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# Sexual selection and extinction in deer

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## Abstract

By performing a comparative analysis and using phylogenetic relationships of the Cervidae family this study aimed to address whether or not sexual selection may play a role in the extinction of species by making species more vulnerable to extinction. The role of sexual selection in making species more vulnerable to extinction is largely unexplored, and several factors such as ecological and life history traits may increase the risk of extinction.

In all species of the family Cervidae (Gilbert et al. 2006, Geist 1998, Groves and Grubb 2011, Meijaard and Groves 2004, Price et al. 2005, Goss 1983) sexually selected characters play a main role in determining species status and thus potentially their probability of extinction. In this study the intensity of sexual selection (measured as sexual size dimorphism, antler size and mating system) and the rate of extinction (IUCN classification and anthropogenic effect) were counted as factors to determine the role of sexual selection intensity in both species-rich and species-poor clades.

By using the programme MESQUITE and phylogenetic trees, the results show an association between species with larger body size and dimorphism, living in open habitats and having larger antler size expanded to more than three tines; such species are mostly non-territorial and form harems during the rutting season. The small species are territorial, live in closed habitats, are monomorphic and have small antler size limited to two tines or less. Moreover species that are more subjected to habitat degradation and anthropogenic effects tend to become smaller in size.

Extinction risk for the species-rich clades with small sized, territorial and small antler sized species is lower than for those consisting of species with larger antler size, larger body size, living in open habitats and using harems as mating system.

To sum up, the intensity of sexual selection in larger species in deer family put them in risk of extinction; but on the other side, small species are more adapted to the environment by choosing different strategy in mating system, and reducing antler and body size thus diminishing the extinction risk.

*Keyword: Sexual selection, Extinction, Cervidae, Size dimorphism, mating system*

## Introduction

Darwin in the “Origin of species” (Darwin 1859) indicated that there is struggle for existence among species that leads to variation. He stressed the term “selection” as a principle for extinction or adaptation (Darwin 1872). In the “Descent of man”, Darwin (1871) mentioned two types of selection, natural selection and sexual selection; he defined natural selection as struggle for existence among individuals and sexual selection as advantages in reproduction which some individuals have over others in the same sex within species (Darwin 1871). Based on natural selection, alleles are selected which raise the competitive allocation of appropriate resources in to reproduction with investment in maintenance, repair and survival (Flatt 2011). At the beginning, sexual selection was a part of natural selection but later on, Darwin developed his theory that sexual selection can work against natural selection and that it can be non-adaptive for survival. On the other hand, Fisher (1930) gave Wallace opinion in which that sexual selection existed and Wallace tried to stress on natural selection as a principle of evolutionary description for biological phenomenon. These debates followed until middle of nineteenth century, the time that Ronald Fisher developed the concept of sexual selection as a Darwinian biologist (Fisher 1930). The modern approach talks about sexual selection as a special aspect of the natural selection theory with difficulties arising from unavoidable interactions between these two selections (Gayon 2010). The term of sexual selection and its mechanism is discussed and modified by many researches. The role of sexual selection in generating species biodiversity is a relatively well researched field and the emerging picture seems to be there is consensus that sexual selection may lead to divergence among populations and thus to speciation (Panhuis et al. 2001, Seehausen et al. 2008). Darwin’s explanation of the concept of sexual selection in “The Descent of Man and Selection in Relation to Sex” is followed by many researches that sexual selection could lead to sexual isolation and consequently speciation (Ritchie 2007).

### *Sexual selection*

Sexual selection is known as a struggle to reproduce between individuals of the same sex, generally male- male competition, which necessarily do not lead to death but less offspring; and female choice by which females prefer the most attractive individuals to mate with (Darwin 1871, 1872). Sexual selection is an important driver for morphological trait evolution in both male secondary sexual traits and female life history characters. Sexual selection is not limited by access to copulations as Parker (1994) mentioned, it can continue after mating (e.g. sperm competition after mating with different males). Female fitness increases through mating by multiple mating with

one male or mating with several males; female gets benefits from direct and indirect selection (i.e. direct phenotypic benefits and indirect genetic) (Andersson and Simmons 2006, Kolm et al. 2006).

– *Male-male competition*

Male-male competition and female choice both happen during pre and post copulatory competition. Pre-mating competition between males consists of combat or non-aggressive display and post-mating competition includes sperm competition and/or infanticide. Secondary sexual characters are used in male competitions in the most competitive sex. Traits that influence mating decisions can be phenotypic such as morphological, acoustic, olfactory, tactile or behavioural traits; they can be resources defended or produced by a signaller for example a nest or a territory (Candolin 2003). Male-male competition is important for females by facilitating female choice by increasing differences among males, it decreases risk of predation, spending energy and saving time and it prevents losing mate opportunities; overall it speeds up intensity of sexual selection. Any alteration in signalling and trait expression might affect female choice. Therefore, if the signalling trait is costly for males during competition, then the cost declines by male condition; otherwise there is no adaptive female choice in response to that trait (Candolin 1999). Sometimes males try to overcome female resistance by evolving traits which is followed by evolving resistance in female as well; thus males tend to evolve new display traits that make them more adorned by new multiple ornaments. Preferences for new traits may cause indirect benefits due to increasing offspring's reproductive success. These new traits might not be useful anymore to overcome female resistance and cause species extinction because those traits decrease fitness or are costly (Candolin 2003). Generally male signalling traits are under influence of inter and intra-sexual selection which they perform as quality indicators in mating choice and condition factors in male-male competition (Delaney et al. 2007, Faivre et al. 2003).

– *Female choice*

Cryptic female choice and differential allocation is categorized as post copulatory female choice. Godin and Briggs showed that mate preference in female guppy decrease by predation risk; this decrease associated with cost of viability of females. This response may affect the intensity of sexual selection and thus further evolution of sexually selected traits and female choice (Godin and Briggs 1996). Many researches have shown secondary sexually characters to evolve by female choice (Witte et al. 2000), also males can affect female traits by distinguishing between females ready to mate and therefore drive the trait in females. Witte et al. (2000) found that preferences to

adorned females or males increase by juveniles whom grow up with adorned parents by sexual imprinting; this result shows that the preferences for ornaments might change species without ornaments to species with conspicuous traits. The last result was in accordance with the conclusion from experiments on flycatchers that females learn to mate with artificially novel adorned males. If preference of exaggerated imprinted traits spread in populations then the proportion of females interested in novel ornamented individuals increase due to mating activities; the preferences of novel traits could drives pre-zygotic isolation before it happens genetically, thus rapid divergence is possible by sexual selection within species (Qvarnström et al. 2003).

– *Sexual conflict*

Many studies have shown that sexual selection gives benefits to females but on the other side, it can also be costly due to sexual conflict. Sexual conflict could be defined as a negative relationship between average fitness of males and females involved in mating activities that speeds up during reproduction (Pizzari and Snook 2004). Studies have stressed the effect of sexual conflict in co-evolution of male manipulation and female resistance, risk of extinction, influencing speciation and evolution of senescence. Hall et al. (2008) declared that any changes in environment that influence sexual conflict will have consequences for sexually selected traits in male and maintenance of genetic variation of those trait. They concluded that by manipulating the ability of both sexes to influence spermatophore attachment (sexual conflict due to attachment time of an external spermatophore), the intensity of sexual selection on male courtship call and body size is influenced by sexual conflict. Males may harm females directly (e.g. toxicity of the seminal fluid) or by reducing female survival during persistent courtship (Holland and Rice 1999). Because of negative consequences for females, conflicts between sexes may raise the resistance of females to signal traits, and also sometimes lead to sexually antagonistic co-evolution (Andersson and Simmons 2006). Moreover, in allopatric populations sexual conflict could accelerate the evolution of diversifying reproductive traits and consequently lead to reproductive isolation (Svensson and Gosden 2007).

*Secondary sexual traits and mating system*

As Darwin declared, differences in colour, ornaments or structures between males and females of any species that live in the same environment, is driven by sexual selection (Darwin 1872). He stressed that sexual selection drive the evolution of secondary sexual characters that cannot be explained by natural selection (Gayon 2011). The interactions between natural and sexual selection

determine evolutionary dynamics and changes in secondary sexual traits. Mathematical models and comparative studies have shown that secondary sexual traits might cause rapid evolutionary changes (Svensson and Gosden 2007). Sexually selected traits vary in expression and these differences are driven by sexual selection since they determine the reproductive success. Sexually selected traits vary among individuals, both in response to life history trade-offs and in short timescale as a response to environmental conditions (Griffith et al. 1999). Decrease in sexually selected traits due to predation is one example of response to life history trade-off.

Variation in secondary sexual traits correlates with intensity of male-male competition that finally determines reproductive success. Because of intra-sexual competition, male size dimorphism and weaponry evolve in response to sexual selection. For example, in species with high sexual size dimorphism, it has been shown that males in polygynous ungulates are more successful in reproduction with higher body size/mass and bigger horn or antler size/mass. Low sexual size dimorphism is associated with low levels of sexual selection but males may be more active than females in behaviour; these behavioural characters affect reproductive success more than morphological ones in such species. On the other hand, according to the agility-hypothesis small body size can determine sexual selection on small size in reproductive success. Vanpé et al. (2010) also concluded that in species with low sexual dimorphism, if females are selected for higher body size or mass, then the male body size is selected for smaller size. Dunn et al. (2001) also indicated that many factors influence the evolution of sexual dimorphism such as mating system and sperm competition. Mating system for each species is different and includes one of six categories, which are monogamy, polyandry, mostly monogamy but occasional polygyny, mostly polygyny, cooperative breeding and promiscuous mating systems. Dunn et al. (2001) declared that all the four types of dimorphism which they used in their research (testis size, plumage dimorphism, wing and tail length), are associated with mating system and sperm competition, except for body mass which had no relation to sperm competition.

According to the traditional explanation, variation in sexual dimorphism is driven by variation in mating system and type of parental care in species. Owens and Hartley (1998) showed that not all type of variation in sexual dimorphism is related to mating system, such as plumage-colour dimorphism that was associated with female choice and frequency of extra-pair paternity. In another study, Møller and Briskie (1995) indicated that testes size is correlated to sperm competition and extra-pair paternity. Sexual selection not only influences secondary sexual traits in males but also affects female life history traits; as Kolm et al. (2006) showed, sexual selection is a driver of high level of sexual size dimorphism and influences larger body mass and egg size in female Galliforms.

