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Article *in* Mammal Review · January 2005

DOI: 10.1111/j.1365-2907.2005.00048.x

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Mammal Rev. 2005, Volume 35, No. 1, 25–50. *Printed in Great Britain*.

The taxonomic status, distribution and conservation of the lowland anoa *Bubalus depressicornis* and mountain anoa *Bubalus quarlesi*

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ABSTRACT

1. The anoas are two species of dwarf buffalo, the lowland anoa *Bubalus depressicornis* and mountain anoa *Bubalus quarlesi* that are endemic to the island of Sulawesi, Indonesia. The classification of the subgenus *Anoa* within *Bubalus* is upheld by assessment of recent genetic and morphological research. The classification of anoas into two species is still debated, but with the absence of significant opposing evidence, this position is adopted here.

2. Information about the distribution of the two species is presented that adds to but largely supports existing reports. However, it is still uncertain whether the two putative species are sympatric or parapatric in their distribution. A review of anoa distribution from historical reports and recent field data (1990s to 2002) highlights their decline throughout Sulawesi, especially in the southern and north-eastern peninsulas. The decline has been attributed to local hunting for meat and habitat loss. Most populations are rapidly becoming fragmented, suggesting that the conservation of viable populations may eventually require management of metapopulations.

3. There is an urgent requirement for conservation efforts to: (i) protect anoas from hunting; (ii) prevent habitat loss in key sites; (iii) complete genetic studies to better determine the number of anoa taxa and Management Units and assess their distribution; and (iv) determine the status of the remaining anoa populations.

Keywords: buffalo, conservation, dwarf buffalo, Indonesia, Sulawesi, Wallacea

INTRODUCTION

Anoas are dwarf buffaloes, endemic to the Indonesian island of Sulawesi (and offshore islands). They are the smallest of the Bovini, standing about 1 m tall at the shoulder. Two species are presently recognized, the lowland anoa *Bubalus depressicornis* and the mountain anoa *Bubalus quarlesi* (Groves, 1969; Corbet & Hill, 1992; Wilson & Reeder, 1993). Both anoa species are classified as Endangered by International Union for the Conservation of Nature (IUCN) (IUCN, 2002), are legally protected under Indonesian law (Jahja, 1987) and are included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UNEP-WCMC, 2000). There is much debate over the taxonomic status and distribution of these two species (Mohr, 1921; Bohlken, 1958; Dolan, 1965; Groves, 1969; Weise, 1979; Kakoi *et al*., 1994; Pitra, Furbass & Seyfert, 1997; Schreiber

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et al., 1999). Nevertheless, the anoas are important 'flagship species' for conservation, being the largest endemic mammals on the highly bio-diverse island of Sulawesi. Conservation of the anoas to date has focused on the protection of forested areas and on captive breeding (Nötzold, 1999). The captive population doubled in size in the 10 years prior to the stud-book's publication; there were 125 animals in European, North American and Asian zoos in December 1998. However, management of the captive breeding programme is hampered by the uncertain taxonomic status of the anoas, and the uncertain classification of those animals already in zoos (Nötzold, 1999). Protected areas on Sulawesi cover 2223 km^2 or 11.9% of the island (total area 181 000 km^2), and 82% of the area under protection is reportedly still forested (Aden *et al*., 2001). Unfortunately, until recently little information has been available about the status of the anoas in these areas. This paper summarizes current knowledge about the taxonomy and distribution of the anoas, and presents new data collected by the authors and their colleagues. The conservation requirements of the anoas are also assessed.

BIOGEOGRAPHY OF SULAWESI

Sulawesi is situated within the Wallacea bioregion, renowned for its high level of endemism. Of the mammal species found on Sulawesi, 61% (98% excluding bats) are endemic, compared to just 18% on the neighbouring island of Borneo and 58% in Papua New Guinea (Whitten, Mustafa & Henderson, 1987). Thirty-four per cent of Sulawesi's bird species are endemic, compared to just 6% on the neighbouring island of Borneo and 52% in Papua New Guinea (Whitten *et al*., 1987). Being at the boundary of the Asian and Australasian biogeographical regions, Wallacea comprises a mix of the Asian and Australasian fauna and flora, including two cuscus species (*Ailurops ursinus* and *Strigocuscus celebensis*) from Australasia, and two suids (babirusa *Babyrousa babyrussa* and Sulawesi warty pig *Sus celebensis*) and the tarsiers (*Tarsius* spp.) from Asia. The anoas are thought to have originated from Asia, as they are close relatives of the Asian water buffalo *Bubalus arnee* (Groves, 1969).

Fossil and subfossil remains of anoas have been found in the Sulawesi Recent Faunas of Late Pleistocene to Holocene age (van den Bergh, de Vos & Sondaar, 2001), but not from earlier deposits as suggested previously (Hooijer, 1950). Both species of anoas were believed to be present throughout the island's forests in historic times (Weber, 1890; Sarasin & Sarasin, 1901; Mohr, 1921; Harper, 1945; Groves, 1969). However, their date of arrival on Sulawesi and geological history of the island is less well understood. A number of theories have been proposed to explain the presence of two morphologically similar species on Sulawesi, and to clarify the taxonomic uncertainty. These include environmental variation resulting from altitude (Heller, 1889; Whitten *et al*., 1987); and two separate immigrations (Kakoi *et al*., 1994; Kikkawa *et al*., 1997). Schreiber *et al*. (1999) suggest a number of additional possibilities. In essence, their theories suggests that two populations of anoas were geographically separated for a period on two landmasses before Sulawesi was finally formed (Hall, 1996, 1998), or after being spilt into smaller islands by rises in sea level. The latter is known to have occurred during the Pleistocene from pollen records found in the south-western peninsula (Fooden, 1969). Alternatively, variation in climate may have reduced forest cover as well as led to forest fragmentation during the Pleistocene period (Whitten *et al*., 1987). This could have led to the isolation of anoa populations and subsequent divergence, thus giving rise to the two species thought to occur today. Unfortunately, there are currently insufficient data to choose between these alternative explanations (van de Berg *et al*., 2001).

It is still unclear if the anoas currently live sympatrically, or whether they are separated, for example, by altitude. However, the distribution of Sulawesi's other mammal species may provide insights into the distribution of the anoas, and help answer the question. Between five and seven *Macaca* species are present on Sulawesi (Fooden, 1969; Albrecht, 1978; Bynum, 1999). Their distribution is thought to be parapatric (Bynum, 1999), although interbreeding between some of these populations is known to occur in hybrid zones (Ciani *et al*., 1989; Watanabe & Matsumura, 1991; Evans, Supriatna & Melnick, 2001). However, the regional distribution of these species does not appear to follow the island-wide distribution pattern of the anoa species and the fine scale distribution of anoa species remains unclear; they may live in localized forest patches at different altitudes or sympatrically. Distinct species or forms are found in another group of primates, the tarsiers of Sulawesi (Niemitz *et al*., 1991). At least two species occupy distinct regions within Sulawesi's lowland forests, *Tarsius dianae* and *T. spectrum*, while a further species, *T. pumilus*, is found at high altitudes (Shekelle *et al*., 1997; Groves, 1998). This altitudinal separation of tarsier species is likely to lead to a parapatric distribution resulting from the uninhabited altitudinal band between high- and low-altitude species. Further species such as squirrels and other small mammals, divided by boundaries of unknown origin, have been recorded on Sulawesi (Musser, 1987; Groves, 2001). In comparison, the distribution of anoa species appears to be more localized than the above-mentioned mammal species.

TAXONOMY AND SYSTEMATICS

Systematics

The systematic status of the anoas has been a source of much confusion ever since the first specimens were described. Despite the close similarity between the anoas and the Asian water buffalo, several authors have placed the anoas in a specially erected genus, *Anoa* H. Smith (1827) (Mohr, 1921; Pilgrim, 1939; Hooijer, 1948, 1950). However, Dolan (1965) considered *Anoa* to be a subgenus within *Bubalus* and Groves (1969) also concluded that the anoas show all the specialized characters of *Bubalus* and few significant or absolute differences. Groves advocated employing *Anoa* H. Smith (1827) as a subgenus to better indicate the relationship between the anoas *Bubalus (Anoa) depressicornis* and *B. (A.) quarlesi*, and the water buffalo *Bubalus (Bubalus) arnee* and the tamaraw *B. (B.) mindorensis.* Recent analyses of the anoas' haemoglobin β chain amino acid sequences (Kakoi *et al*., 1994), and the cytochrome *b* region of their mtDNA (Tanaka *et al*., 1996), support the placing of *Anoa* as a subgenus within *Bubalus*. Tanaka *et al*. (1996) estimate a coalescence time (mean estimated divergence time) for the present *Bubalus* species at around 2 million years, using the divergence time of *Bos* and *Syncerus* for comparison (corroborated from fossil records) (Savage & Russell, 1983).

