67.6 0.121	58.8 0.060	73.6 0.158	49.6 -0.013	49.8 -0.012	38 -0.129	33.4 -0.185
Bovidae	Trinil	8718	79.7 0.110	68.4 0.043	87.4 0.150	62.4 0.003	60.4 -0.011	45.8 -0.131	42.4 -0.164
Bovidae	Trinil	8719	72.9 0.123	62.9 0.059	81.3 0.171	52.1 -0.023	53.3 -0.013	41.8 -0.118	34.7 -0.199
Bovidae	Trinil	8720	83.8 0.112	72.6 0.050	93.4 0.159	65.9 0.008	66 0.009	46.9 -0.140	41 -0.198
Bovidae	Trinil	8747	80.8 0.120	70.5 0.061	88.6 0.160	60.7 -0.004	62.6 0.010	43.2 -0.152	39 -0.196
Bovidae	Trinil	8749	83.2 0.118	73.9 0.066	92.8 0.165	66.7 0.022	61.9 -0.011	44.8 -0.151	39.3 -0.208

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM</b> raw <sup>1</sup> s.c. <sup>2</sup>	<b>LI</b> raw s.c.	<b>LL</b> raw s.c.	<b>WI</b> raw s.c.	<b>WD</b> raw s.c.	<b>TI</b> raw s.c.	<b>TD</b> raw s.c.
Bovidae	Trinil	8750	82.9 --	71.5 --	88.2 --	-- --	63.1 --	46.9 --	39 --
Bovidae	Trinil	8751	83.2 0.112	73.1 0.056	90.6 0.149	64.9 0.004	61.7 -0.018	47.8 -0.129	43 -0.175
Bovidae	Trinil	8756	81.1 --	-- --	89 --	65.9 --	62.9 --	44.3 --	39.1 --
Bovidae	Trinil	8757	75.1 0.121	65.1 0.059	81.6 0.157	57.8 0.007	54.9 -0.015	41.6 -0.136	36.5 -0.193
Bovidae	Trinil	8758	75.5 0.128	64.3 0.059	78.9 0.148	53.5 -0.021	58 0.014	40.8 -0.139	36.4 -0.188
Bovidae	Trinil	8760	80.8 0.125	68.7 0.054	88.1 0.162	63 0.017	60.3 -0.002	41.7 -0.162	38.8 -0.194
Bovidae	Trinil	8768	80.4 0.119	69.3 0.055	87.8 0.158	63.4 0.016	59.6 -0.011	44 -0.142	39 -0.195
Bovidae	Trinil	8769	79.1 0.106	69.2 0.048	89.1 0.158	65 0.021	61.5 -0.003	45.3 -0.136	39.5 -0.195
Bovidae	Trinil	8771	77.6 0.137	65.1 0.060	85.4 0.178	57.9 0.009	54 -0.021	39.6 -0.156	35.1 -0.208
Bovidae	Trinil	8782	69.6 0.114	61.7 0.062	77 0.158	51.9 -0.013	55.9 0.019	38.6 -0.142	33.9 -0.198
Bovidae	Trinil	8880	79.7 0.121	68.5 0.056	90 0.174	62 0.012	58.5 -0.013	42.8 -0.149	37.8 -0.202
Bovidae	Trinil	8913	85.1 0.109	72.7 0.040	93.7 0.151	67.2 0.006	64.7 -0.010	51.2 -0.112	43.4 -0.184
Bovidae	Trinil	9154	83.5 0.121	74.1 0.069	94.9 0.177	65.1 0.013	60 -0.022	44.6 -0.151	39.2 -0.207