### *Intensity of sexual selection*

Sexual selection intensity, as explained by Wade and Arnold (1980), is a function of variance in fitness in the two sexes, which itself depends on mating system and reproductive success. They mentioned this because sexual selection is regarded as an intra-sexual phenomenon (excluding sexual conflict), therefore male reproductive success could be a strong factor when measuring the intensity of sexual selection. According to what has been discussed above any differences on male attributes, female choice, sex ratio, sperm competition etcetera can affect the intensity of sexual selection in pre and post mating sexual selection (Wade and Arnold 1980). For example, male investment in resources affects the intensity of sexual selection by the fact that when food is scarce females tend to have larger size in order to compete with other females on nurturant males (due to the fact that male resource investment affects the number of copulations also affects female fitness by accessing the amount of resources to produce eggs). From the other side, sexual selection on females arises through male mating preference when nutrients limit the male mating frequency. Moreover, the intensity of sexual selection differs between females and males (Castillo and Núñez-Farfán 2008). In another example, Bro-Jørgensen used breeding group size with mating system to measure the intensity of sexual selection and he suggested that horn size and sexual body size increase with the size of breeding group and decrease with territoriality. These variations in secondary sexual traits could be explained by intensity of sexual selection within mating system (Bro-Jørgensen 2007).

On one side, Darwin stated, traits can evolve despite not being favoured by natural selection, and it leads to populations in an unstable state (Darwin 1871). On the other side, some theories predict that by the action of sexual selection, the rate of adaptation will increase in relation to environmental changes (Morrow and Fericke 2004). There are many ways by which environmental changes might result in evolution of male sexual signals and female choice. Changes in signals might cause sexual selection by changing female preferences or by changes in signalling environment. Also, the cost of having a signal might change by alteration in natural selection such as predation risk or parasitism. Moreover, changes in traits will cause changes in mate preferences by changes in the value of the altered signals or by changes in the cost of expressing a given preference (Easty et al. 2011). Thus, it is unknown whether there is a net gain or loss of species due to sexual selection. Modern comparative methods using phylogenetic relationships can be applied to identify evolutionary patterns and processes. Subsequently this leads to better understanding of the origin of character states and if they have evolved independently, and which factors could be responsible for extinction or speciation (Harvey and Pagel 1991).

The role of sexual selection in making species more vulnerable to extinction is largely

unexplored. There are several factors which may predict a risk of extinction, consisting of ecological and life history traits of species. By affecting the rate of mortality and natality, sexual selection can increase the risk of extinction; for example in a population under intense sexual selection that may face increasing rates of predation, parasitism, raised sensitivity to environment and demographic stochasticity, including the possibility of Allee effects (Doherty et al. 2003, Kokko and Brooks 2003). Theory have shown that in a changing environment, a number of new selection pressures arise in the population due to the cost of sexual selection, and this might lead to extinction by intense female choice. For example, in a population that faces environmental degradation, the cost of signalling causes only a few males to survive until the breeding season and consequently may lead the population to extinction; the process of extinction continues until the signalling disappears due to decreasing the cost of trait (Tanaka 1996, Doherty et al. 2003). Overall the cost of sexual selection deals with ecological and genetic factors; ecological factors could be explained by “reduced effective population size because of reproductive skew, antagonistic co-evolution between sexes, tradeoffs between the size of sexual traits, and the size of other morphological character” (Doherty et al. 2003).

In this project I want to address whether sexual selection may play a role in the extinction of species by making species more vulnerable to extinction. I am doing this by performing a comparative analysis of the extant species of deer (Cervidae).

### *Goal and scope*

Estimating the trade-off between life history traits and viability is the major principle to understanding the causes of extinction. For example, it has been proposed that the Irish elk became extinct because it evolved very large antlers (up to 40 Kg weight) (UCMP 2013). Males with larger antler was probably preferred by females but the excessive size of antler made it difficult for Irish elk to feed and consequently led to its extinction (Kokko and Brooks 2003).

My research is based on the following hypotheses: sexual selection not only leads to elevated levels of speciation but also to more extinction; also it is predicted that species subjected to intense sexual selection are also more extinction prone.

To measure the relation between sexual selection and extinction within the deer family I ask several questions. Does intensity of sexual selection lead species to be more vulnerable to environmental changes? How and in which way may the risk of extinction affect species to adapt to their environment? Are the changes in behaviour and secondary sexual traits similar in all clades in the Cervidae family? And do anthropogenic effects push deer species to choose different

reproductive strategies?

In this project a combination of extinction threat with estimates of sexual selection was used to test the hypotheses stated above. Referring to Issac et al. (2007), a phylogenetic tree was applied to represent evolutionary history of species, mode of divergence and phylogenetic diversity. In a large phylogeny with many species (such as the tree of life), rate of extinction can be measured by the form of clades (e.g. monotypic, old or species-poor clades). However, there are some limitations to apply phylogenetic diversity: the length of branches is not available for dated species thus phylogenetic diversity mostly focuses on pattern of branches; also when using phylogenetic diversity, the focus is not on species. Using evolutionary distinctiveness combined with extinction risk has been used to identify endangered species with distinct evolution (Isaac et al. 2007). Using published records I aimed at deriving proxies for extinction risk for species by using IUCN data (IUCN 2006) following previously described approaches (Isaac et al. 2007). Thus extinction risk was scored as one or several categories according to IUCN-The World Conservation Union Red List- categorization system, such as: critically endangered, endangered, and vulnerable taxa. This system was used to identify threatened, non-threatened taxa. Other IUCN-listed categories such as extinct, extinct in the wild, lower risk, and data deficient were used (Spielman et al. 2004).

Exaggerated sexually selected structures (ornaments or weapons) may impose costs for animals during their different life stages such as by reducing viability, retarded growth of nearby organs (Nijhout and Emlen 1998, Emlen 2001). Hence there is a need to assess the level of intensity. Estimating the level of intensity of sexual selection was addressed using various proxies for intensity such as levels of social mating system, sexual dichromatism and sexual size dimorphism which have all been suggested to be measures of pre-mating sexual selection (Møller and Briskie 1995, Owens and Hartley 1998, Dunn et al. 2001, Kolm et al. 2006).

Species level analyses were conducted using supertrees of deer (Price et al. 2005). This is an excellent group for the proposed project since deer varies greatly in mating system (Greenwood 1980), sexual size dimorphism and sexual ornaments (antlers) and also varies in threat status.

## Methods

The research is based on published literature and data collected from the internet and IUCN data. The list of species in the Cervidae family has been combined with the data of extinction risk by applying the different categories from the IUCN Red List. First, I identified the species within the family Cervidae with substantial variation in the traits (levels of social mating system, sexual dichromatism, secondary sexual characters and sexual size dimorphism) for assessing intensity of sexual selection (Appendix 1, Species descriptions). During the second stage, I collected a database with information on those traits. Assembling a phylogeny for the Cervidae was the next step which was followed by tree transformation and data (e.g. based on branch lengths, discrete traits, continuous traits), then I ran analyses under a phylogenetic comparative framework using the Mesquite program (Maddison and Maddison 2011).

For analysing the data, I used the supertrees methodology which assembles a consensus from smaller phylogenetic trees sharing some taxa in common (Sanderson 1998). The source of data for the phylogeny was gathered via articles consisting of phylogenetic data and web sites such as BIOSIS and BioScience. Bibliographies were used for additional data.

### – *Intensity of sexual selection in deer*

Estimating the intensity of sexual selection in this study was based on social mating system, sexual ornaments (antlers) and sexual size dimorphism that have all been counted as a pre-mating measurement of sexual selection. The following types of sexual dimorphism have been used in other studies: body size, body composition, skeletal composition, brain and nervous system, other organs and metabolism, and weaponry (McPherson and Chenoweth 2012). In this study, body size, body height, antler size/shape and the level of mating system was chosen as measurements of sexual selection intensity.

### – *Data analyses*

Data analyses were done with the software Mesquite (Maddison and Maddison 2011). In this program, I used sexual dimorphism, body size, body weight, antler size, IUCN classification, antler size as a secondary sexual trait, mating system and territoriality and mating behaviour as the main characters in a matrix. On the character states, the traits were traced on the phylogeny tree and in

this case I used the phylogeny of Gilbert and co-workers (Gilbert et al 2006). For the species that are not included in Gilbert et al. (2006), trees from Meijaard and Groves (2006), Pitra et al. (2004) and Price et al. (2008) were used to shape the final phylogenetic tree. From the tree I derived reconstruction coordinates of ancestral states by maximum likelihood. Currently each node is estimated independently (i.e., corresponding to PAUP's marginal reconstruction). The out-group consists of two species belonging to two different taxa of the suborder Ruminantia: *Antilocapra americana* (Antilocapridae) and *Moschus moschiferus* (Moschidae).

Sexual dimorphism was based on the weights of females and males; those species with slight differences in weight between sexes were considered as monomorphic and those with large differences in weight (more than 1.5 times) were considered as dimorphic.

Body size was considered as shoulder height and species with less than 650 mm in shoulder height were included as “small” and more than 650 mm assigned as “large” species. For those species with lacking data in shoulder height, I used body length; species with a body length less than 1250 mm were considered as “small” and more than 1250 mm set as “large” species (Gilbert et al. 2006).

I used two IUCN classifications. First, eight categories were included: extinct, extinct in the wild, critically endangered, endangered, vulnerable, least concern, near threatened and data deficient. The second set of categories consisted of 1) Extinct, extinct in the wild, critically endangered, 2) endangered, vulnerable, near threatened and 3) least concern and data deficient. In addition, according to IUCN database, I considered anthropogenic effects such as hunting for trophy or meat, land use changes, habitat degradation, hunting by domestic animals etc. The severity of these effects was marked as severe, moderate and less impact in three categories.

Secondary sexual traits were scored as having antler or tusk in the males; in some species, tusk and antlers both exist and in some, there is lack of antler or tusk. Antler size was classified in five groups according to the following: 1) <15 cm; 2) 15- 50 cm; 3)50-100 cm; 4)>100 cm and 5) without antler (= 0).

As mating system, I put species in six categories based on the existence of: harems, leks, defending a spaced out territory, courting pairs, having a dominance hierarchy or a fission-fusion system. Moreover, the size of breeding group was taken into account as 1) small-medium group size and 2) medium-large group size. Being territorial was counted as one of the main factors and considered separately for each species.

The behaviour was divided into two groups, mating behaviour and daily behaviour. As mating behaviour I considered aggressive behaviour, non-aggressive behaviour, fighting and defending female/s. Daily behaviour habits included being solitary/sociable, crepuscular, nocturnal/diurnal, living in a small group or in pair, or in a family group.