Comparative studies of present day anoa skulls and fossil buffalo remains from between 3.20 and 1.78 million years ago (Mya) suggest that the anoas might be members of the most plesiomorphic clade of wild cattle (Bovini: oxen, bison, yak and buffalo) (Geraads, 1992; McDougall *et al*., 1992). Other studies of allozyme data and antigenic epitopes of the transferin molecule also support this theory (Hartl *et al*., 1988; Schreiber, Erker & Bauer, 1990). However, recent analysis of nuclear DNA (partial nucleotide sequences of the aromatase cytochrome P450 and lactoferrin genes) suggests that lowland anoa are most closely related to *Boselaphus* not *Bubalus* (Pitra *et al*., 1997). Pitra and co-workers also argue that their nuclear DNA data indicate that the *Anoa* and boselaphine lineage diverged from the ancestral bovine lineage before the buffalo and cattle lineages, some 12.4 Mya. This contradicts the hypothesis that *Anoa* diverged much more recently (*c.* 2 Mya) from the ancestral *Proamphibos–Hemibos* lineage leading to the living Asiatic buffaloes (Groves, 1981). If Pitra and co-workers are correct, *Anoa* should probably be treated as a genus of Asiatic antelope (i.e. included in an expanded Boselaphini tribe) rather than a subgenus within *Bubalus*. Nevertheless, as Pitra *et al*. (1997) noted, further studies are needed to test their conclusions. Therefore, *Anoa* will here be treated as a subgenus of *Bubalus* following Groves (1969).

How many species?

Most classifications accept the existence of two forms, lowland anoa and mountain anoa, and many authorities have treated these forms as two species, with or without additional subspecies (Harper, 1945; Groves, 1969; Honacki, Kinman & Koeppl, 1982; Corbet & Hill, 1992; Wilson & Reeder, 1993). Nevertheless, uncertainty remains over the validity of these two species. The English common names relate to a putative altitudinal separation (Groves, 1969), with the large form (lowland anoa) inhabiting low-lying areas and the smaller form (mountain anoa) living at higher elevations. The locality records of available specimens suggest this altitudinal separation, according to Groves (1969). However, no detailed comment on habitat variation was given to explain this supposed altitudinal boundary between the ranges of the two species. Furthermore, it has also been suggested that altitude would cause a clinal variation within one species of anoa, rather than indicate the existence of two parapatric species (Heller, 1889; Whitten *et al*., 1987).

Weise (1979) attempted a multivariate analysis using 26 measurements from 57 anoa skins and skulls (a greater number of skulls and measurements than Groves' study). However, Weise found insufficient data to show a statistically significant clinal range in skull size and also concluded that there were no biometric differences between lowland and mountain anoas that could not be explained as a result of allometric transformations because of the smaller (by 15%) size of the mountain anoa. Careful analysis of Weise's paper indicated that this is not a surprising finding because the criteria he used to classify 36 of the 57 skulls of unknown locality into mountain or lowland anoas were based on horn and size characters. We feel that the conclusions of the morphological analysis should be interpreted cautiously because a priori skull size and horn characteristics were used to identify the anoa species. Weise (1979) analysed 49 skull characteristics in pairs and in 40 of these correlation cases showed only size-dependant proportional difference when using multivariate analysis plots: mountain anoa skulls overlapped well within the lowland anoa grouping. He points to inconsistencies with characteristics used to identify the forms. He also stated that from the morphological data and from suggestions that there is contact between the populations and possible admixture in the wild, anoas can only be differentiated to subspecies level.

Others have also reported intermediate forms in the wild and in captive collections, suggesting interbreeding between the two species (Schreiber & Nötzold, 1995; S. Hedges, personal observations; J. Burton, personal observation). In addition, the different pelage characters of both species described in Table 1 have been observed in a single animal from birth to sexual maturity (J. Burton, personal observations).

Nevertheless, recent genetic studies of anoas in zoo collections support the two species hypothesis. For example, analysis of partial mtDNA cytochrome *b* gene sequences (285 bp) revealed clear differences between mountain anoas (from Krefeld Zoo) and lowland anoas (from Berlin, Leipzig and Antwerp zoos) (Schreiber *et al*., 1999). Of the eight animals sampled, four haplotypes were identified, within which 11 sites (3.9%) were variable. This level of nucleotide substitution was far higher than the intraspecific difference found in three other species [two dwarf zebus, *Bos (Bos) taurus*; two American bison, *Bison bison*; and four gaur, *Bos (Bibos) frontalis*]; indeed these species showed no variation. Three further species had 0.4% nucleotide substitutions, also lower than in the anoas [four African buffalo, *Syncerus caffer*; three European bison, *Bison bonanus*; and five banteng, *Bos (Bibos) javanicus*]. The interspecific variation within the anoas (between mountain anoa and lowland anoa) was

Table 1. Summary of anoa taxonomy

	Species	
	Lowland anoa	Mountain anoa
Valid name	*Bubalus (Anoa) depressicornis* (Smith, 1827).	*Bubalus (Anoa) quarlesi* (Ouwens, 1910)
Synonyms	*Antilope depressicornis*, *Bos bubalus anoa*, *Bos depressicornis fergusoni*, *Oreas platyceros*, *Probubalus celebensis*	*Anoa quarlesi*, *Anoa anoa*, *Bubalus depressicornis quarlesi*
Holotype	Nearly complete skull with horns of *Antilope depressicornis* Hamilton Smith, 1827; in the British Museum (Natural History), London (B.M. 607a)	Three specimens in the Amsterdam Museum are labelled as syntypes: skin and skull from a juvenile (first molar present) (a male?) (ZMA 9288); skin and skull from an older juvenile (second molar present) (a female?) (ZMA 9289); the third, an infant skull (ZMA 9295), is considered by Groves (1969) to be erroneously labelled as a type because Ouwens only refers to two animals in his paper
Type locality	Celebes [= Sulawesi, Indonesia]	Mountains of central Toradja [= Toraja] district, Celebes [= Sulawesi, Indonesia]
Paratype	Skull from an unsexed subadult (third molars erupted but unworn); in the British Museum (Natural History), London (B.M. 8.12.23.1)	

3.1%. Comparing these data with the interspecies variation between recognized species, the anoas have greater per cent nucleotide substitution rates than between domestic yak *Bos (Poephagus) grunniens* and American bison (2.1%); gaur and banteng (3.2%); and gaur and yak (3.3%). These results clearly corroborate the two species hypothesis.

Two further studies using complete mtDNA cytochrome *b* gene sequences (1190 bp) also support the two species hypothesis (Tanaka *et al*., 1996; Kikkawa *et al*., 1997). These studies were conducted using samples from two and five captive anoas from Indonesian zoos, respectively. The results of the study by Tanaka *et al*. (1996) suggest that the mountain anoa and lowland anoa should be regarded as two species as they found the weighted genetic distance between lowland and mountain anoas to be 0.0354. This was similar to the weighted genetic distance between the anoas (mountain and lowland) and water buffalo (both river and swamp types), clearly distinct species. The weighted genetic distance between anoas was greater than the intraspecific variation of domesticated water buffalo (swamp and river buffalo) (0.0256).

Kikkawa *et al*. (1997) analysed samples from five anoas. Without clarifying criteria for describing subspecies, they identified these animals into three subspecies of anoa, ‘lowland’, ‘mountain’ and ‘quarlesi’. The estimated sequence divergence between their ‘lowland’ and ‘mountain subspecies’ was 3.6%, and between their ‘lowland’ and ‘quarlesi subspecies’ was 3.3%. These sequence divergence differences are closer to those found between ‘good’ species such as the anoas and water buffalo of the swamp type (3.33%), than those found within water buffalo (i.e. between river and swamp type buffaloes) (2.67%). Even though the morphological descriptions of the different ‘subspecies’ are unclear, variation between these animals is equivalent to that seen between other distinct species. Kikkawa *et al*. (1997) state differences between anoas and water buffalo were not significant at the genus level, but that the results showed there are two lineages within anoa.

Earlier work (Schreiber, Nötzold & Held, 1993), which looked at allozyme distances and gross body morphology, agreed with, but raised some doubts about the two species hypothesis. The researchers suggested that there was less variation between the anoas in European zoos than could be found between other closely related species. Electrophoretic distance of allozymes was used to investigate differences between 25 anoas. Pairwise comparisons of Nei's genetic allozyme distances for anoa were $D = 0.0206$ to $D = 0.0505$, while for distinct wild bovid species the values were $D = 0.1389$ to $D = 0.7621$ (Hartl *et al.*, 1988). Therefore, these allozyme distances were more similar to those found between geographical races or subspecies (Nei, 1987). However, Schreiber and his co-workers cautioned that the taxonomic relevance of these genetic distances was open to question because of the effect of bottlenecks and incestuous breeding. In addition, we would argue that these results are also weakened because of uncertainty over the zoo animals' origins and lineages. Schreiber *et al.* (1993) concluded that the coincidence of differences encountered in karyotypes, polymorphic genes, body size, hair texture and other phenotypic characters (including horn shape) indicated that the anoas comprise differentiated taxa, but that the electrophoretic distance variation is less than is typical for bovine species.