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM</b> raw <sup>1</sup> s.c. <sup>2</sup>	<b>LI</b> raw s.c.	<b>LL</b> raw s.c.	<b>WI</b> raw s.c.	<b>WD</b> raw s.c.	<b>TI</b> raw s.c.	<b>TD</b> raw s.c.
Bovidae	Trinil	9193	77.2 0.112	66.4 0.046	85.1 0.154	43.9 -0.133	61.7 0.014	63 0.024	36.2 -0.217
Bovidae	Trinil	9195	69.9 0.125	59.1 0.052	78.5 0.175	50.5 -0.016	49.6 -0.024	39.2 -0.126	34.2 -0.186
Bovidae	Trinil	9197	85 0.111	75.5 0.060	93.7 0.154	63.2 -0.017	62.3 -0.024	52.2 -0.100	43.1 -0.184
Bovidae	Trinil	9228	79.8 0.109	70.1 0.053	88.9 0.156	62.8 0.005	63.6 0.010	44.8 -0.142	40 -0.191
Bovidae	Trinil	9236	69.8 0.142	60.1 0.078	74.4 0.170	43.6 -0.062	48.8 -0.013	38.7 -0.114	31.6 -0.202
Bovidae	Trinil	9237	68 0.137	59.6 0.079	73 0.167	45.3 -0.040	45.7 -0.036	38.5 -0.110	31.5 -0.198
Bovidae	Trinil	9364	82.4 0.117	71.5 0.055	92.8 0.168	64 0.007	61.5 -0.010	46.6 -0.131	39.2 -0.206
Bovidae	Trinil	10235	69.1 0.133	60.4 0.074	75.7 0.172	46.9 -0.035	47.2 -0.033	38.9 -0.117	32.5 -0.195
Bovidae	Trinil	5823	83.7 0.119	75.1 0.072	93.7 0.168	62.1 -0.011	63.6 0.000	45.7 -0.144	39.7 -0.205
Bovidae	Trinil	8497	83.7 0.105	74.1 0.052	95.3 0.161	65.5 -0.002	64.8 -0.006	49.8 -0.121	42.6 -0.189
Bovidae	Trinil	8627	84 0.121	71.8 0.053	90.9 0.155	62.3 -0.009	63.8 0.002	48 -0.122	40 -0.201
Bovidae	Trinil	8745	86 0.108	75.8 0.053	94.5 0.149	68 0.006	65.7 -0.009	51.5 -0.115	43 -0.193
Bovidae	Trinil	8754	84 0.118	74.3 0.065	93.8 0.166	61.9 -0.015	59.2 -0.034	50.7 -0.101	40.6 -0.198
Bovidae	Trinil	8755	84.1 0.109	76.2 0.066	93.1 0.153	66.6 0.007	64.4 -0.007	49.9 -0.118	40.5 -0.209

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM raw<sup>1</sup> s.c.<sup>2</sup></b>	<b>LI raw s.c.</b>	<b>LL raw s.c.</b>	<b>WI raw s.c.</b>	<b>WD raw s.c.</b>	<b>TI raw s.c.</b>	<b>TD raw s.c.</b>
Bovidae	Trinil	8759	78.7 0.110	70.3 0.061	86.9 0.154	60.8 -0.002	58.7 -0.017	46.5 -0.118	39.5 -0.189
Bovidae	Trinil	8761	80.7 0.107	71.4 0.053	90.3 0.155	64.4 0.009	61.2 -0.014	46.2 -0.136	42.2 -0.175
Bovidae	Trinil	8881	84.2 0.111	74.5 0.058	93.5 0.156	65.6 0.003	62.6 -0.018	50.2 -0.114	41.5 -0.196
Bovidae	Trinil	8911	84.7 0.109	73.4 0.046	96.8 0.167	63.6 -0.016	63.9 -0.014	51.8 -0.105	42.9 -0.187
Bovidae	Trinil	9153	80.7 0.118	71.9 0.068	91.2 0.171	61.5 0.000	59.4 -0.015	44.8 -0.137	38.2 -0.206
Bovidae	Trinil	9365	85 0.111	73.5 0.048	92.7 0.149	68.2 0.015	63.2 -0.018	50 -0.120	43 -0.185
Bovidae	Trinil	9414	81.2 0.116	71 0.057	88.7 0.154	62.2 0.000	61.3 -0.006	46.5 -0.126	39.8 -0.194
Bovidae	Trinil	5822	79.5 0.119	67.3 0.047	86.3 0.155	61 0.004	57.1 -0.025	46.3 -0.116	39.5 -0.185
Bovidae	Trinil	5824	75.9 --	-- --	82.8 --	55.7 --	59.7 --	44.4 --	38.2 --
Bovidae	Trinil	8427	81.1 0.136	70 0.072	87.3 0.168	58.7 -0.004	56.8 -0.018	43.3 -0.136	35.8 -0.219
Bovidae	Trinil	8763	79.1 0.103	70.7 0.054	90 0.159	63.4 0.007	60.9 -0.011	46.9 -0.124	40.6 -0.187
Bovidae	Trinil	8882	78.1 0.116	66.2 0.045	84.7 0.152	56.6 -0.023	59.5 -0.002	46.3 -0.111	39.7 -0.177
Bovidae	Trinil	9151	79.5 0.121	69.1 0.061	88.1 0.166	59.6 -0.004	57.5 -0.019	45.7 -0.119	37.4 -0.206
Bovidae	Trinil	9194	78.8 0.130	65.7 0.051	85.4 0.165	55 -0.026	56.2 -0.017	45.3 -0.110	37.5 -0.193