Habitat type was classified in two groups based on IUCN data and were scored according to the following: open/disclosed (D) or closed (C) habitat. The first category consists of grasslands, marshlands, and open forests and closed habitat includes dense forests and marshes with reeds (Gilbert et al 2006).

## Results

The phylogenetic trees used were made based on complete mitochondrial *cytochrome b* gene sequences (Pitra et al. 2004), mitochondrial protein-coding genes, *Cyt-b* and *CO2*, and four nuclear regions (Gilbert et al. 2006), elements of skull shape as determined by morphometrics (Meijaard and Groves 2006) and some other molecular studies (Wilson and Reeder 2005, Groves and Grubb 2011, Geist 1998). In this study, I used four different phylogenetic trees (see below).

The Cervidae family is traditionally taxonomically divided into two groups: the old world deer (Muntjacinae and Cervinae) and the new world deer (Odocoileinae and Hydropotinae).

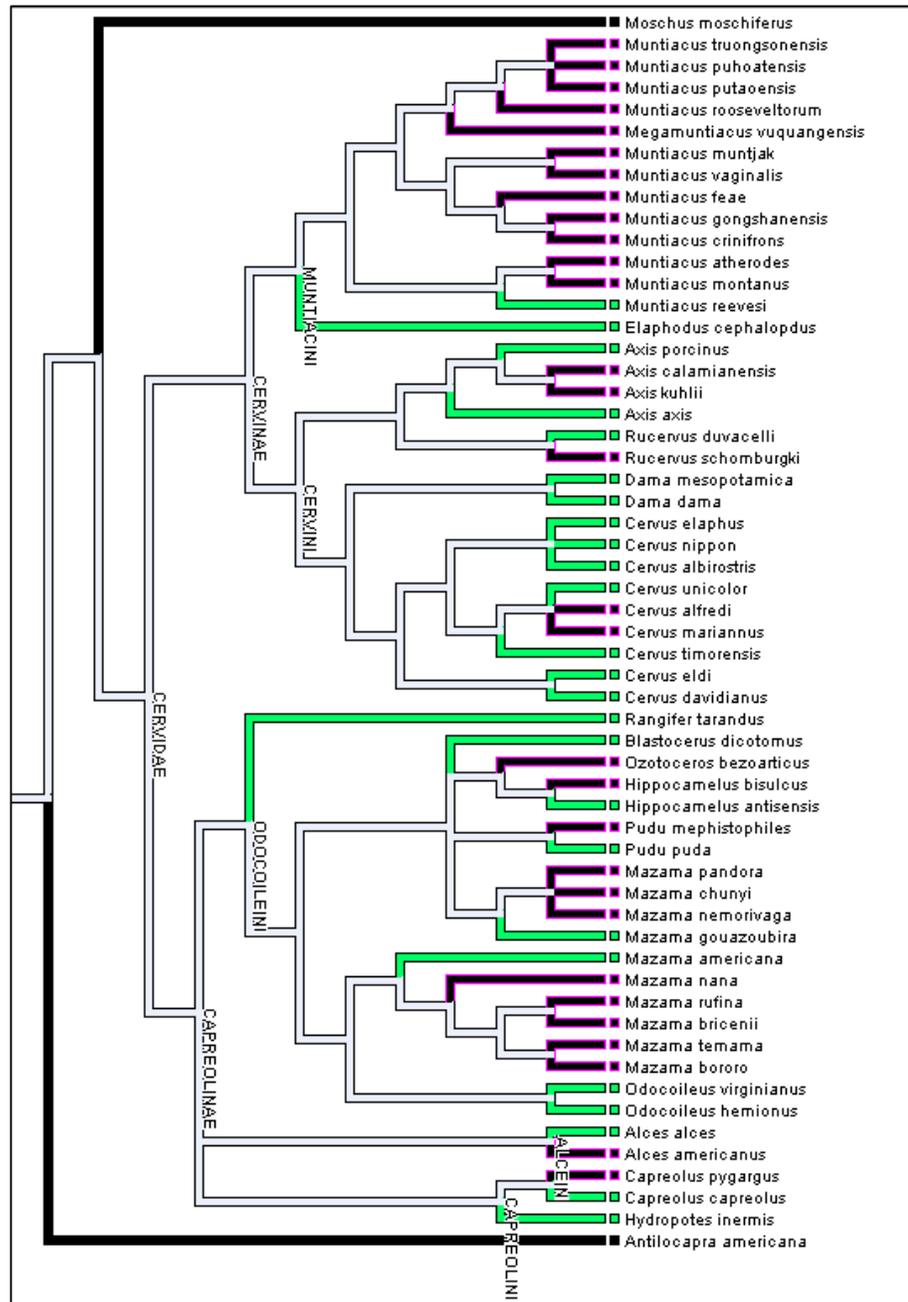


Figure 1: The Cervidae family is divided to two main clades: Cervinae and Capreolinae. The Cervinae clade itself is divided into two main clades known as Cervini and Muntiacini. Also Capreolinae is divided into three main clades consisting of Capreolini, Odocoileini and Alcini. Two species, *Moschus moschiferus* and *Antilocapra Americana* have been assigned as out-groups. In the case of accessing different data on each species, the Gilbert paper (Gilbert et al. 2006) was used as a reference (■ the species which referred to Gilbert et al. 2006; ■ the species which gathered from other researches - Wilson and Reeder 2005, Groves and Grubb 2011, Geist 1998, Pitra et al. 2004, Meijaard and Groves 2006).

According to nuclear and mitochondrial markers, the Cervidae is also divided into two main clades: Cervinae and Capreolinae. The Cervinae clade itself is divided into two main clades known as Cervini and Muntiacini. Also Capreolinae is divided into three main clades consisting of Capreolini, Odocoileini and Alcini. Two species, *Moschus moschiferus* and *Antilocapra americana* have been assigned as out-groups. In the case of accessing different data on each species, Gilbert et al. (2006) was used as a reference, Figure 1.

To compare the trees, results was confirmed by other studies, in which all ancestors of species were more or less placed in the same positions and the different trees showed similar results (Mejaard and Groves 2006, Pitra et al. 2004, Price et al. 2008). Using pairwise comparisons by testing character correlations also confirmed the results by Gilbert et al (2006). In the ancestor of *Cervidae*, the males were large (shoulder height >650mm), bigger than females, with three-tined to four-tined antlers, without upper canines, and they lived in open habitats. However, the ancestors of *Muntiacus* + *Elaphodus* and *Capreolus* + *Hydropotes*, the analyses suggest a completely different pattern: they lived in closed habitats, and the males were small (shoulder height <650mm), similar in body mass to females, with two-tined antlers (Figure 2, 3).

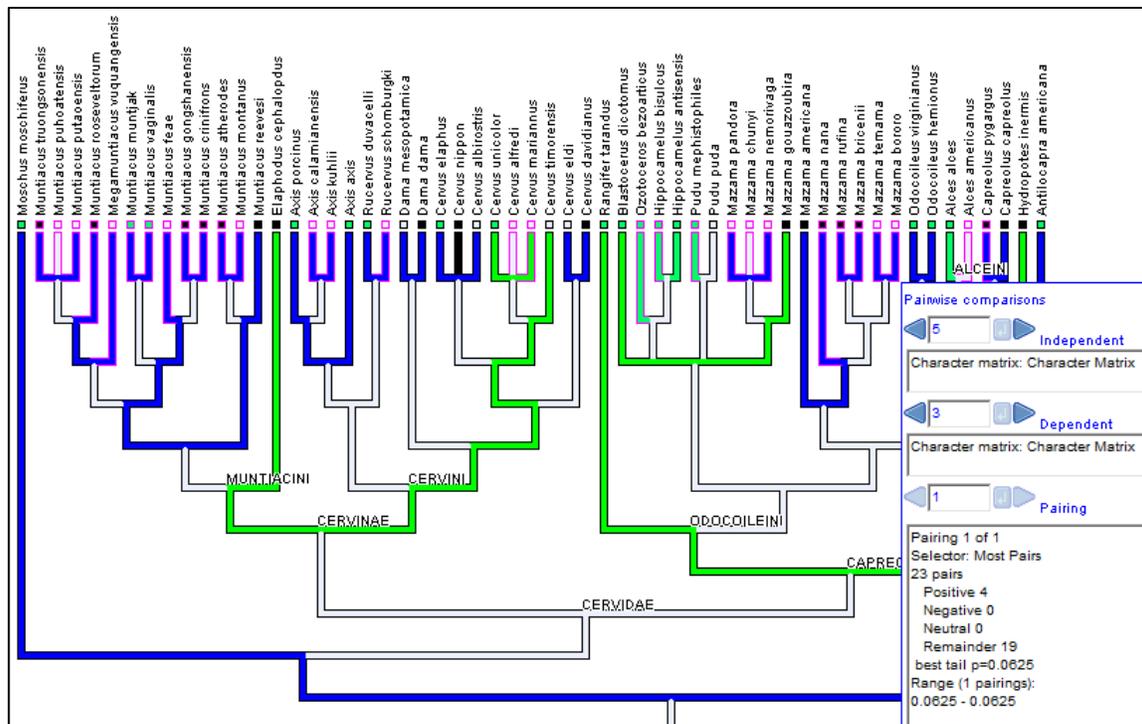


Figure2: Correlation between body size (independent character) and antler size (dependent character). Positive (Green): cases in which one of the taxa has a 1 for both characters and the other taxon has a 0 for both. (00 vs 11); Negative (Red): cases in which one of the taxa has a 1 for one character and a 0 for the other and the other taxon has the opposite. (01 vs 10); Neutral (Grey): cases in which the taxa disagree in the independent character, but have the same dependent character. (01 vs 11) or (00 vs 10); Reminder (Blue): cases in which the independent character is the same for both taxa. Here, body size is considered as independent character and antler size as dependent character.

The results show that 49% of all species have large body and are dimorphic and 40% are small and monomorphic. It also indicated that 95% of smaller size species are monomorphic and 85% of the large species are dimorphic.