There are at least two possible explanations for the difference in mtDNA and allozyme distance results discussed above. First, mountain and lowland anoa are well-separated species but hybridization in the captive population caused the observed pattern of protein variation (Schreiber *et al.*, 1993), whereas the maternally inherited mtDNA sequence reflects only the genotype of the founder females (Tanaka *et al.*, 1996; Kikkawa *et al.*, 1997; Schreiber *et al.*, 1999). Alternatively, the differences in the mtDNA sequences could be a chance effect caused by the sole female founder of the *B. quarlesi* species belonging to another mitochondrial lineage. Such polymorphism would have no taxonomic implications but would merely indicate the presence of very deep mitochondrial lineages and testify to the great age of the taxon. Recent studies of well-differentiated haemoglobin sequences are in accordance with the second possibility (Schreiber & Goltenboth, 1990; Schreiber *et al.*, 1993). Schreiber *et al.* (1999) suggest limited gene flow between populations could be sufficient to explain the lack of distinct variation in the wild, but would be insufficient to prevent differentiation within mtDNA over long periods. This has been shown to occur in other species (Avise, 1994), including Sulawesi macaques in zones of hybridization (Evans *et al.*, 2001).

Recently, it was suggested that there might be more than two species of anoa (Sugiri & Hidayat, 1996). Sugiri and Hidayat took samples from five wild-caught anoas from the mountains of Central Sulawesi. Three animals from one area had the same chromosome number of $2n = 46$ as captive mountain anoas, but another of the wild anoas had a chromosome number of $2n = 44$. The fifth animal's chromosome number was not reported. Captive lowland anoas reportedly have a chromosome number of $2n = 48$. Sugiri & Hidayat (1996) suggest that further work is needed, especially as the chromosomes of the individual with $2n = 44$ 'could not be identified' as being 'meta-, sub or acro-centric'. Schreiber *et al.* (1993) also argue that the biological meaning of anoa chromosomal variation needs to be investigated, as published chromosome numbers vary considerably, with $2n = 44$, 45, 47 and 48 in European zoos (Koulischer, Tyskens & Mortelsmanns, 1972; Schreiber *et al.*, 1993). In addition, lowland anoas in Indonesian zoos have been reported to have chromosome numbers of $2n = 36$ and $2n = 38$ (Amano & Martojo, 1983). More recently, anoas at Ragunan zoo have been reported to have chromosome numbers of $2n = 48$ in lowland anoa, $2n = 46$ in mountain anoa, and $2n = 42$ and $2n = 38$ in anoas of unidentified type (Pranadewi, 1998; Marsono *et al.*, 2001). If this variation exists, then it may show that the taxonomic diversity of anoas has been underestimated in the current classification. Other closely related species such as the water buffalo have chromosome numbers of 2n = 48 and 50 (swamp and Murrah types) and the tamaraw 2n = 46, less variation than found between anoa species. Clearly this issue requires further investigation.

A number of studies have suggested the existence of distinct subspecies (Heller, 1889; Dolan, 1965; Bartikova & Dobroruka, 1973; Foead, 1992; Schreiber & Nötzold, 1995; Kikkawa *et al*., 1997). Groves (1969) also discussed the possibility of subspeciation within the anoas. However, he concluded that while there did appear to be some geographical variation in size, the number of specimens available was insufficient to assess the significance of this variation.

In conclusion, with the absence of any overwhelming evidence to contradict the systematic position of the anoas presented by Groves (1969) and adopted by Honacki *et al*. (1982), Corbet & Hill (1992) and Wilson & Reeder (1993), the two species, *B. depressicornis* and *B. quarlesi*, are accepted as valid taxa here. However, it does seem likely that revisions will need to be made within the subgenus *Anoa*.

MORPHOLOGY

The anoas are the smallest of the extant wild cattle species (Groves, 1969). They are stocky, short limbed and thick necked. Young anoas are generally reported to have a thick covering of yellowish-brown woolly hair but there is much variation; newborn calves in zoos have brown or black pelage. Adults are also variable in colour but are predominantly brown or black. Males are usually darker than females and both have horns. The anoas are reputed to have exceptionally thick hides. The following descriptions of the two (putative) species (Table 2) should be regarded as a guide only, given the apparently high levels of individual variation shown by these animals and the uncertainty that remains about their taxonomic status.

Schreiber *et al*. (1993) concluded that the phenotypic characters conventionally used to distinguish lowland and mountain anoas including horn cross-section, shoulder height, body markings and hair characteristics are ambiguous, particularly if only a few animals are available for comparison. Their conclusions were based on an examination of animals in zoological collections. Unfortunately, doubts have been raised about these animals' origins in Sulawesi. Furthermore, incestuous breeding and possible hybridization between lineages reduce the value of these conclusions (Schreiber *et al*., 1993; Nötzold, 1999).

Criteria for identifying anoa species

Morphological criteria were identified from previous descriptions of anoas (Heller, 1889; Dolan, 1965; Groves, 1969; Walker *et al*., 1975; NRC, 1983; Groves, 1985; Grzimek, 1990). We reviewed all those characters we judged likely to be of utility to select a subset that was not disputed and that was congruent with our own experiences of examining both live anoas and skeletal material (Table 2).

These criteria are used in the present review of anoa distribution and status. However, if an individual showed morphological characteristics from both species, or if no data relating to these characteristics were available, we consigned the record to the 'Unknown *Bubalus* species' category. Juvenile *B. depressicornis* are similar to adult *B. quarlesi* in some features. In order to identify a juvenile *B. depressicornis*, either white leg markings had to be present or there had to be clear proof that the animal was indeed a juvenile (indicated by the lack of third molar teeth). Much uncertainty still remains, which is confounded by the overlap in morphological characteristics (Table 2).

Table 2. Morphological characteristics of two anoa species: *Bubalus depressicornis* and *Bubalus quarlesi*

	Species	
	Lowland anoa *Bubalus depressicornis*	Mountain anoa *Bubalus quarlesi*
Body size	Shoulder height: 60–100 cm; mass < 300 kg† Body length 170–188 cm¶	Shoulder height: < 75 cm; mass < 150 kg; body length 122–153 cm
Horns*†	**Triangular cross-section flattened, marked transverse ridges & marked external keel;** horn length: lowland male 271–373 mm; female 183–260 mm*‡	**Short, conical and rounded cross-section, no marked ridges or external keel in juvenile & adult;** both sexes: horn length 146–199 mm*
Overall body pelage colour	**Black & sparsely** (woolly brown in juvenile [M3]); sparse & straight, often rubbed off with age*	**Dark brown to black adult & thick & woolly haired into adulthood;** female coat especially woolly*
White facial/neck markings	White facial markings present* Often white throat markings*†‡¶	White facial markings sometimes present White throat markings never present*
White leg markings (see age dimorphism)‡§	**Forelegs: always white to yellowish-white from knee to hoof (black strip down front & across pasterns).** Hind legs: conspicuous white spots above hooves. Yellow in juvenile, to white in adult†	Foreleg: only whitish-yellow spots above hooves, sometimes absent§
Tail length (as percentage of total body length)*‡	19.8–25.8% (9 skins)*	14.6–17.8% (5 skins)*
Groin	Light coloured to white*	Light coloured but not white*
Age-related dimorphism	Juvenile form resembles adult mountain anoa (in following characteristics: pelage colour, texture, horn shape, body size), BUT lowland anoa always has white forelegs, conspicuous white spots on hind legs above hooves (see Dolan, 1965)*	Horn index of least–greatest basal horn breadth (anterio-posterior to bilateral)*
Skull length	Male 293–322 mm; female 290–300 mm*	Both sexes skull length 244–290 mm*

*Groves (1969). Species Identification Characteristics for the two species.
‡Hedges (1996). Species Identification Characteristics. Taken from: Harper (1945); Dolan (1965); Groves (1969); Walker *et al.* (1975); NRC (1983); Groves (1985); Grzimek (1990);
†Schreiber *et al.* (1993). Species Identification Characteristics.
§National Research Council (NRC, 1983) states that the entire lower limbs of mountain anoas are creamy white in colour, but all other published descriptions have emphasized the generally dark-coloured legs of this species.
¶A. H. Mustari, unpublished observation. Note on body mass: all those recorded ($n = 8$) have been below 150 kg for individuals identified as *B. depressicornis* as well as *B. quarlesi.*
The features in **bold** face are those used by the present authors to provisionally identify the species.

ECOLOGY AND BEHAVIOUR

Very little is known about the ecology and behaviour of the anoas, although they are thought to be solitary, forest-dwelling browsers (Whitten *et al.*, 1987; Foead, 1992). In a recent study, 21 of 40 field observations were of a single animal (Mustari, 1995). Anoas reportedly use many types of forest, from lowland forest, including secondary formations and mangroves, to montane forest at up to 2300 m above sea level (NRC, 1983; Mustari, 1995). In lowland habitats, anoas have been estimated to occur at densities of 1.3 animals/km^2 (with a 95% confidence interval of 0.5–3.1 animals/km^2) in Tanjung Peropa Nature Reserve (NR) (389 km^2) and 1.1 animals/km^2 in Tanjung Amolengu Wildlife Reserve (WR) (5 km^2) (A. H. Mustari, unpublished data). These densities were estimated using direct observation/encounters calculated from line transects, totalling 372 km in Tanjung Peropa and 124.3 km in Tanjung Amolengo. However, the density estimate for Tanjung Amolengu WR may have been higher than was sustainable, as animals were known to cross to this forest from adjacent areas. The typical life span in captivity is reported to be 20–30 years (Walker *et al.*, 1975; NRC, 1983; Grzimek, 1990). Sexual maturity is attained in the second to third year (in captivity), with generally only a single calf born per year (NRC, 1983; Jahja, 1987).