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM</b> raw <sup>1</sup> s.c. <sup>2</sup>	<b>LI</b> raw s.c.	<b>LL</b> raw s.c.	<b>WI</b> raw s.c.	<b>WD</b> raw s.c.	<b>TI</b> raw s.c.	<b>TD</b> raw s.c.
Bovidae	Trinil	10324	79.8 0.115	67.8 0.045	89.5 0.165	61.7 0.004	59.5 -0.012	46.9 -0.115	38.5 -0.201
Bovidae	Trinil	10644	79.7 0.115	70.3 0.061	86.9 0.153	62.4 0.009	60.5 -0.004	45.5 -0.128	38.1 -0.205
Bovidae	Trinil	5825	79.6 0.118	72.5 0.077	90.2 0.172	59 -0.012	57.4 -0.024	44.2 -0.138	38.8 -0.194
Bovidae	Trinil	8418	80.5 0.102	73.5 0.063	91.3 0.157	63.5 -0.001	61.8 -0.013	47.4 -0.128	42 -0.180
Bovidae	Trinil	8498	81 0.125	72.1 0.074	87.7 0.160	62.8 0.014	61.6 0.006	41.6 -0.164	37 -0.215
Bovidae	Trinil	8572	85.6 0.124	75.2 0.068	92.1 0.156	66.1 0.012	62.7 -0.011	49.2 -0.116	37.6 -0.233
Bovidae	Trinil	8626	80.4 0.108	69.1 0.043	88.7 0.151	65.7 0.021	61.1 -0.011	45.9 -0.135	41.7 -0.177
Bovidae	Trinil	8753	81.1 0.113	71.1 0.056	90.8 0.162	62.1 -0.003	59.3 -0.023	45.7 -0.136	42.5 -0.168
Bovidae	Trinil	8765	83 --	73.9 --	-- --	63 --	57.6 --	48.4 --	40.1 --
Bovidae	Trinil	8767	76.6 0.106	70 0.067	85.3 0.152	60 0.000	60.7 0.005	43.4 -0.141	39 -0.188
Bovidae	Trinil	8891	83 0.124	72.1 0.063	91.8 0.168	60.8 -0.011	62.2 -0.001	43.3 -0.158	40.6 -0.186
Bovidae	Trinil	9152	77.9 0.107	67.8 0.046	86.8 0.154	63.9 0.021	61 0.000	46 -0.122	38 -0.205
Bovidae	Trinil	9229	87.2 0.116	75.4 0.053	91.7 0.138	68.8 0.013	66.5 -0.002	48.8 -0.136	43.8 -0.183
Bovidae	Trinil	9271	83.8 0.125	74 0.071	91.8 0.164	61.5 -0.010	61.3 -0.011	44.7 -0.148	40.5 -0.191