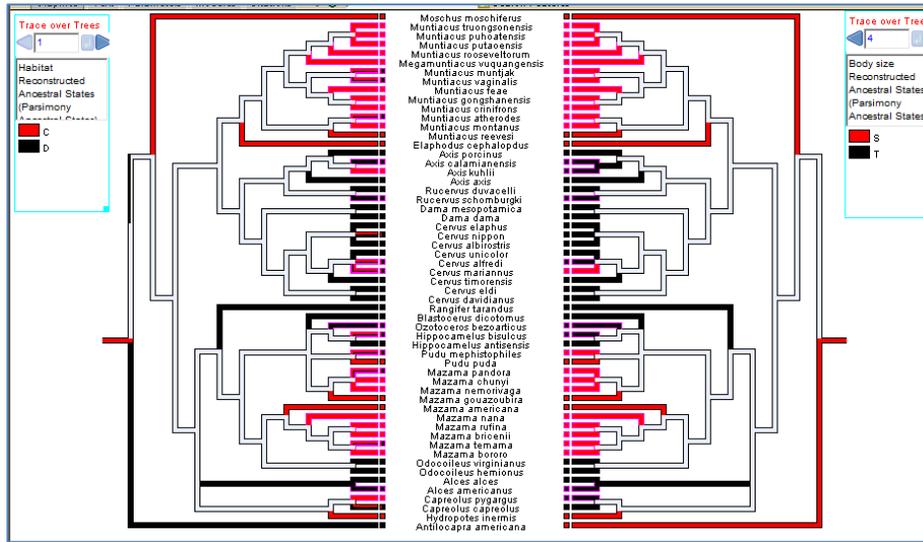


Figure 3: Character correlations have tested by comparing reconstructions visually. Correlation between habitat openness (C=close; D= Open) and body size (S=Small; T= Tall). Likelihoods using a speciation/ extinction model reduced from the BiSSE model (Maddison, Midford and Otto 2007)

Antler size in the ancestors of Alceini and Odocoileini ranked as four (>100 cm), in Muntiacini 1 (>15 cm), in Capreolini 2 (15-50 cm) and in Cervini 3 (50-100 cm). Also in Muntiacini and Hydropotes the tusks or upper canines are developed. In the ancestor of Odocoileini (*Rangifer tarandus*) both sexes carried antlers.

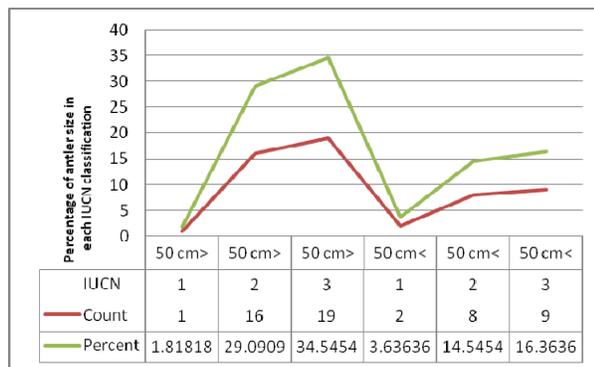
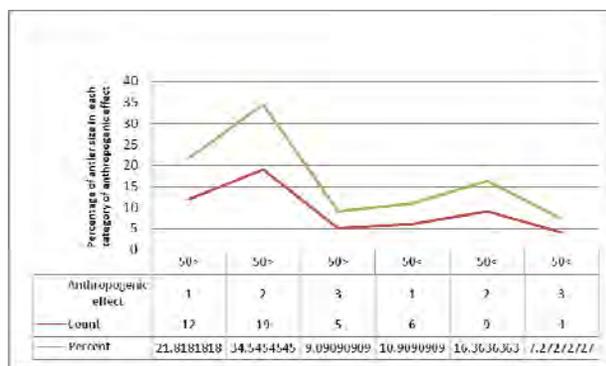


Figure 4: Correlation between Antler size and IUCN classification as an extinction risk. Both species with large and small antler size have shown extinction risk as located in second category of IUCN (Vulnerable, near threatened, endangered).

Based on the IUCN red list classification, the ancestors of the species in the subfamily of Muntiacini, Alceini and Capreolini are categorised as data deficient or least concern while species from Odocoileini are near threatened, vulnerable or endangered and the Cervini subfamily is classified in the extinct, extinct in the wild and critically endangered

Figure 5: In the Cervidae family, all subfamilies are under moderate impacts of human life, but *Cervinae* endures severe effects of habitat degradation, wild life mismanagement, pollution, chasing by domestic dogs and illegal hunting.



categories.

The correlation between antler size and extinction criteria shows (Figure 6) that the highest percentage of species with smaller antlers are placed in third IUCN category but both groups (large

Table1: The correlation between body size and IUCN classification. Both small and large size deer are in category two and three with 5.2% of extinct or extinct in the wild of large species. The results show moderate to severe anthropogenic effect on both small and large size deer.

Body size	IUCN	Count	Percentage
S	1	0	0
S	2	13	22.81
S	3	17	29.82
T	1	3	5.26
T	2	13	22.81
T	3	11	19.30

Body size	Anthropogenic effect	Count	Percentage
S	1	9	15.79
S	2	17	29.82
S	3	4	7.02
T	1	9	15.79
T	2	13	22.81
T	3	5	8.77

and small antler size) show extinction risk by being locating in the second category of IUCN (vulnerable, near threatened, endangered). 50 percent of the species with smaller size of antlers are less concerned or data deficient while 38% of species with larger antlers are listed in first or second IUCN categorisation (Figure 4). Moreover the effect of human impact is moderate to severe on both large and small antler size species (Figure 5).

The correlation between body size and IUCN classification shows that both small and large sized deer are in the categories two and three and 5.2% of the large species are in first category of extinct/extinct in the wild. In addition there are moderate to severe anthropogenic effects on both small and large sized deer (52.5 % moderate, 31.5% severe impact) (Table 1).

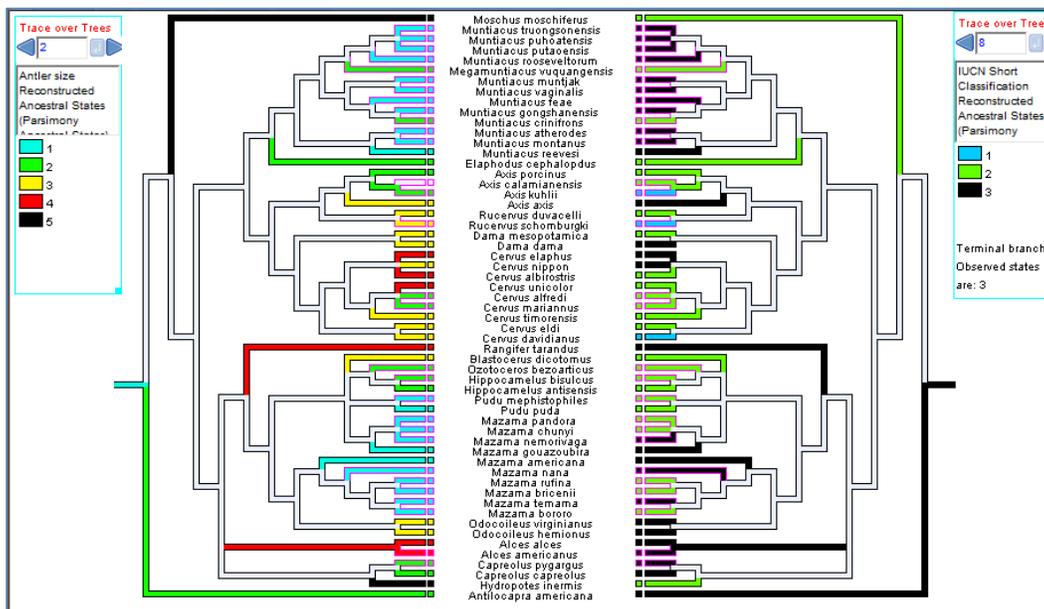


Figure 6: Character correlations have been tested by comparing reconstructions visually. Correlation between Extinction criteria (1: Extinct, extinct in the wild, critically endangered, 2: endangered, vulnerable, near threatened, 3: least concern, data deficient) and antler size (1: <15 cm; 2: 15- 50 cm; 3:50-100 cm; 4 :> 100 cm; 5: without antler = 0). Likelihoods using a speciation/extinction model reduced from the BiSSE model (Maddison, Midford & Otto 2007)

As results show, in Cervidae family, all subfamilies are under moderate human impact, but

*Cervinae* endures severe effects of habitat degradation, wild life mismanagement, pollution, chasing by domestic dogs and illegal hunting.

The ancestors of Muntiacinae and Capreolinae were territorial while Cervini, Alceini and Odocoileini were not territorial and their mating system consisted of harems and protecting females. In total, 72% of the small species are territorial and 72 % of the large species are not; my analyses suggested that most monomorphic species are territorial and 80% of dimorphic species are non-territorial. Among these species, Muntiacini has aseasonal reproduction and the other groups reproduce seasonally.

My analyses also show that there is a significant correlation between mating system/territoriality and anthropogenic effects. In addition the correlation between extinction rate (IUCN classification) and antler size/number of tines/ territoriality and habitat openness is significant. Species with larger body size, larger antlers and being territorial are more prone to extinction.

The group of large species mostly posed in first and second category of IUCN red list (1: Extinct, extinct in the wild, critically endangered, 2: endangered, vulnerable, near threatened) while the rest of species in this family were assigned to the category of least concern or data deficient.

Based on the IUCN data of species distribution, species mapping by GIS (ESRI Inc. 1999) shows different distributions among small and larger deer. Based on Giest (1998), smaller species live in low latitudes while those with larger body size are more common in higher latitudes. This follows Bergmann's rule, species with smaller size live in warmer region and larger size in colder areas. This means that in low and high latitudes, body size decrease and in seasonal climate regardless of regular but temporary food access, the size of body increases and the peak is at 60 N° (Figure 7).

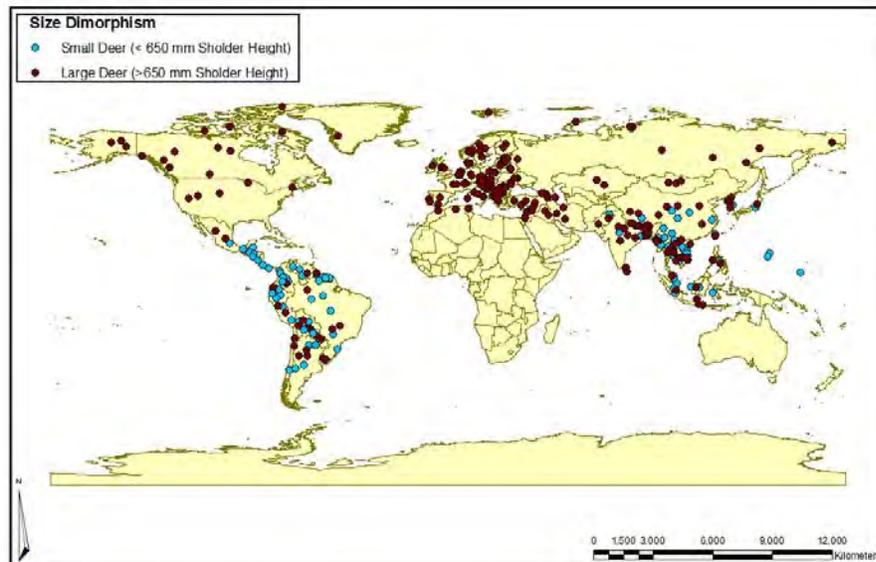


Figure 7: The distribution of small and large deer in the world based on IUCN map. Smaller species live in low latitude while those with larger body size are more common in higher latitude

## Discussion

Sexual dimorphism and secondary sexual characters not only reflect adaptation in those species with high reproduction success but also represent species with high risk of extinction. Increasing rate of predation, parasitism, raised sensitivity to environment and demographic stochasticity, including the possibility of generating Allee effects, changing environment due to increasing the number of selections and cost of sexual selection in population might lead to extinction.