DISTRIBUTION

Mohr (1921) provided the first distribution map of the anoa but this had little detail. More recently, Groves (1969) presented a much more detailed map of the anoas' historical distribution. However, Weise (1979) challenged the taxonomic attribution by Groves of some of the specimens examined, such as the skulls from the Boro-Boro Mountains area. Since 1990, the present authors have conducted a detailed assessment of anoa distribution, as well as a review of published information. Criteria for identification of anoa species are described above. Data were collected during forest surveys. Surveyors recorded both direct and indirect signs (tracks, faeces and feeding traces), although obviously these indirect signs could not be used to identify anoas to species. Direct observations of anoas are rare, as indicated from transect data in three areas in South-East Sulawesi: two animals were seen during 182.1 km of transects in Tanjung Peropa; three anoas during 50 km of transects in Tanjung Batikolo; and three in 202.7 km of transects in Rawa Aopa Watumohai National Park (NP) (Riley, Hunowu & Soleman, 2001a; Riley *et al.*, 2001b). Furthermore, even the use of automatic cameras ('camera-traps') produces few records; for example, only one individual was photographed during a total camera-trapping time of 4930 hours in Tanjung Peropa (Riley *et al.*, 2001b), while in Rawa Aopa Watumohai NP none were photographed in 3523 hours of camera-trapping (Riley *et al.*, 2001a). We also conducted semi-structured questionnaire surveys, and recorded all observations of skeletal remains found. The majority of information relating to the identification of species came from skulls collected by hunters. These data were used as an indicator of distribution (presence/absence) of the two species. Questionnaire data were treated with caution because of the misidentification of the different age- and sex-classes of anoas as distinct species in some local nomenclature.

Survey areas are shown in Fig. 1; the distribution of both anoa species recorded since 1990 is shown in Fig. 2. Further information on anoa distribution and the threats to anoas in each area can be found below and in Appendix 1. Most mountain anoa records are from the central region of Sulawesi where much of the forest is above 1000 m asl; the only other mountain anoa record is from Buton Island, in Buton Utara WR (49) where there are also mountains of around 1000 m asl (Fig. 2). Lowland anoas records are distributed mainly

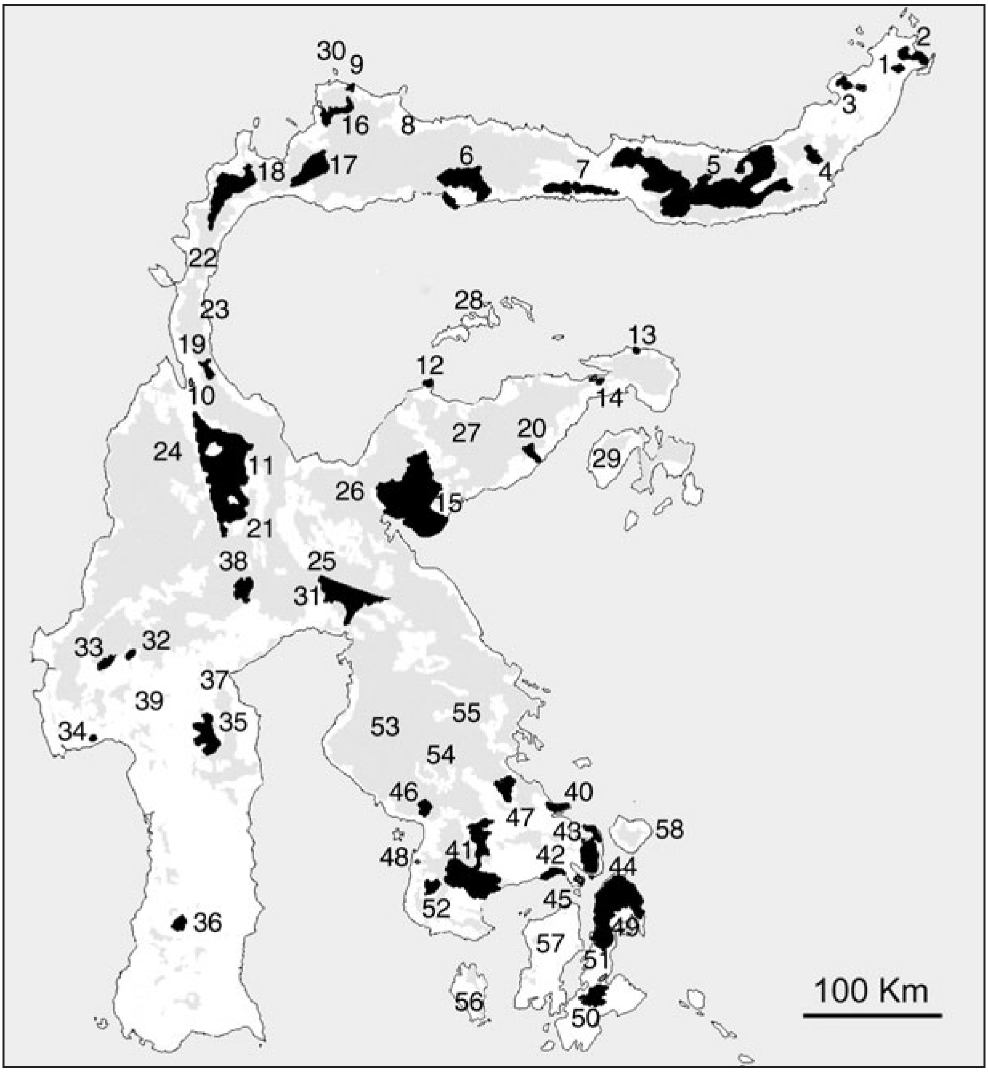

Fig. 1. The location of survey areas and forest cover in Sulawesi. Protected areas are shaded in black. Forested areas are shaded in light grey according to surveys between 1989 and 1995 (MacKinnon, 1997).

below 1000 m asl. Thus, the data collected during this study tend to support either the suggested altitudinal separation of the two anoa species (Groves, 1969) or the altitudinal cline suggestion (Heller, 1889; Whitten *et al.*, 1987). Nevertheless, the resolution of the map is rather poor (location of symbols do not exactly represent the location of data points because of the collection of data from villages and the altitude ranges are broad). So it is worth noting that MacKinnon (cited in Thornback, 1983) states that in mountainous areas one tends to find mountain anoa, but within this region this species can be found at sea level as well as at higher elevations. Meanwhile in areas with lowland anoa, this supposedly lowland form ranges up to at least 1500 m asl (e.g. in the Gunung Tangkoko and Gunung Ambang areas). Again, further survey work is required.

Figure 1 shows the location of Sulawesi's protected areas relative to the island's forest cover. Significant areas of unprotected forest remain between Panua NR/Marisa Complex (6), Gn.