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM raw<sup>1</sup> s.c.<sup>2</sup></b>	<b>LI raw s.c.</b>	<b>LL raw s.c.</b>	<b>WI raw s.c.</b>	<b>WD raw s.c.</b>	<b>TI raw s.c.</b>	<b>TD raw s.c.</b>
Bovidae	Trinil	9272	78.4 0.109	73.5 0.081	88.1 0.160	62.1 0.008	58.3 -0.019	43.3 -0.148	39.2 -0.192
Bovidae	Trinil	9366	83.6 0.115	74.8 0.067	95.1 0.171	62.7 -0.010	61.5 -0.019	45.7 -0.147	42.8 -0.176
Bovidae	Trinil	4486	66.8 0.116	57.9 0.054	74.8 0.165	48.9 -0.020	49.1 -0.018	39 -0.118	33.9 -0.179
Bovidae	Trinil	7830	64 0.129	55.2 0.065	70.8 0.173	40.2 -0.073	43.4 -0.040	37.9 -0.098	33.2 -0.156
Bovidae	Trinil	8624	70.1 0.121	61 0.060	77.5 0.164	51.5 -0.013	53.2 0.001	39.2 -0.132	33.4 -0.201
Bovidae	Trinil	8766	72.1 0.120	62 0.055	80.5 0.168	51.3 -0.028	53.7 -0.008	41.8 -0.117	35.3 -0.190
Bovidae	Trinil	8773	69.5 0.136	59.3 0.068	76.4 0.178	44.2 -0.060	48.5 -0.020	39.2 -0.112	32.8 -0.190
Bovidae	Trinil	8780	68 0.120	59.2 0.060	75.3 0.165	48.9 -0.023	49.6 -0.017	37.8 -0.135	34.8 -0.171
Bovidae	Trinil	8883	67.7 0.113	62.2 0.076	74 0.151	48.2 -0.035	49.6 -0.022	40 -0.116	35.6 -0.166
Bovidae	Trinil	8914	75.8 --	-- --	83.5 --	50.7 --	53.1 --	40.4 --	35.9 --
Bovidae	Trinil	8946	69.7 0.125	60.3 0.062	76.8 0.168	50.6 -0.014	52.6 0.003	37.7 -0.142	32.7 -0.203
Bovidae	Trinil	10310	69.7 0.116	61.9 0.065	75.3 0.150	49.7 -0.031	50.2 -0.026	41.2 -0.112	36.8 -0.161
Bovidae	Kedoeng Broeboes	8684 --	70.3 --	59.7 --	-- --	49.4 --	55.7 --	41.9 --	34.4 --
Bovidae	Kedoeng Broeboes	9099	75.7 0.119	66.5 0.063	83.6 0.162	58 0.004	53.5 -0.032	42.7 -0.129	37.4 -0.187