Antler development has been a debatable subject among scientists for a long time and several theories to explain the adaptive significance of these ornament has been put forward. One theory proposed antlers develops as a weapon for mutual combat during rutting, which is used for pushing or wrestling rather than killing. This theory is supported by the fact that during the period after rutting is followed by shedding the velvet and casting off solid/ bony antlers (Goss 1983). Another theory discusses the displaying, which is also supported by the previous theory but not necessarily head-to-head combat (Goss 1983). Antler growth by accentuating the size of the head (especially in larger deer species) plays the same role as horn size, mane development, and swollen necks in other species. For example in Irish elk, the growth of antler out to the sides rather than upwards is evidence that antlers were developed to impress others visually. Moreover, a third theory argues that antlers are used for thermal radiation by releasing excess body heat (Goss 1983). This theory says that losing velvet and casting antlers in the winter is preventing heat loss. However, this cannot explain the presence of antlers of tropical species should then be larger or being permanent, but they are not. The last theory is based on olfactory projection in which the antler has an abundance of sebaceous gland in the skin. Rubbing antlers to the tree or body is used when scent marking (Goss 1983). To sum up, antlers can be used as weapons in aggressive behaviour but may also have secondary functions (Goss 1983). Antlers have appeared in female rein deer and have also been reported to be common in female roe deer, white-tailed deer and mule deer, while less common in sika, red deer, wapiti, and moose (Goss 1983).

The other measurement of sexual selection intensity is sexual size dimorphism. Sexual dimorphism has evolved through sexual selection or adaptation for gender-specific niche divergence under the pressure of ecological or reproductive factors. Body size for those species with a polygynous mating system is greater and depends on the ratio of males to females in local area (*Alces alces*) (McPherson and Chenoweth 2012). Generally body size dimorphism is correlated to weaponry, (lack of) parental investment, access to resources and aggression (McPherson and Chenoweth 2012).

Mating system may also drive dimorphism among species having polygynous mating system. Species that have harems are more dimorphic than territorial ones; and this is suggested to be a result of the intensity of sexual selection (Weckerly 1998, Bro-Jørgensen 2007).

Geist (1998) showed that species at the beginning of colonisation of a new habitat had larger body size but after reaching their carrying capacity, populations tend to reach smaller size. This supports the result of this study in which derived species tended to be smaller especially in *Mazama* and *Muntjacus* species. These species face more habitat degradation and anthropogenic effects, thus they have become smaller. Moreover, the connection between body size and environment arises in the terms of a predator-limited and resource-limited fauna. In a predator-limited fauna, the body size increases, competitive ability reduces and food acquisition organ has not developed (e.g. teeth size decrease and are less complex in structure), while in resource-limited fauna body size decreases and it is followed by high level of competitive ability and improved food acquisition organ (for example teeth size increase and become more structural complex). In the second category the ornaments remains modest (Geist 1998). However, by an alternative view in some species of the deer family, the female body size increases in resource-limited areas in order to compete with other individuals (Castillo and Núñez-Farfán 2008) and the probability of sexual size dimorphism decrease as observed in some species in *Muntjacus*, the *Mazama* subfamily and the Pampas deer.

My results show that species with larger body size are more dimorphic. Larger species live in open habitats and have larger antler size, the number of tines is higher and they are mostly non-territorial and form harems during the rutting season. However, the small species (*Muntjacus* and *Elaphodus*) are territorial, monomorphic with small antler size and the number of tines limited to two. As noted by Randi et al. (1998), a dramatic size reduction of spiked antlers in the South American genera *Pudu* and *Mazama*, suggests that the reversal of morphological trends is possible as consequence of selection for small body size (Randi et al. 1998). In addition, according to Merino and Rossi (2008), the first deer that entered South America was a medium-sized species with branched antlers; these would have given rise to taxa with the appearances that it is more conservative, have smaller size and simple antlers as in *Mazama* and *Pudu* (Merino and Rossi 2008). This result also follows the conclusions by Gilbert et al (2006) in that *Mazama* species choose the closed habitats with dense vegetation, therefore their antler size, body size have become reduced and sexual size dimorphism tends to become absent. In addition, the antler size depends on the environment (open or closed) and the resource limitation; in resource-limited and closed habitats, antlers are smaller while the size of antlers increase with the degree of food availability and openness of the habitats (Geist 1998). Existence of tusks in smaller species (*Muntjacus*) is adding to their small antler, and these are known to be used as weapons to defend their territories and used in fights with other males. The regularity of antler shedding in muntjacs depends on

continually defending resource-rich territories (irregular shedding) or relates to seasonal defence and reproductive functions (regular shedding) (Giest 1998).

The pattern of the tree in Muntjacini clade shows deep split between Muntjacus and Elaphodus. The clade of Muntjacus also is rich in species therefore the risk of extinction of clade is less than other sister clade (Elaphodus). The same result comes up with the clade of Odocoileini; *Rangifer tarandus* has higher risk of extinction than sister clades Mazama because of species-poor clade. Moreover, in Capreolinae clade, Capreoloni and Alcini have higher risk of clade-extinction than Odocoileini clade (sister group).

Extinction risk for those clades with small species, territorial and small antler size is less than those clades consisting species with bigger antler size, larger body size and shaping harem as mating system.

To sum up, in all species of the Cervidae family, sexual selection seems to play a main role for the probability of extinction. Clearly, the intensity of sexual selection (sexual size dimorphism, antler size and mating system) and the rate of extinction (IUCN classification and anthropogenic effect) differ among species and clades. The extinction rate has been affected by human impact and anthropogenic effects. The overall estimate of the likelihood of extinction/speciation indicates 85.57587659 with lambda (speciation rate) 0.46228503 and mu (extinction rate) 1.943431099E-5 in the Cervidae family. In some subfamilies (Muntjacus and Mazama), the risk of extinction (such as habitat degradation and chasing by domestic dogs) causes the species to have evolved smaller body and antler size. Finally the intensity of sexual selection in larger species in deer family put them in risk of extinction; but on the other site, small species are more adapted to the environment by choosing different strategy in mating system, reducing antler and body size thus diminishing the extinction risk.

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## Appendix 1

### Species descriptions

- *Alces alces gigas* (Eurasian elk)

*Alces alces gigas* (the weight is over 385 kg) is restricted to circumpolar boreal forest in Eurasia. It is seasonally polyestrous (Franzmann 1981) and its mating behaviour consists of digging a rutting pit or wallow to urinate in (Whittle et al. 2000). The mating system in *Alces alces gigas* is a form of harem system in which dominant males defend, herd and mate with females (Bowyer et al. 2011). Female wallows in the dig and completely fill its pelage with urine. The urine has a strong and sharp odour which males also impregnate themselves with. This is kind of attraction of female instead of interaction amongst males. Rutting digs and deposition of urine is categorised as a secondary sexual trait that is related to body condition. High quality males try to invest more on cost-reducing traits rather than weak individuals. Based on that, females choose males with high quality phenotypes, and consequently the best genotype (odour is a sign of honest advertisement). In addition, Bowyer indicated that female choice in the shape of protest moan helps to reduce harassment by smaller males that could play an important role in evolution of mating system in polygynous mammals (Whittle et al. 2000, Bowyer et al. 2011). Body size dimorphism in *Alces alces gigas* results from varies condition on energy expenditure, rutting activities and nutritional requirements in different age and sex classes (male >40 kg heavier than female - Bowyer et al. 2011).



Figure 8: Male elk grazing (*Alces alces gigas*) Sarek National Park, Lapland, Sweden. Photographer: Staffan Widstrand. www.arkive.org

Males with larger body size are more successful in reproduction than smaller ones. On the other side, this size dimorphism increases the risk of predation; also forces males to spend more energy during mating season which ends to lower fat reserves during winter, therefore males tend to choose a different habitat and foraging strategy to reduce energy expenditure (male weight: 398- 633 kg; female: 500 kg) (Miquelle et al. 1992). Another secondary sexual character

in *Alces alcesgigas* is antler size (> 155 cm) (Figure 8). Studies have shown that a male with larger antler size mates more often than a smaller-antlered male. Bowyer suggested that larger antlers with more symmetry are connected to strength, size and resistance to breakage (Bowyer et al. 2001). The male body length is 2.4 to 3.1 m, and 2.3 to 3.0 m for the female, and they are not territorial (De Bord 2009).

- *Alces americanus* (Moose)



Figure 9: Moose bull feeding, beginning to shed antler velvet.  
Photographer: To & Mat Leeson, www.arkive.org

Moose (Figure 9) inhabits northern North America from Alaska, Canada, northeast of USA and all the way to the Rocky Mountains in Colorado. It prefers forest areas close to water body. Males are larger than females (2.5 to 3.2 meters compared to 2.4 to 3.1 meters) with large, wide and elaborated antlers (up to 2 m in width from tip to tip). The male body

weight ranges from 360 to 600 kg, and 270 to 400 kg for the female. Females attract males by vocalizations and scent signals. Other documents showed that males wallow in urine-soaked mud for scent marking to attract females. Males compete to access females in breeding season; they gather in the mating period in tundra and alpine habitats. The moose is solitary and crepuscular. Depending on the time in a year, populations migrate between suitable sites or mainly remain in the main area. The moose is the largest deer with the largest antler worldwide (Bartalucci and Weinstein 2000, Wildscreen 2003).