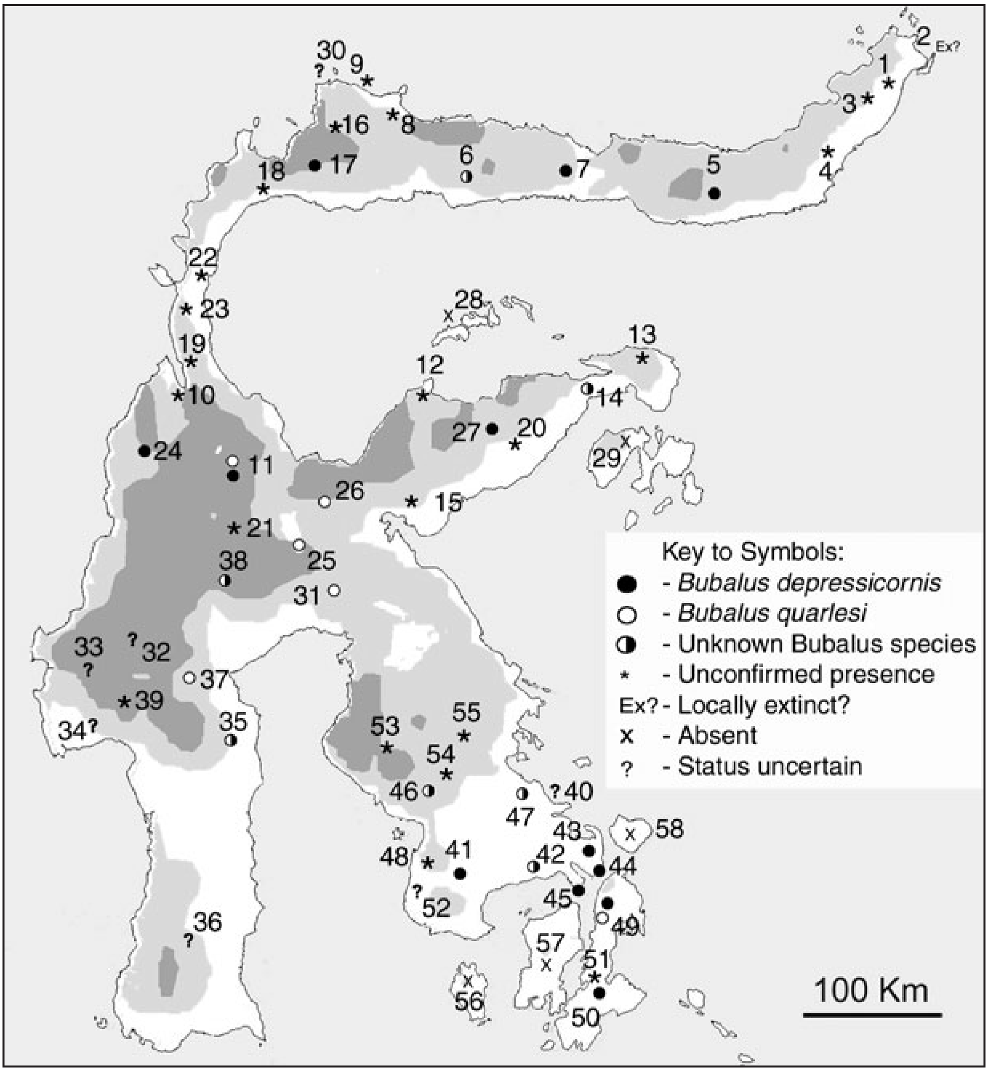

Fig. 2. Distribution of lowland *Bubalus depressicornis* and mountain anoa *Bubalus quarlesi* after 1990 and altitude (m asl). The map symbols represent locations where data have been collected. Each symbol may represent between 1 and 19 data points from a single location (e.g. numerous skeletal remains, direct observations or indirect signs on different occasions or locations within the site). See Appendix 1 for key to survey areas.*Key to criteria for anoa distribution*: *B. depressicornis* and *B. quarlesi* – see Table 1; Unknown *Bubalus* species – if an individual showed a morphological characteristic from both species or there was no data on characteristics, then the individual was included in the data set as 'Unknown *Bubalus* species'; Unconfirmed presence – secondary data indicating presence since 1990; Locally extinct? – anoa presumed extinct during the period since 1990, after extensive field surveys or area no longer suitable for anoa; Absent – anoa never reported from this area; status uncertain – near local extinction.*Altitude key*: white 0–200 m asl; light grey 200–1000 m asl; dark grey +1000 m asl. Altitude measured in metres above sea level. Data courtesy of E. Colijn.

Dako Proposed NR (16) and Gn. Tinombala (17) in the north; in the Gn. Lumut/Gn. Hohoban (27) area in the east; around Pengunungan Tangkeleboke (including Gn. Menkonga) (53), P. Abuki (54) and P. Matarombea (55); and to the west and south of Lore Lindu NP (11). It is not known whether most of these unprotected areas contain anoas. Nevertheless, anoas were still present throughout much of the island of Sulawesi in the 1990s (Fig. 2). The data compiled and reviewed here and depicted in Fig. 2 are in good agreement with the distribution map of Groves (1969); for example, both species were present in the south-east and central regions of Sulawesi. Additional information collected since 1990 has shown that lowland anoa inhabit the eastern peninsular, where it was previously unreported. Anoas were thought not to have reached most of Sulawesi's small neighbouring islands, except for Buton Island in the south-east. Both species were reported from Buton Island, which is again noteworthy, as previously only mountain anoa was known to occur. Both species appear to inhabit Lore Lindu NP and Buton Utara WR. In addition, there are a number of areas where anoas are known to occur, but they have been incompletely identified as 'Unknown *Bubalus* species'. This is mainly caused by the lack of morphological descriptions of the anoas present. More detailed surveys are needed.

The north-eastern and the southern parts of the island are notable for their lack of forest cover (Fig. 1), and it appears that only small and isolated populations of anoas remain in these areas (i.e. in Gunung Manembo-nembo WR, Gunung Ambang WR and Bulu Saraung NR). These populations are at high risk of local extinction. In Tangkoko – Dua Saudara NR, hunting is thought to have been the main cause of the estimated 90% decline in lowland anoa numbers between 1978/79 and 1993/94 (O'Brien & Kinnaird, 1996). The need to protect anoas and their habitat is discussed below.

From our review of the anoas' distribution and status, it is possible to identify areas that are likely to be of key importance for the conservation of these animals. Lore Lindu NP in Central Sulawesi (2310 km^2) still has abundant signs of anoa in the high elevation central areas (Burton, 2002). This park still has much undisturbed montane forest, forming one continuous area. In 2002, anoas signs were observed in a number of locations within the park. In Bogani Nani-Wartabone NP (2871 km^2) in North Sulawesi and Gorontalo Provinces, there are reportedly still significant numbers of anoa judging by the frequency of indirect signs seen in the forest (J. Riley, personal communication). Anoas have also been seen and photographed (using camera-traps) in the area in 2000–2001 (Pangau, 1997; J. Riley, personal communication). In South-East Sulawesi, camera-trap photographs were taken of anoa in Tanjung Peropa NR (389 km^2) (Riley *et al*., 2001b). Frequent sightings have also been made in this area. On Buton Island, observations of lowland anoa have been made in Lambu Sango WR (250 km^2) (Burton, 2001).

CONSERVATION STATUS

Hunting (mainly for meat) and the loss of suitable habitat are the major threats to the anoa, and recent reports indicate that hunting is by far the more serious of the two (Appendix 1). In rural areas, there appears to be little awareness of the protected status of anoas, and villagers readily recounted their hunting experiences to researchers (Schreiber & Nötzold, 1995). Recently, anoas have been extirpated from Tangkoko – Dua Saudara NR (J. Riley, personal communication), and this is thought to have largely resulted from hunting (O'Brien & Kinnaird, 1996). In the far larger protected area of Rawa Aopa Watumohai NP (968 km^2), there have been major losses of anoas because of severe anthropogenic effects of habitat degradation for logging, agriculture and settlements, as well as hunting pressures (Burton, 2001). In Lore Lindu NP, anoas have apparently declined, and it is suggested that they are now restricted to core areas that are less encroached upon by humans (Appendix 1). There have apparently been significant declines in distribution within many other protected areas too (Harper, 1945; Groves, 1982; NRC, 1983; Thornback, 1983; Jahja, 1987).

Hunting

Although many hunters are still willing to discuss their activities, this is becoming less common, making collection of accurate information on hunting pressures more problematic. However, minimum hunting rates and the reasons behind these are discussed below. Identification of skeletal remains and hunting location data gathered from hunters in eight villages around Lore Lindu NP (2130 km^2) showed that about 13 anoas were taken from the park per year by this small number of villages. In Lambu Sango WR (250 km^2), a minimum of 15 animals per year were caught by hunters in 19 villages (J. Burton, personal observations). The recording of anoa skulls found in villages in Central Sulawesi showed a catch rate of 1.5 anoa/village/year (11 villages, within boundaries of 600 km^2). In this area a total of 161 skulls or skins (from different individuals) were observed, and questionnaires suggested 443 animals had been collected over a 40-year period (Kasim, 2000). The latter figure is a catch rate of 1 animal/village/year. A similar survey in Kecamatan Palolo (near Lore Lindu NP) identified 34 skulls from animals caught in 1998, six skulls in 1999 and three in 2000. A further 153, 22 and 2 anoas having been caught in these years according to questionnaire surveys (Nurlaela, 2001). The actual numbers of anoas caught in each of these study areas is likely to be much higher, as people forget the number of animals caught or will be frightened to admit to the full scale of the hunting of these protected species.

In Morowali NR, Central Sulawesi, hunter-gatherers (from the Wana ethnic group) are thought to be catching anoas at an unsustainable rate (Avalard, 2000). Avalard suggested that the Wana would require about 700 km^2 of forest containing anoa to sustain a population large enough for them to hunt at current levels, whereas Morowali is only 225 km^2. As the anoas comprise 40% (by weight) of the large game animals harvested by the Wana, it is likely that anoas will be hunted to near extinction in Morowali and the Wana will then have to concentrate hunting effort on other species (Avalard, 2000).

Recent field surveys in Lore Lindu NP showed that areas close to settlements had a lower frequency of indirect signs of anoas (tracks and faeces) recorded on transect surveys (Burton, 2002a). An indication of human pressure was given a subjective category of Low, Medium or High Human Disturbance relating to the number of trails, agricultural fields, traps and people observed in the forest. Areas of higher disturbance level had a low frequency of anoa indirect signs (Burton, 2002).