**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM raw<sup>1</sup> s.c.<sup>2</sup></b>	<b>LI raw s.c.</b>	<b>LL raw s.c.</b>	<b>WI raw s.c.</b>	<b>WD raw s.c.</b>	<b>TI raw s.c.</b>	<b>TD raw s.c.</b>
Bovidae	Kedoeng Broeboes	9100	66.9 0.121	58.6 0.064	72.7 0.157	40.8 -0.093	51 0.004	41.2 -0.089	34.7 -0.164
Bovidae	Kedoeng Broeboes	9102	63.1 --	53.4 --	67.6 --	-- --	45.8 --	-- --	32.7 --
Bovidae	Kedoeng Broeboes	9105	62.5 0.129	53.6 0.062	68.6 0.170	38.7 -0.079	42.4 -0.039	36.7 -0.102	33.6 -0.140
Bovidae	Kedoeng Broeboes	9106	79.9 0.123	70.8 0.071	88.3 0.167	58.6 -0.011	59.1 -0.008	44.1 -0.135	37.3 -0.207
Bovidae	Kedoeng Broeboes	9255	70.8 0.147	59.8 0.073	73.3 0.162	45.2 -0.048	46.8 -0.033	38.5 -0.118	33.2 -0.182
Bovidae	Kedoeng Broeboes	9103	61.3 0.134	53.7 0.077	65.6 0.163	43.5 -0.015	44 -0.010	32.4 -0.143	28 -0.206
Bovidae	Kedoeng Broeboes	9123	63.2 --	58.3 --	69.8 --	-- --	48.3 --	35.5 --	-- --
Bovidae	Kedoeng Broeboes	8846	80.9 0.138	70.1 0.076	86.4 0.167	52.3 -0.051	58.2 -0.005	44.3 -0.124	37.1 -0.201
Bovidae	Kedoeng Broeboes	9089	79.5 0.126	68.6 0.062	87.3 0.167	57.3 -0.016	53.1 -0.049	46.1 -0.111	39.5 -0.178
Bovidae	Kedoeng Broeboes	9184	65.8 0.131	56.8 0.067	71.5 0.167	40.7 -0.077	44.5 -0.039	38.7 -0.099	34.4 -0.150
Bovidae	Kedoeng Broeboes	9091	72.2 0.117	61.6 0.048	79.8 0.161	49.6 -0.046	52.8 -0.019	43.4 -0.104	38.4 -0.157
Bovidae	Kedoeng Broeboes	9092	66.2 0.120	57.2 0.056	72.4 0.159	46.6 -0.033	47.4 -0.025	38.1 -0.120	35 -0.157
Bovidae	Kedoeng Broeboes	9093	70.4 0.135	61.4 0.075	76.2 0.169	45.8 -0.052	50.1 -0.013	39 -0.122	33.2 -0.192
Bovidae	Kedoeng Broeboes	9094	70.7 --	62.2 --	78.4 --	-- --	48.7 --	36.6 --	34.8 --



**Appendix D: Continued.**

<b>Taxon</b>	<b>Locality</b>	<b>Dubois Collection Number</b>	<b>LM</b> raw <sup>1</sup> s.c. <sup>2</sup>	<b>LI</b> raw s.c.	<b>LL</b> raw s.c.	<b>WI</b> raw s.c.	<b>WD</b> raw s.c.	<b>TI</b> raw s.c.	<b>TD</b> raw s.c.
Bovidae	Kedoeng Broeboes	9095	68.2 0.112	60 0.057	74.6 0.151	49 -0.031	50.6 -0.017	41 -0.109	36.1 -0.164
Bovidae	Kedoeng Broeboes	10875	70.4 0.143	60.3 0.076	73 0.159	45.9 -0.043	48 -0.023	37.4 -0.132	33.4 -0.181
Bovidae	Kedoeng Broeboes	9087	59.5 0.123	52.5 0.068	66.6 0.172	39.6 -0.054	44.1 -0.007	33.9 -0.122	29.7 -0.179
Bovidae	Kedoeng Broeboes	9088	63.2 0.130	55.3 0.072	69.1 0.169	40.2 -0.067	43.5 -0.032	37.6 -0.096	31.3 -0.175
Bovidae	Kedoeng Broeboes	9089	62.6 0.121	54.1 0.058	67.7 0.155	43.6 -0.036	45.8 -0.015	37.7 -0.099	31 -0.184
<i>Duboisia santeng</i>	Trinil	3238b	33.7 0.142	29.7 0.087	36.4 0.176	21.5 -0.053	21 -0.063	18.8 -0.111	16.1 -0.178
<i>Duboisia santeng</i>	Trinil	2178a	34 0.161	29.7 0.102	36.6 0.193	21 -0.048	20.6 -0.057	17 -0.140	14.4 -0.212
<i>Duboisia santeng</i>	Trinil	2178b	29.8 0.123	26.2 0.067	33.2 0.169	19.4 -0.064	20.5 -0.040	18 -0.096	15.6 -0.159
<i>Duboisia santeng</i>	Trinil	264a	32 0.142	27.9 0.083	34.4 0.174	20.6 -0.049	20.7 -0.047	17.2 -0.127	15.4 -0.175
<i>Duboisia santeng</i>	Trinil	264b	33.9 0.143	29.2 0.079	36 0.169	21.3 -0.058	21.8 -0.048	18.7 -0.115	16.5 -0.169
<i>Duboisia santeng</i>	Trinil	5797a	31.8 0.135	28.7 0.090	34.8 0.174	21.3 -0.039	20.3 -0.060	17.3 -0.130	15.8 -0.169
<i>Duboisia santeng</i>	Trinil	5797b	32 0.135	28 0.077	33.9 0.160	22 -0.028	21.2 -0.044	18.1 -0.113	15.3 -0.186
<i>Duboisia santeng</i>	Trinil	5797c	29.7 0.131	26.5 0.082	32.9 0.176	20.1 -0.038	19.9 -0.042	16.3 -0.129	14.5 -0.180
<i>Duboisia santeng</i>	Trinil	5797d	33 0.145	29.7 0.100	35.5 0.177	20.8 -0.055	20.9 -0.053	18.5 -0.106	14.6 -0.209