- *Capreolus capreolus* (European roe deer)

Roe deer (Figure 10) are distributed all over Europe and Asia Minor. The most aggressive behaviour occurs before the rut and during seizing of territories. However, during rutting the mating system (territoriality) is not violent; also



Figure 10: Roe deer buck running during rut.  
Photographer: Andy Rouse, www.arkive.org

vocal signalling is the main factor in their social life (Sempéré et al. 1996). In roe deer, sexual size dimorphism is almost insignificant and they shape small groups of less than five individuals. They tend to be polygynous, (Gaillard et al. 1993). According to Gaillard, sex does not affect body size in roe deer (60–70 cm high at the shoulder and with a live weight of 18.0–28.5 kg). He mentioned that based on sexual selection, differential allocation of maternal investment for each sex might have been seen in dimorphic and polygynous species. In roe deer this allocation comes to the male at the beginning of birth but it lasts a short time, and female fawn gets more benefits over longer period – even through life time (Gaillard et al. 1993, Hemami et al. 2004).

Despite of low sexual size dimorphism, antler size is as an honest signal to female and males, in which heavy old males invest more in antler size and vigorous males assess the potential threat of younger males by their antler size (Vanpé et al. 2007). Yearlings with larger testis and antler size are more probable to be attacked by territorial males. Antlers (15-30 cm long) are used as weapons to defend the territory and to signal mating success (Vanpé et al. 2007). The European roe deer is territorial and defends the territory by scratching the ground with the front hooves or rubbing and scraping antlers against trees trunk or bushes. This is a kind of scent communication because of glands on the head and hoof and counts as a signal to the female to assess the status of a male during rutting. This function of fraying is different between species; for example the white-tailed deer is not territorial but the act of rubbing and scraping occurs frequently (Johansson et al. 1995, Johansson and Liberg 1996). Melis mentioned that the polygynous mating system in roe deer and territoriality are the reasons that the male in this species does not put much time in mating and is a tactic to reduce the aggressive interactions and competition (bucks keep their territory up to 5-6 month). Moreover, it apportions reproductive success for several years (Melis et al. 2005). Antler size and asymmetry also express the condition of individuals, in the same way as for the Eurasian elk. Pélabon mentioned that individuals with more asymmetric antlers are more vulnerable than individuals with larger and symmetric antlers (Pélabon and van Breukelen 1998).

- *Capreolus pygargus* (Siberian roe deer)

The Siberian roe deer is larger in body, skull and antler than the European roe deer and the male is slightly larger than the female. It is distributed in the temperate regions of Europe and Asia. The Siberian roe deer is territorial and aggressive behaviours decrease after reproductive period (Danilkin 1995). The male is polygamous but does not defend a harem (Gonzalez and Tsytsulina 2008). Males define their territory by olfactory signs (by rubbing head, cheek and

neck against trees and shrubs), and also by visual marks (frayed trunk caused with antler). As for the European roe deer, vocal signalling plays an important role in the social system (Danilkin 1995).

- *Hydropotes inermis* (Chinese water deer)

The Chinese water deer (Figure 11) distribution is in the subtropical zones of southwestern China and Korea. It prefers river body areas with small trees and shrubs. It has a low sexual dimorphism and males do not have antlers but tusks instead (up to 8 cm long- Wildscreen 2003). Therefore, it has been considered as a primitive Cervidae and females are slightly smaller than males (14-15 kg average by Dubost; 10.8 kg male and 9.9 kg female -by Hastings; 9-14 kg by Mauget) (Wildscreen 2003, Mauget et al. 2007, Dubost et al. 2011, Hastings 1998). Molecular analyses placed it within Odocoileinae, the nearest relative to the rest of the clade. The Chinese water deer is territorial and during breeding season aggressive behaviour and defending territory has been recorded (Mauget et al. 2007). They mark their territory by rubbing forehead to tree (but there is lack of forehead gland) and depositing dung in a wallow (Katopodes 1999). They are solitary, stable pairs and sometimes shapes of small groups has been recorded (Wildscreen 2003).



Figure 11: Male Chinese water deer standing on grass showing the tusks. Photographer: Martyn Chillmaid, [www.arkive.org](http://www.arkive.org)

- *Blastocerus dichotomus* (Marsh deer)

The marsh deer originally inhabited marshy areas south of the Amazon River into northern Argentina. They form groups of up to five seasonally and there is no sign of harem formation (Pinder and Grosse 1991). The antler is not shed and the male keeps them almost two years (Figure 12). There is no evidence of aggressive behaviour among males during the reproductive season (Epps



Figure 12: Marsh deer stag. Photographer: Christopher Courteau. [www.arkive.org](http://www.arkive.org)

2000). Sexual size dimorphism has been recorded in marsh deer (males up to 150 kg; females up to 100 kg; average between 80 and 125 kg) (Duarte et al. 2008, Politis et al. 2011, Pinder and Grosse 1991). There is strong size dimorphism (male weighs 1.57 times more than the female) and antlers are heavy (1.65 to 2.5 kg) with four pronged with radical branching (which makes the antler different from those of the mule deer) (Geist 1998). Males have larger home range than females (Epps, C. 2000).

- *Ozotoceros bezoarticus* (Pampas deer)

The pampas deer is distributed in open rangelands of eastern South America. González found strong skull width and sexual dimorphism in pampas deer but no differences in length measurements (30 - 40 kg). This sexual size dimorphism is related to mating system and degree of polygyny. In addition, there is higher intra-population variability among males (González et al. 2002, Politis et al. 2011). Despite the slightly larger body size in males, there is no marked sexual dimorphism in size, weight, or pelage (D'Elia 1999). Antlers are three-tined and shed in winter. During the rutting time, males strike low bushes or shrubs by polished antlers and rub the base of the antlers on plants or other objects; males also paw the ground, followed by urinating and curling tail. Sparring is common among different sized males and no evidence of territoriality or pairs or shaping harem has been recorded in wild populations of pampas deer but several males may fight for the access to recipient females (Jackson 1987). It is a sedentary species with unknown size of home range. They live in small groups but are mostly solitary (D'Elia 1999). Males have a larger home range than females (more than 9.9 km<sup>2</sup> for males and 5.9 km<sup>2</sup> for females) (Rodrigues and Monteiro-Filho 2000).



Figure 13: Adult male huemul with velvet peeling of antlers. Photographer: Simon Littlejohn. www.arkive.org

- *Hippocamelus bisulcus* (Patagonian huemul)

The Patagonian huemul inhabits Southern Chile and Argentina (Jiménez 2008). Povilitis showed that unlike other members of the Cervidae family, male and female huemul does not stay together after the rut and no significant association between them were recorded. Males are polygynous and the dominant male tends to mate with females serially, and later on leaves the ranges to avoid any resource competition. However, when there are few suitable patches left, the huemul tends to use a pairing strategy. Sexual size dimorphism in the huemul could be a reason for diminishing resource competition and

reproductive behaviour (Povilitis 1983). Males have antlers up to 35 cm and it is branched, shedding every year, Figure 13 (Wildscreen 2003).

- *Hippocamelus antisensis* (Taruca)

The original distribution of the taruca (Figure 14) consists of the Andean highlands from north-western Argentina through western Bolivia and north-eastern Chile, Peru and Ecuador, but nowadays the population has decreased, and is limited to some parts and extinct from some countries. Sexual size dimorphism is significant in the taruca. Males are larger (74 to 91 cm compared to 70 cm for females). Aggressive behaviour has been recorded during courtship and breeding occurred throughout the year (Roe and Rees 1976). They have been recorded in small groups of 6-7 individuals with males following groups of females (Wildscreen 2003). They have seasonal reproduction. They shape larger groups during mating and both females and males move between groups. There are no territoriality and the male guards the female with which he has mated. Males fight with their antlers over female in oestrous (Putz 2003).



Figure 14: Taruca (*Hippocamelus antisensis*).  
Photographer: Enrique Berligieri. [www.arkive.org](http://www.arkive.org)

- *Mazama americana* (Red brocket)

The red brocket deer is the largest species in the genus *Mazama* (30 to 40 kg). Red brocket deer is distributed in northern Latin America from Mexico to the north of Argentina (Durate et al. 2008, Abril et al. 2010). This species has seasonal reproduction (Julia and Peris 2010). It is the largest brocket with has the greatest range of distribution. Males have short spiky antlers, which may be shed during the year or kept all year round. They are solitary and have sometimes been seen in pairs. The red brocket avoids very wet habitats and prefers to live in woodland and forest up to 5000 metres. This species is both active during night and day



Figure 15: Red brocket rear view. Photographer: Patricio Robles Gil, Sierra Madre. [www.arkive.org](http://www.arkive.org)

(Wildscreen 2003, Jansa 1999). A red brocket has upper milk canines (appeared in 20 % of individuals). It defends resources with short and non-branching antlers (Figure 15). There is a lack of pre-orbital gland or it is very small. It has been recorded in some specimens that the antlers has up to four tines. Rubbing forehead and antler thrashing, jumping over each other and pawing has been recorded in red brocket as a territorial defender species. Moreover, they mark with urine and faeces (Geist 1998).

- *Mazama bricenii* (Mérida brocket)

The Merida brocket is distributed in the high Andes in northern Colombia and western Venezuela and the largest population is in Venezuelan national parks. They are solitary and nocturnal, and they have been recorded alone or in pairs within small territories (Lizcano and Alvarez 2008). The size of the antler is 5 cm and the weight is 12.5 kg (Geist 1998, APUS 2003).

- *Mazama chunyi* (Peruvian dwarf brocket)

The Peruvian dwarf brocket inhabits southern Peru and northern Bolivia (Rumiz and Barrio 2008, Rumiz et al. 2007). A small spiky-antler size (Figure 16) seems to be adapted to high dense mountain forest where they live (Rumiz et al. 2007). They are solitary, active both during day and night; also it seems that their reproductive strategies are the same as in other brockets (Wildscreen 2003). This species is smaller than *M. rufina* (rufous brocket) about 8- 12 kg in weight and it looks like the pudu superficially. The pre-orbital gland is well developed but small. The antler size is less than 3.5 cm (Geist 1998, Calderon 2013).



Figure 16: Dwarf brocket deer with researchers.  
Photographer: Daniel Blanco, Peru verde.  
www.arkive.org

- *Mazama gouazoupira* (Gray brocket; brown brocket)

This species is distributed from southern Uruguay to the north of Mato Grosso State in Brazil and from the Andes mountains to the Atlantic coast. It has the widest distribution among all brockets and the body colour changes according to the habitat it uses (colour varies from gray to brown depending on forest, savannah and shrub-land; body weight 16.4 to 17.9 kg) The Gray brocket is a small deer. Females are polyoestrous and males are polygynous. It invests and

allocates more energy in testicular mass which it is related to reproductive behaviour and success. Large testicular size is determined by multi- male mating system as well (Costa et al. 2011); males have simple antlers about 7 to 10 cm in length. Moreover, the gray brocket is known as a polyphyletic species. Seasonality of reproduction has been recorded in this species and males are highly territorial (Julia and Peris 2010, Kufner et al. 2008). This species is smaller than the red brocket, pre-orbital glands are small and they are more diurnal (Geist 1998).