In North Sulawesi, where hunting is thought to be a more serious problem than in other parts of Sulawesi, anoas are still being hunted (Pangau, 1997). However, little anoa meat has been sold in markets since the mid-1990s, apparently because of the local peoples' fear of punishment for engaging in these illegal activities (Clayton & Milner-Gulland, 1999). Patrolling with the aim of stopping the trade in illegally hunted meat on the roads and in the markets of Minahasa, North Sulawesi has shown that there is less anoa meat on sale relative to that of the other Sulawesi ungulates (Clayton & Milner-Gulland, 1999). However, it is now thought that people consume anoa meat in local villages and the forest, instead of transporting it to market and risk being caught.

Hunting methods vary between regions, but the most common techniques are snares or spears and dogs, and less commonly guns (Whitten *et al*., 1987; Mustari, 1995; Avalard, 1999; O'Brien & Kinnaird, 1999). Hunters also set fires to encourage new growth and so attract anoa and make hunting easier (Whitten *et al*., 1987).

The main reason for the widespread hunting of anoa is to obtain meat for local consumption (Thornback, 1983; Schreiber & Nötzold, 1995). For example, in South-East Sulawesi, 14 hunters were questioned: over the last 5 years the majority hunted occasionally, catching between one and 10 anoa each. However, one hunter said he caught 10 animals in 1 year.

Five of the hunters said they sold the meat, while the others consumed it in the forest or within the local community. Anoa meat was usually sold for Rp5000–7500/kg (*c.* £0.50/kg), but one hunter said he could sell anoa meat for Rp22 500/kg (*c.* £1.60/kg) (J. Burton, personal observations).

Anoa skulls and horns do not seem to be particularly valued as trophies by hunters, and while quantitative data are unavailable, trade in trophies does not appear to pose a serious threat to the anoas (Schreiber & Nötzold, 1995; S. Hedges, personal observations). There have been occasional reports of illegal trade in live animals in the past; for example, it was reported that an animal trader in South-East Asia offered to sell a pair of lowland anoas at US$3000 each (Anonymous, 1976). However, no significant international trade in either live animals or body parts has been reported in recent years. Trade does exist within Sulawesi, where live animals are sold for later slaughter or as pets. An animal can be sold for £29.00–36.00 (Rp400 000–500 000), although prices can reach as much as £71.00–142.00 (Rp1 000 000–2 000 000) in extreme cases (Lee, 1999a; J. Burton, personal observations).

The effect of hunting on the long-term survival chances of populations of anoa in Sulawesi was estimated during the Anoa Population and Habitat Viability Analysis Workshop (PHVA). Available data on life history were used with the VORTEX Program to estimate the population viability of different population sizes under three levels of hunting pressure (Manansang *et al.*, 1996). Hunting rates were taken from the estimated 15% per year decline of the Tangkoko – Dua Saudara NR population (O'Brien & Kinnaird, 1996) and lower levels of 8% and 4%. Population viability estimates were calculated for initial populations of 25, 100, 360, 1500 and 2860 animals during a 100-year simulation, with the carrying capacity set at twice the original population size. It is currently unlikely any population in a protected area is larger than the greatest population modelled above. The simulations showed that all populations became extinct with the 15% off-take hunting level. The 8% hunting level caused the local extinction of all except the two largest populations (1500 and 2860 individuals) within 100 years, but even the largest populations were at high risk of extinction soon after 100 years. Even an initial population size of 2860 anoas with 4% hunting loss caused a greater than 90% decline in 100 years to just 232 animals. These simulations highlight the threat that even the largest anoa populations face from hunting levels that could now be occurring throughout Sulawesi.

Loss of suitable habitat

Habitat degradation and loss is the second most significant threat to the anoas. Many anoa populations are becoming isolated as the forest around the protected areas is cleared or converted to plantations. Total forested area remaining on Sulawesi in 1985 was estimated to be between 42 and 49% of the land area of the island (Holmes, 2000; Mathews, 2002). The loss of lowland forest between 1985 and 1997 was estimated to be 89% (Holmes, 2000). Recently, it has been said that 'Sulawesi's lowland forest has already been reduced to statistical insignificance' (Aden *et al.*, 2001).

Although 11.9% of the island is protected, loss of suitable anoa habitat within protected areas is as much a problem as in unprotected forest (Aden *et al.*, 2001). For example, the expansion of agricultural and settled areas, logging, mining and fires have encroached into many protected areas. Large protected forest areas such as the eastern end of Bogani Nani-Watabone NP and the Besoa and Lindu areas of Lore Lindu NP are being fragmented by roads (Burton, 2002). The fragmentation of these once contiguous forests will reduce the natural movement of anoas between forest patches. This may cause the loss of genetic diversity and increase the chance of population extinctions (Gilpin, 1991; Wang & Caballero, 1999). However, assessing the scale of the threat posed to the anoas by shifting agriculture and fires is hampered by the lack of knowledge of their habitat requirements. Furthermore, the effects of disturbance resulting from human presence in the forest (e.g. collecting forest products or traversing anoa areas) on anoa populations are unknown.

In addition to hunting and the loss of suitable habitat, diseases present a potential threat to the species. The increased presence of domestic or feral cattle, as well as introduced deer populations, heightens this risk.

Captive breeding

A total of 125 (58, 67) anoas were reported to be in captivity on 31 December 1998. These animals were held in 35 institutions: 17 in Europe, 10 in North America and 8 in Asia (Schreiber *et al*., 1993; Schreiber & Nötzold, 1995; Nötzold, 1999). Of these 125 animals, seven were listed as founders. These seven animals were imported from zoos in Indonesia or Malaysia, or obtained from animal dealers. Their places of origin within Sulawesi are unknown.

Studbook breeding recommendations have, of necessity, been rather general because of the uncertainty surrounding the taxonomic affiliations of the captive animals. All 125 animals were listed as *B. (A.) depressicornis* (Nötzold, 1999) although there has been discussion about their taxonomic status. Biometric and photographic assessment of the founders of the Antwerp, Rotterdam and Leipzig lines (lowland anoa) has indicated their phenotypic similarity. These populations have subsequently been hybridized. The anoas at Krefeld, Berlin and Decin Zoos, which are the descendants of three animals originally imported by Berlin Zoo, have been listed as mountain anoa. The small number and close relationship of these animals raise questions about the long-term value of this population for the captive breeding programme.

Suggestions for an anoa conservation programme

Overall objectives

It is clear from the information presented in this paper that our knowledge of the systematics, distribution, abundance and general biology of the anoas is still rather scant. As effective conservation strategies require firm biological foundations, the recommendations made below emphasize the need to gather biological information, while at the same time attempting to conserve as much of the remaining anoa diversity as possible. The top priorities are: (i) to protect anoas from hunting and prevent habitat loss and degradation in all key sites; (ii) to complete the genetic studies currently underway in order to determine how many anoa taxa exist; and (iii) determine the status of the remaining anoa populations (i.e. determine population size or relative abundance, and monitor population trends) in Sulawesi to allow the design and implementation of an effective anoa management strategy.

The largest protected area in Sulawesi is 2871 km^2. In most protected areas anoa numbers will be below carrying capacity because of hunting pressure. So, if we use the estimated density of anoas reported by Mustari above of 1.1 and 1.3/km^2, we see that the largest remaining protected anoa populations are likely to be smaller than 3000 animals, probably half this population size, with a far smaller number of breeding individuals. A large proportion or the total number of anoa will probably exist in small non-viable populations, as has been reported recently using similar surveys of the Gaur (Choudhury, 2002). Therefore, for the long-term conservation of these species active management of the genetic resource may be required. This could take the form of the movement of individuals between populations to increase gene flow.

Protect anoas from hunting

Anoas need to be protected from hunting by enforcing the existing laws of the Indonesia, particularly the Conservation of Natural Resources and Ecosystems Act (Udang-Udang Republic of Indonesia (UURI) No. 5). Law enforcement should be combined with an environmental education campaign that stresses that the anoas are unique to Sulawesi and in danger of being lost forever. Successful anti-poaching activities require frequent patrols of key protected areas, which should result in the arrest and effective prosecution of poachers. In addition, realistic fines for people caught selling live anoas, anoa meat, horns or other parts or for keeping pet anoas need to be imposed (Lee, 1999b).

Complete genetic research aimed at determining the number of anoa taxa

Until we know more about the genetics of these animals, we cannot ensure that our efforts are being directed towards conserving the greatest possible proportion of the anoa gene pool. Genetic research is currently being conducted (by J. Burton) to determine whether the two presently accepted species of anoa, *B. depressicornis* and *B. quarlesi*, are in fact sufficiently distinct to warrant specific status. The study will also allow the identification of the distribution of both species and of Management Units that will allow effective preservation of the greatest genetic diversity. Management Units are classified as populations with morphological or genetic variation caused by isolation or loss of mixing between populations (Moritz, 1994). The information collected includes photo-documentation, body measurements and DNA samples, as well as such information as is available about the animals' likely places of origin on Sulawesi. Such information will also help overcome some of the difficulties (the small number of founders, interlineage hybridization and incest breeding) that have hampered conservation breeding of the captive population in Europe (Schreiber & Nötzold, 1995; Nötzold & Schreiber, 1996). Results of the genetic work will be a key component in the design of an *in situ* management plan for the anoas.