**Appendix D: Continued.**

Taxon	Locality	Dubois Collection Number	LM	LI	LL	WI	WD	TI	TD
			raw <sup>1</sup> s.c. <sup>2</sup>	raw s.c.	raw s.c.	raw s.c.	raw s.c.	raw s.c.	raw s.c.
<i>Duboisia santeng</i>	Trinil	5797e	33.8 0.139	31.4 0.107	38.1 0.191	20.8 -0.071	22.2 -0.043	17.2 -0.154	16.6 -0.169
<i>Duboisia santeng</i>	Trinil	5797f	34.3 0.144	31.1 0.101	36.5 0.171	21 -0.069	21.1 -0.067	18.6 -0.122	17.2 -0.156
<i>Duboisia santeng</i>	Trinil	5797g	30.7 0.140	26.6 0.078	33.3 0.175	19.1 -0.066	19.8 -0.051	16.6 -0.127	15.8 -0.149
<i>Duboisia santeng</i>	Trinil	5797h	32.1 0.140	28.9 0.094	35.3 0.181	20.2 -0.061	20.9 -0.046	17.6 -0.121	15.1 -0.187
<i>Duboisia santeng</i>	Trinil	5797i	34.5 0.136	30.6 0.084	38.1 0.179	22.6 -0.047	24.3 -0.016	18.4 -0.137	15.9 -0.200
<i>Duboisia santeng</i>	Kedoeng Broeboes	6925a	33.5 0.152	28.4 0.080	35.5 0.177	22.1 -0.029	21.5 -0.041	17.9 -0.121	14.3 -0.218

<sup>1</sup>Raw measurements in mm.

<sup>2</sup>Size-Corrected values.

## VITA

Daniel Charles Weinand was born in Atlanta, Georgia on July 24, 1969. In Atlanta, he attended Montclair Elementary School and graduated from Cross Keys High School in 1987. From there, he attended the University of Georgia in Athens where he received a Bachelor of Science degree in Zoology in 1991. Immediately upon graduation, he took over as the Zooarchaeology collection manager at the Georgia Museum of Natural History where he continued to work while completing the Master of Science degree program in Geology in 1997. Although his emphasis was geoarchaeology, animal bones remained his primary interest as exemplified by his thesis, “Increment Studies of White-Tailed Deer (*Odocoileus virginianus*) from Coastal Georgia.”

It was finally time for a change of scenery, and he left for Knoxville, Tennessee to pursue his Doctor of Philosophy degree in Anthropology. Fortunately, this move also led to meeting and marrying his wife Laura Taylor in 2000. While pursuing his degree, he also obtained training in the radiocarbon dating method and has worked to establish the first radiocarbon dating lab at the University of Tennessee. The completion of this dissertation marked the end of the requirements necessary to obtain his Ph.D. in August 2005.

Daniel currently resides in Knoxville with his wife. They are expecting their first child. He is currently employed as a Post-Doctorate researcher in charge of the radiocarbon laboratory at the University of Tennessee.