- *Mazama nana* (Brazilian dwarf brocket)

This species is distributed in the southeast Paraguay, north of the Misiones Province in Argentina, and in some of the Brazilian states. It probably resembles other dwarf brockets such as *M. chunyi* and *M. rufina* in behaviour and ecology. This species is the smallest deer in Brazil (15 kg weight and 45 cm height). An antler annual cycle has been recorded but not in Brazil and no record of reproductive seasonality. It is solitary, nocturnal and territorial (Abril and Duarte 2008, CAB Direct 2010, ICMBio 2013). They have shorter legs than red and grey brocket but larger pre-orbital glands (Geist 1998).

- *Mazama rufina* (Dwarf red brocket)

The dwarf red brocket's distribution is restricted to the Andes. The original range of habitat is from Columbia to northern Peru. Its favourite habitat is cloud forest. Their population has been decreased because of deforestation and land use changes. They seem to be solitary and they are active nocturnally and diurnally. It has been recorded in pairs or alone and within small territories (Lizcano and Alvarez 2008). In size, it is similar to *M. nana*. It has pre-orbital glands, well developed. The antler rarely grows more than 8 cm in size (Geist 1998).

- *Mazama bororo* (Small red brocket)

The small red brocket is a native species in Brazil, ranging from São Paulo to Paraná. This species, based on morphology and karyotype, is categorised as an intermediate form between *M. nana* and *M. americana*. It weighs between 11.3 to 13.5 kg and it appears just in primary and secondary forests. *Mazama bororo* is solitary and nocturnal and uses olfactory marking to define the territory (Duarte 2008, Gonzales et al. 2009, TERRA da gente 1999, Vogliotti and Duarte 2009).

- *Mazama nemorivaga* (Amazonian brown brocket)

The Amazonian brown brocket is native in Brazil, Colombia, Ecuador, French Guiana, Guyana, Panama, Peru, Suriname and Venezuela. Based on records, it seems that this species prefer to live in tropical and subtropical moist forests, restricted to non-flooded forest (20 kg; 110cm long). Reproduction happens all around the year (Rossi and Duarte 2008, IPAM 1996, Calderon 2013). It was first classified as *M. gouazoubira superciliaris* but recent research shows that this species is placed in the clade of Odocoileinae that also groups together *Blastocerus*, *Ozotoceros*, *Hippocamelus*, and *Pudu*, and which includes *M. gouazoubira* (Fiorillo et al. 2013).

- *Mazama pandora* (Yucatan brown brocket)

This species is listed as recently re-discovered species and the distribution is limited to Belize, Guatemala and Mexico. Little is known about the Yucatan brown brocket ecology apart from it being a habitat generalist (Weber et al. 2008).

- *Mazama temama* (Central American red brocket)

The range of the Central American red brocket is Belize, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua and Panama. This species prefer well-preserved forests such as perennial forest, cloud forest and low-dry forest. In some areas it avoids cropland or open lands but they are recorded in some cultivated areas. In areas with high rate of hunting, *Mazma temama* prefers low flooded forests for a better protective strategy. The antler is about 10 cm and its bodyweight is 25-48 kg with an average of 1 m in length and a shoulder height of 70 cm (Belo et al. 2008, La Otra Opcion A.C 2010).

- *Odocoileus hemionus* (Mule deer)

The mule deer is a medium sized deer; the male is larger than the female. Its distribution is mostly in the North America. The mule deer has perfect binocular and colour vision; also, it is sensitive to movement. Production of sperm, testosterone and testis size is at a higher level during the reproduction season. The rate of mortality depends on predation, population density and hunting. The mule deer is polygynous, their mating system includes tending-bond, and some records mentioned shaping harem in this species means that courtship and mating happens within group. A dominant male (which is defined by antler and body size 3.5 – 8 cm and 70-

150 kg respectively) stimulates female to mate with and just dominant male is territorial (Anderson and Wallmo 1984). Genetic variation in isolated populations is high (Peles et al. 1999). The reproductive behaviour consists of sparring, tending, circling, antler thrashing and fighting (Relyea and Demarais 1994). A V-shaped mark starts from between eyes and continues to the sides; this mark is more visible in male than female (Misuraca 1999). The size of antler is about 88, 5 cm and sexual size dimorphism is significant in this species (Plard et al. 2011).

- *Odocoileus virginianus* (White-tailed deer)

The white-tailed deer inhabits southern Canada throughout most of the border with United States, southward to northern South America. Sexual size dimorphism is shown by larger body size in the male (20-40% more than the female). Mortality depends on maternal nutrient, predators (today mostly domestic dogs) environmental changes and hunting; Webb showed that most non-hunting mortality depends on rutting related-stress (Smith 1991, Webb et al. 2007). Males are not territorial and they live in a group with females, but they have no sexual contact except in the mating period. During the rutting time, the male is solitary but there is an exception when they stimulate oestrous females. Dominance hierarchies exist among individuals, marking and rubbing with head and antler has been recorded during the mating period. Both female and male have been observed scraping, but it is specifically done by male during rutting time (Smith 1991). Aggressive behaviour is rare in this species. The dominance rank changes and is unstable hierarchy; males could be attacked by subordinate males and not just the males in their rank (Bartoš et al.2010). The size of antler is about 65,6 cm, and sexual size dimorphism is significant in this species (Plard et al. 2011).

- *Pudu mephistophiles* (Northern pudu)

The northern pudu is limited to the Andes high altitude forest (Stahl and Athens 2001). It is the smallest deer and native in Colombia, Peru and Ecuador. According to IUCN, its distribution includes fragmented ranges from mountain forest to humid grassland. The small size of this species is a good strategy against predators (Barrio and Tirira 2008). The hair in front of the head tends to raise and hide the antlers. It is half the size of the southern pudu. Antlers are renewed annually. The northern pudu is aggressive and there is no record of being territorial in this species. Horning, licking, butting and marking have been recorded; in oestrous time, female urinates, lets male sniff, and lick the urine and they have seasonal mating and no copulatory bound are shaped. The body weight is about 3.3 to 6 kg and antler size is 6 cm. The pre-orbital

gland is small and upper milk canine has been recorded commonly. There is lack of tarsal and metatarsal gland but the inter-digital gland exists (Geist 1998).

- *Pudu puda* (southern pudu)

The southern pudu's distribution is limited to humid forests in Chile and south-west of Argentina (Meier and Merino 2007, Jimenez and Ramilo 2008). It is solitary except during rutting period. It has wider hooves than the northern pudu; pre-orbital glands are bigger and antler is larger (5.3 to 9 cm). The body weight is about 6.4 to 13.4 kg and upper milk canine is rarely to be found. By changing light, antler growth cycle and breeding shifts quickly (Geist 1998). There are a range of behaviours during the mating season including marking, jumping, chasing, butting and kicking. Studies show that the amount of hormone related to antlerogenesis behaviour in dominant male increases during the second period of antler growth (Bartos et al. 1998, Jimenez and Ramilo 2008). Another study suggested that the pudu, similar to roe deer, has two peaks of reproductive hormones; one related to mineralization of antler and the other one connected to rutting. These two peaks might be related to an increased period of testicular activation and fertility (Bubenik et al. 2002). Habitat changes, hunting (especially with domestic dogs), predation and competition with other deer are mortality factors in this species (Jimenez and Ramilo 2008).

- *Rangifer tarandus* (Reindeer/Caribou)

The reindeer is distributed in the circumpolar, tundra and taiga zones of northern of Europe, Siberia, and North America. Sexual dimorphism (antler and body size) has been recorded in reindeer. Nomadic species mostly migrate in North America but in Europe tend to be more sedentary (Henttonen and Tikhonov 2008). This species as other Cervidae is polygynous in which competitive abilities define reproductive success. A high-ranked male has higher reproductive success; he prevents any lower-ranked male's approaches to female (Røed et al. 2005). One study showed that young males with less-developed rutting behaviour cause extra stress. Also experiments shows that males lose more weight during rut rather than females and



Figure 17: Reindeer bull in velvet. Photographer: Eric Baccega. [www.arkive.org](http://www.arkive.org)

this is connected to variation between the sexes during reproductive allocation. The loss of weight in young males is more than in the adults therefore, according to the concept of female choice, males tend to keep a larger body during the mating system. Losing weight might have connection to the demand of less energy during winter; the risk of limitation in foraging is high in some herd. Dominant bucks shape the large harem; females connect to different harem-holding males and live in fission–fusion systems. In highly female biased population, if harassment by males is costly for females, they tend to gather in harems or territories which are controlled by high-ranked males (Holand et al. 2007, Barboza et al. 2004). The opportunity for subordinate males to mate is only untended females in large harem in taiga also the time that a dominant male migrates between herds in the tundra (Barboza et al. 2004). Thus in game populations where high-ranked males are removed, the behaviour and sex ratio alter. On this case, various behavioural effects on reindeer population and a high rate of mortality in males are observed (Røed et al. 2005, Barboza et al. 2004). As in other deer, antler size and asymmetry are negatively related in the reindeer and antlers are expressed as a condition-dependent character. Antler weight, size and volume, all relate to body size (Figure 17). In addition, there is a positive relation between parasite burden and asymmetric antlers (Markusson and Folstad 1997). Antlers exist in both sexes and the antler is asymmetric (Goss 1983).

- *Axis axis* (Chital)

The chital is distributed in India, Nepal, Bhutan, Bangladesh, and Sri Lanka. *Axis axis* is a gregarious species of medium size. They have a small home range and do not migrate (Jog et al. 2005). It inhabits all kind of habitats except dense forests or desert/semi desert habitat, and preferably chooses open land and valley area. The chital exhibits a fission-fusion system, or fluid group formation and dissolution. In open land, they shape larger group size (consisting of two or more families) and this size will change by joining males during rutting period and peak fawning. The mating consists of a dominance-based hierarchical system. Males are more vulnerable to predation because they are far apart from the group (Ramesh et al. 2012, Duckworth et al. 2008). Compared to hog deer, antler and tines are longer and the body mass is twice as much as for the hog deer. It seems that chital share some characteristics of social behaviour and morphology with the fallow deer. Males die faster than females but this rate is even higher among the hog deer (80 stags to 100 females in chital, 56 stags to 100 females in hog deer) (Geist 1998). Males are darker and the body height is about 0.6 to 1 m. The antler reaches almost 1 m and consists of three tines (body weight: 27 to 45 kg) (Lundrigan and Gardner 2000). Chital reproduction, as for other tropic Cervidae, depends on food availability

affected by the climate condition. However, in temperate regions the reproduction is seasonal (Bubenik et al. 1991). Female biased sex ratios are significant. Illegal hunting, disease and forest fragmentation are mortality factors (Duckworth et al. 2008).