Conduct an island-wide status survey

While the work described earlier in this paper has done much to bring up to date our knowledge of the distribution of anoas on Sulawesi and its offshore islands, we still know rather little about likely population sizes and population trends. For the majority of sites we merely know that anoas are present or are absent/likely to be absent. This makes it difficult to focus conservation efforts effectively. There is therefore still a need for an island-wide survey to identify major anoa populations. In order to devise the most representative conservation strategy, the surveys should aim to locate populations throughout the island in order to preserve the full biogeographical variation exhibited by these species.

The proposed island-wide status survey has five components: (i) confirm the presence and estimate density of anoas in key areas to identify where sufficient numbers are present for likely population viability in the long term. These should include Lore Lindu NP, Bogani Nani-Wartabone NP and environs, the Upper Paguyaman/Nantu area, Morowali NR, Tanjung Peropa WR, Lambu Sango WR or Buton Utara NR (at a later date, the following areas should also be assessed: G. Lumut/G. Hohoban, Pengunungan Tangkeleboke, Pengunungan Abuki, Dako Proposed NR and Gn. Tinombala). It would also be desirable to survey all those areas where anoa have been reported since 1990 (Fig. 2); (ii) determine whether anoas are present in blocks of suitable habitat for which only pre-1990 data exist (Pulau Dolongan, Masupu Proposed Game Reserve, Sumarorang Katena Rompi Protection Forest, Lampoko Mampie GR, Bulu Saraung NR, Lasolo-Sampara Proposed NR and Padang Mata Osu WR), or no reports exist [Gn. Kambuna area (Masupu Proposed WR to Lore Lindu NP), Pungunungan Verbeek area (the border between South-East, South and Central Sulawesi)]; (iii) assess the feasibility of methods for increasing anoa gene flow between protected areas; (iv) identify major threats to the anoa populations in each site; and (v) collect samples (dry skin, horns, skulls and, wherever possible, DNA samples) for genetic and morphological analysis. However, DNA samples should only be collected from pets (or other captive animals).

Development of protected areas

On paper Sulawesi boasts an impressive system of protected areas, but unfortunately many of these areas are poorly managed, understaffed, and lack the basic resources required for effective conservation. Once the island-wide survey data have been collected, the need for, and feasibility of creating additional protected areas should be determined. The priority areas for conservation management should also be assessed; however, in general the largest areas of habitat are likely to be the top priorities, because these areas are likely to contain the populations most resilient to demographic and genetic problems and the effects of hunting. Management planning for conserving the anoa will have to incorporate logistical considerations such as local infrastructure, Forestry Department support and interest, regional development plans and local community support (Anonymous, 1991; Collins *et al.*, 1991; McCarthy, 1991).

Management of domestic and feral animals to reduce threats to anoas and other wildlife

Domestic water buffalo or other livestock are known to enter into protected areas where anoas occur (UNDP/FAO, 1982; Zwahlen, 1992). This should be prevented to avoid the risk that diseases and parasites will be transmitted to the anoas. It is appreciated that genuine conflicts of interest over grazing rights may exist between protected areas and the people living around them. In the event of an outbreak of a serious disease such as rinderpest or foot and mouth disease, domestic livestock in the areas surrounding nature reserves and national parks identified as containing major anoa populations should be vaccinated.

Ecological and behavioural research to facilitate effective conservation

A detailed field study should be regarded as a high priority. We know so little about the ecology and behaviour of these animals that plans drawn up for their conservation inevitably have to rely on numerous assumptions. The field study should concentrate on those aspects of anoa biology most pertinent to their conservation. For example, the habitat requirements of the anoas are still little known. We know next to nothing about what constitutes high-quality habitat for anoas, or about seasonal variations in habitat utilization. Similarly, almost nothing is known about the effects of varying degrees of habitat modification (e.g. selective logging) or disturbance (cattle grazing, collection of forest products, etc.) on anoa populations. Additionally, following suggestions that anoas avoid areas frequented by deer and pigs, their distribution and ranging behaviour with respect to these species should be studied. A radio-tracking study would provide much valuable data. Furthermore, research should aim to determine whether opportunities for improving the quality of available habitat exist and whether such manipulations would be desirable.

In order to help identify the limiting factors affecting anoa populations, it would be very useful to gather information about anoa population dynamics (especially recruitment and mortality) in those areas where hunting intensity, degree of habitat modification and other disturbances are being assessed. The impact of hunting may be assessed by studying how anoa density and behaviour varies with distance from villages, and with respect to the income structure and occupation profile in those villages.

Sociological/anthropological research

It is recommended that a study of the uses local people make of the areas in and around the most important sites should be made. Conducting Rapid Rural Appraisals around these sites would be a useful way of identifying major conflicts of interest between protected areas and the surrounding communities.

Education and training

For effective management of wildlife, it is necessary for protected area staff to be adequately trained in surveying and monitoring techniques; as already discussed above, the lack of sufficient numbers of well-trained staff has been identified as a major limiting factor for the successful implementation of conservation programmes in Indonesia. It is necessary to explain to people living around protected areas why their activities need to be controlled and why wildlife, which they might otherwise utilize, should be conserved. The fact that anoas, along with many other species, do not occur outside Sulawesi should be stressed because many people on the island are unaware of their heritage (S. Hedges, personal observations).

Recommendations relating to captive breeding of anoas

Until genetic or morphological studies have provided a clearer idea of the number of anoa species and their distribution, there should be no further movement of animals from *in situ* to *ex situ* locations or vice versa.

ACKNOWLEDGEMENTS

The authors would like to thank: The Indonesian Ministry of Forestry, Jakarta (PHKA), Sulawesi's Provincial Forestry Departments (BKSDA); The Indonesian Institute of Science (LIPI); and the Indonesian sponsor, Ir. Harayanto MS, Bogor Agricultural University (IPB) for permission and support to conduct this work. For their collaboration in Indonesia thanks goes to numerous people: Moh. Yasin; Andi Faisal Alwi; Yusran Zainudin and Jabar Lahadji; Kaharudin Kasim; Vitri and Piton; Yani Mile and Ridwan; Imran, Ading, A'o; La Ode Nafiu; Hally Day; Margaretha Pangau; Arfan Polontalo and Jemi Monoarfa; Duncan Neville and Edward Pollard; Steve and Puji Oliver. This work was supported by the Stichting Dierentuin Helpen (Consortium of Dutch Zoos), the University of Edinburgh Development Trust, Royal Geographical Society, London, Royal Zoological Society of Scotland and The Nature Conservancy. A.H. Mustari was additionally supported by AusAID. For their support in the UK and Indonesia as well as their helpful comments on the manuscript, the authors would like to thank Dr Alastair A. Macdonald, Dr Roy Wiles and Jon Riley. For assistance in producing the maps we thank Ed Colijn and Colin Warwick. Thanks are also due to Dr R. McDonald and an anonymous referee for helpful comments on the manuscript.

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Submitted 14 April 2003; returned for revision 6 June 2003; revision accepted 16 December 2003
Editor: RM

APPENDIX 1

Summary of anoa distribution, status and threats in major forested areas of Sulawesi

Map code	Province & area name	Status (area – km^2)	Anoa status (data type)	Comments (reference codes in [] brackets, see below for details)	Threats
1	Gunung Klabat	P. NR (53)	Unconf (LR)	Report by local people during questionnaire [20]	Hunting, encroachment [1]
2	Tangkoko Batuangus – Dua Saudara	NR (75)	Ex?	Present in 1994, limited range [11]. Comparisons of 1993/4 [14] and 1979 [MacKinnon & MacKinnon, cited in 2], showed decline of 90%; repeat Wildlife Conservation Society surveys showed no signs in 1999 & 2001 [21, 24]	Agricultural encroachment and heavy hunting pressure [7, 11, 12, 14,]
3	Gunung Manembo-nembo	WR (65)	Unconf (LR)	Listed 1982 [1] and twice reported in 1994 [11]. Report by conservation staff [20]	Encroachment and hunting [1]. Hunting threat more recently [12]
4	Gunung Ambang	NR (250)	Unconf (LR)	Anoa killed in 1992. Report by forestry staff [20]	Hunting and habitat loss [12]
5	Bogani Nani-Wartabone	NP (2871)	B.d (Skull)	Anoa photographed in 1996 [27] skulls seen of lowland species. Field sightings in 1995 [20]	Illegal gold-miners hunting [7]
6	Panua (in Marisa Complex)	NR (940)	Conf (LR)	Rangers saw anoa in 1995, reports in 1990s [20]. Advantage being within Marisa Complex (940 km^2)	Hunting [1, 12]
7	Upper Paguyaman/ Nantu area	None (315)	B.d (Sighting)	Present in early 1990s [11]. Two lowland anoa seen in 7-day survey in 1991 [6]. Reported sightings in 1990s [20]. Skulls of Lowland form seen & 2 reports observed 5 and 9 anoa since 1992 [27]	Reports of animals snared in 1993, 1994 and 2002 (inc. *B. depressicornis* skulls) [27]. Other threats include habitat loss, road building) [6]
8	Buol/Toli-Toli	P. NR (225)	Unconf (LR)	Reported by local people in 1992 [12]	Hunting & habitat loss [12]
9	Pinjam/Tanjung Matop	WR (16)	Unconf (LR)	Footprints reported (1995) by forest rangers [12]. Questionnaires [26]	

APPENDIX 1. *Continued*

Map code	Province & area name	Status (area – km^2)	Anoa status (data type)	Comments (reference codes in [] brackets, see below for details)	Threats
10	Poboya	NR (1000)	Unconf (LR)	Questionnaires [26]	
11	Lore Lindu	NP (2310)	B.d, B.q (Skull)	Mountain anoa karyotyped (early 1990s) (unusual sheep-like head) [11, 15]; horns seen in 1994 [29]. Skulls of mountain and lowland anoa seen [23, 24]	Planned hydroelectric development in Lake Lindu area [7]. Hunting at boundary [29]. Expanding enclaves [23]
12	Tanjung Api	NR (42)	Unconf	Reported in 1980s [1], Questionnaires [26]	
13	Pati-Pati	P. WR	Unconf (LR)	Questionnaires [26]	
14	Lombuyan/Pagimanan	WR (36)	Conf (Skull)	Locals reported anoa in 1994, skull observed [17]	Hunting [12]
15	Morowali	NR (2250)	Unconf (LR)	Reported in 1980, 1995, 1996 and 2001 [7, citing the 1980 management plan, 19, 26]	Wana people use spears and dogs [19]. Hunting at unsustainable rate [22]
16	Gunung Dako	P. NR	Unconf (LR)	Questionnaires [26]	
17	Gunung Tinombala	None	B.d (Skull)	Questionnaires [26]	
18	Gunung Sojol	NR (500)	Unconf (LR)	In 1982 contained anoa [1], Questionnaires [26]	
19	Pangi Binangga	P. NR (60)	Unconf (LR)	Questionnaires [26]	
20	Bakiriang	P. WR (10)	Unconf (LR)	Questionnaires [26]	
21	Bada Valley	None	Unconf (LR)	Present in 1989 [29, 10], Questionnaire [26]	
22	Pantai Timur	None	Unconf (LR)	Questionnaires [26]	
23	Pantai Barat	None	Unconf (LR)	Questionnaires [26]	
24	Pengunungan Takolekaju	None	B.d (LR, Skull)	Skulls of lowland anoa seen in 1990 [18]. Questionnaires 2002 [23]	
25	Mayoa area	None	B.q (Skull)	Mountain anoas killed by hunters in 1994 [11]	Hunting reportedly intense [11].
26	Gunung Pompangeo	None	B.q (Sighting)	3 specimens [15] karyotyped as mountain anoa	Hunting is the most serious threat [12]

27	Gunung Lumut, Gunung Tempu, Gunung Hohoban	None	B.d (Skull)	Remains observed by Burton [23]	
28	Togians Islands	(MR)	X (LR)	Questionnaires [26]	
29	Peleng/Banggai Islands	None	X (LR)	Reports from local forest rangers [26]	
30	Dolongan Island	WR	? (LR)	Reported refuge for anoa, no recent data	Human disturbance [1]
31	Pengunungan Faruhumpenai	NR (900)	B.q (Skull)	Mountain anoa may occur (1994), skull seen [11, 29]	Hunting, clearing lowland forest [1, 12]
32	Masupu	WR (25)	? (LR)	Reported 1982 [1], repeated visits saw no signs [26]	Hunting [1]
33	S. Katena/Rompi	PF (100)	? (LR)	Reported 1982 [1], repeated visits saw no signs [26]	
34	Lampoko Mampie	WR (20)	? (LR)	Reported in early 1980s [1]; in late 1980s anoa not mentioned [5]; but may still be present [26]	
35	Pengunungan Latimojong	P. NR (580)	Conf (LR)	Reported present (1987) [29]. 2 skulls reported [10]	Hunting is the most serious threat [12]
36	Bulu Saraung	NR (57)	? (LR)	Possibly not present now [26]	Deforestation, shifting cultivation [1]
37	Makale area	None	B.q (Sighting)	In 1994 a mountain anoa was examined [11]	Hunting is the most serious threat [12]
38	Kambuno Katena	PF	Conf (LR)	Anoa reported [16]	
39	Sumarorang	P. WR	Unconf (LR)	Present in montane forest in early 1980s [1], widespread but uncommon, still hunted [26]	Shifting agriculture and hunting [1]
40	Lasolo-Sampara	P. NR (450)	? (LR)	Reported in forests in Lawe Solo river valley [1]	Hunting and logging [1]
41	Rawa Aopa-Watumohai	NP (968)	B.d (Skull, LR)	Lowland anoa were reported in Rawa Aopa area, not common [4, 7, 9]. Lowland anoa skulls seen [23]	Hunting pressure high, unsuitable savanna, encroachment [8, 12, 23]
42	Polewali	P. WR (80)	Conf (Prints)	Mustari observed field signs in 2000 [27]	Hunting, land clearance [1, 12]
43	Tanjung Peropa	NR (389)	B.d (Sightings, Skull)	Skulls collected and field signs in 2002, direct observation by Mustari in 1996 & 2002 [27]	Hunting 1996, 2002 [12, 27]
44	Tanjung Amolengu	WR (8.5)	B.d (Sightings, Skull)	Estimated 8–12 lowland anoa occurred in this very small reserve in 1995 [13]	Hunting (snares) 10 anoa killed in 1980s & 1995; small and isolated [13]
45	Tanjung Batikolo	WR (55)	B.d (Skull)	Mustari saw skulls footprints [27] in 1994, 2000	Land clearance, hunting [27] in 2000

APPENDIX 1. *Continued*

Map code	Province & area name	Status (area – km^2)	Anoa status (data type)	Comments (reference codes in [] brackets, see below for details)	Threats
46	Kolaka Utara	NR	Conf (Sighting)	Anoa seen by Mustari in 1994 [13]	Habitat loss and hunting [12]
47	Toronipa	NR (20?)	Conf (Prints)	Mustari [13] saw footprints in 1994	Hunting, habitat loss [12]
48	Lamedia	NR (5)	Unconf (LR)	Questionnaires [26]	
49	Buton Utara	WR (820)	B.q; B.d (Sighting, Skull)	Mountain anoa seen in 1995 by Mustari [13]. Skulls observed and identified as lowland anoa [23]	Hunting [12]
50	Lambu Sango	WR (250)	B.d (Skull)	Skulls of lowland anoa, footprints, [23]	Hunting [1]
51	Kakinawe	NR (50)	Unconf (LR)	Questionnaires [26]	
52	Padang Mata Osu	WR	? (LR)	Questionnaires [26]	
53	Pengunungan Tangkeleboke	None	Unconf (LR)	Questionnaires [26]	
54	Pengunungan Abuki	None	Unconf (LR)	Questionnaires [26]	
55	Pengunungan Matarombea	None	Unconf (LR)	Questionnaires [26]	
56	Kabaena Island	None	X (LR)	Questionnaires [26]	
57	Muna Island	None	X (LR)	Questionnaires [26]	
58	Wowoni Island	None	X (LR)	Mustari questionnaire to local people [27]	

Abbreviations: 1. Protected areas: NP, National Park; NR, Nature Reserve; WR, Wildlife Reserve; PF, Protection Forest; P., Proposed status. 2. Anoa status: B.d, *Bubalus depressicornis*; B.q, *Bubalus quarlesi*; Conf, Confirmed presence; Unconf, Unconfirmed presence; Ex?, Locally extinct; ?, Status uncertain, near local extinction; X, Never reported. 3. Data recorded: LR, Local secondary report; Sighting, Direct sighting; Skull, Skeletal remains; Prints, Indirect field data (prints, dung).

References (from numbers in [] brackets above): 1– UNDP/FAO (1982); 2 – Thornback (1983); 3 – Anonymous (1984); 4 – Petocz (1989); 5 – Scott (1989); 6 – Clayton *et al.* (1991); 7– McCarthy (1991); 8 – Zwahlen (1992); 9 – Gunawan (1995); 10 – Melisch (1995); 11 – Schreiber & Nötzold (1995); 12 – Manansang *et al.* (1996); 13 – Mustari (1996); 14 – O'Brien & Kinnaird (1996); 15 – Sugiri & Hidayat (1996); 16 – Tikupadang, Gunawan & Sila (1996); 17 – P. Vercammen, personal communication to Hedges (1996); 18 – N. Sugiri, personal communication to Hedges (1996); 19 – T. O'Brien, personal communication to Hedges (1996); 20 – Pangau (1997); 21 – Lee (1999a); 22 – Avalard (2000); 23 – J. Burton, personal observation; 24 – J. Burton, personal observation; 25 – J. Burton, personal observation; 26 – Questionnaire data from collaborating non-governmental organization (NGO) for J. Burton, 2000–2002; 27 – J. Mustari, personal observations; 28 – S. Hedges, personal observation; 29 – Tikupadang, Gunawan & Sila (1994); Whitten *et al.* (1987).