- *Axis calamianensis* (Calamian hog deer)

The Calamian hog deer inhabits the Philippines and is distributed in three of the four large islands in the Calamians. They live in open land, woodland and secondary forests. Living in a group up to 14 has been recorded. They are diurnal and in areas with intense hunting, they live in smaller groups (Oliver et al. 2008). The Calamian hog deer has longer and darker legs than the hog deer (see below) but is smaller (with the same biology as hog deer), with well-developed pronged antlers (Geist 1998). The body weighs 27 - 110 kg and the antler is horn-like which shed every year. Males rub and hit the antlers to trees or shrubs. It seems that in captivity males mate all year around (Wildscreen 2003)

- *Axis kuhlii* (Bawean deer)

*Axis kuhlii* is originally from the Bawean Island, in the Javan Sea off the northern coast of Java, Indonesia. Bawean deer is a species that prefers hilly forest rather than grassland or marshy areas. According to one study, the morphology of *Axis kuhlii* is similar to *A. calamianensis* and *A. porcinus*. Fossil records show that *A. kuhlii* lived in Java but were extinct from that area because of competition between this species and the Timor deer in forest areas and southern red muntjac in the open lands (Meijaard and Groves 2004). It has seasonal rutting but males in breeding condition might have been seen all over the year. The Bawean deer is nocturnal and solitary; pairs consisting of fawn / female or buck following a female has been recorded (Semiadi et al. 2008). This species has the same size as the hog deer (65 cm in height), with short legs and frequent social vocalization; these characters and hiding strategies led this species to not have specific predators in nature; but nowadays predation with python, aerial predators and domestic dogs cause a decline in Bawean populations (Geist 1998). (Territorial and mark it; Wikipedia) The antler size is small in comparison with other tropical deer. The mating system is courting pairs and males fight for one female (Wildscreen 2003, Ultimateungulate 2013).

- *Axis porcinus* (Hog deer)

The hog deer is distributed in Nepal, Bhutan, Pakistan, eastern India and parts of Ceylon, Bangladesh and Vietnam. The hog deer avoid inhabiting salty and reverine forests and it prefers mostly floodplain areas (Odden et al. 2005, Dhungel and O'Gara 1991). This species is inconspicuous and scattered with short legs and heavy body hiding in tall-grass, which prevents it from being hunted by predators. Males have branched antlers (yearling males have spiky antlers) and sexual size dimorphism (male heavier than female ~ 13 kg) has been recorded (43 kg in male and 32 kg in female) (Durrant et al. 1996). The home range is about 60 to 80 hectare, and in low density, bucks tend to be territorial. It does not seem that the male uses a calling signal or marking but in the rut time, they paw the ground. More over there is no record of harems, and stags defend one female at the time (Geist 1998). They shape a group of an average of 1.9 individuals during the breeding season but larger groups have been recorded – up to 20 individuals. Mixed groups of adult bucks have been recorded at the beginning of the rutting period. Dhungel and O'Gara declared that the most noticeable behaviour during rutting is the rutting call (bellowing) followed by shedding, antler cycle, aggressive behaviour and increase in testosterone hormone in the male (Durrant et al. 1996). The breeding season depends on nutrition and food availability. Home ranges overlap between the sexes (males are not territorial instead they have a roaming strategy) and the home range is smaller than for other large deer in the Cervidae family (Odden and Wegge 2007). The antler, compared to other species in the genus *Axis*, is smaller and covered by velvet most of the year. Males are highly aggressive. Males mate with females as many times as they can; also, it is recorded that the male courts and defends one female. Males are territorial and mark it with secretion (Michelin 2002). The size of the home range differs by food availability, which during spring is smaller, and in the autumn becomes larger due to better access to food. This species is both nocturnal and diurnal and if there is enough food, they are sedentary. The sex ratio is female biased because males are more vulnerable to predation (especially tiger and leopard) and other factors of mortality (Dhungel and O'Gara 1991).

- *Cervus albirostris* (Thorold's deer/White-lipped deer)

The white-lipped deer is native in China and inhabits the eastern Tibetan Plateau and the Qilian Shan area of China. This species prefers an altitude over 3500 m with coniferous forest and alpine grassland. Males are supposed to form small herds and be solitary; the juvenile males shape a group but adult males seem to be solitary. Groups consist of females and yearlings up to 42 individuals during the non-rutting season. They are diurnal and live separately from male except during breeding season. It is extremely hunted for antler, meat and medical reason

(Miura 1989, Harris 2008).

Aggressive behaviour among males during breeding the period has been recorded and the size of herd during this time fluctuated between 50 to 300 deer (Ehler 2002). There is significant sexual size dimorphism in which males weigh around 205 kg plus or minus 13kg and female around 125 kg plus or minus 33.7 kg. Males have large antlers about 7 kg. The pre-orbital gland is large and metatarsal gland is protruded from hind hair. The male face is distinguishably darker than the rest of the body. They shed antlers about two months earlier than the red deer in the same area. There is no resting period between antler shedding and rutting for the white-lipped deer. Older males roar with a deeper voice during the breeding season. Larger males defend females serially, which means few females at any time in the harem (Geist 1998). Aggressive behaviour combined by antler thrashing occurs during rutting and is maybe followed by fighting and sparring (Wildscreen 2003).

- *Cervus alfredi* (Visayan spotted deer)

The distribution of *Cervus alfredi* is limited to the Visayan Islands in the central Philippines. It generally lives in dense forest in the interior of islands and is distributed from the sea level up to mountain regions. This species prefer mostly natural disturbed habitats such as fire fields or slid-slopes. The Philippine spotted deer has short ears and legs; the female is much smaller than the male (36 to 59 kg). Larger males try to mate with females, and during rutting, roaring and aggressive interactions are recorded (Key 2003). The group size is one to three individuals and solitary males have been seen in areas that could be the consequences of high pressure hunting (Oliver et al. 2008). The antler is short (20 cm). It is nocturnal; also, it has been recorded in small groups of 3-5 individuals (Wildscreen 2003).

- *Cervus/Rucervus duvaucelii* (Barasingha/Swamp deer)

At present the barasingha inhabits three reserved areas in India and one wild life reserve in Nepal. The name of swamp comes from the area this species lives in; they also inhabit forest areas as well but close to water. They are dependent on aquatic vegetation because of a need for sodium mineral (Moe 1994, Ferraino 2007). Adult males have a darker coat and up to 15 tines smooth antler up to 1 m (body weight is 172 to 181 kg). During the rutting period, a dominant male forms a harem and gathers up to 30 hinds. Fighting, barking and antler chasing is recorded during this time. A dominant male wallows by urinating and rolling itself in that scent and scraping the ground with hooves. They are social and diurnal; the herd is mixed and leader is a

hind but males sometimes switch between herds (Ferraino 2007, Wildscreen 2003). The females are monoestrous. Mortality factors are predation, flooding and poaching (Duckworth et al. 2008). The hooves of this species are not blunt and small as for other Cervidae (Geist 1998).

- *Cervus elaphus* (Red deer)



Figure 18: Red deer (*Cervus elaphus*) stag bellowing, Bradgate Park, Leicestershire, England, UK, October. Photographer: Danny Green. [www.naturepl.com](http://www.naturepl.com)

*Cervus elaphus* is distributed from Europe and North Africa through central Asia, Siberia, the Far East and North America. They prefer woodlands, mountain areas and in winter, they choose valleys (Lovari et al. 2008). In the male red deer, the level of aggressiveness depends on androgen hormone and testosterone level leading to antlerogenesis behaviour (Bartoš et al. 2010). As red deer is a game animal, selectivity in hunting cause this species to

select different regimes due to body and antler size (Zachos 2011). Red deer is not territorial and males gather harems during rutting period. In other times, females and young shape herds and males are together. During winter they shape bigger herds with mixed sex (Lovari et al. 2008). Males are larger than females (171 to 292 kg in female; male 10 % larger and weighs 178 to 497 kg). The size of the antler (Figure 18), determines the most powerful and more able in fighting behaviour; the larger antler (1.1 -1.5 m) in the male red deer indicates the greater lifetime breeding success in this species. Dominant males shape the harems and defend the territory-like boundary around females; harems consist of one bull and six females (Nie et al. 2011, Fraser 1996, Senseman 2000). The mating strategy of males depends on the spatial distribution of females and temporal availability of oestrous females. A study showed that fights during rut relates to body weight also duration of rutting depends on pre-rut condition in male which all affected by nutritional availability (Gibson and Guinness 1980).

- *Cervus/Rucervus eldii* (Eld's deer)

The original distribution of this species was from India to Indonesia and southern parts of China but nowadays, because of over hunting and habitat degradation the population of Eld's deer is limited to Southeast Asia (Balakrishnan et al. 2003). The cost of reproduction at the age of 5 or 6 years causes high rate of mortality in this species which could relate to the males

fighting during the rutting period. Many males have no access to females gathered in a harem by a dominant male. The age of maturity is determined by first mating, which is older than physical maturity. Thus, males show differences in reproductive success. In *Cervus eldi*, the antler velvet mass has no significant correlation with breeding success which this result might express other factors such as fighting strategy and body size (Nie et al. 2011). Females in the thamin (*Cervus eldi thamin*) deer are polyoestrous with one onset in late winter; they also have seasonal reproductive rhythms and variation of group size. As the hog deer, there is no sex differences home range size. The groups size increase during rutting (unlike chital and barasingha) and it is connected to finding new patches of food sources by females and males in this situation following the oestrous females. Male are solitary except during rutting time when they join the herds (up to 50 individuals). The male's weight (70-130 kg) decreases during the mating period but female body weight increases. The antler is formed in one continuous curve and is less branched (Figure 19). They are nocturnal and they migrate. The home range is about 3.8 to 14.71 km<sup>2</sup> (Aung et al. 2001, Timmins and Duckworth 2008a, Worrel 2004, Wildscreen 2003).



Figure 19: Eld's deer (*Cervus eldi*), Keibul Lamjao Sanctuary, Manipur, India. Known locally as Sangai or Brow-antlered deer. Photographer: Anup Shah. www.naturepl.com

- *Cervus mariannus/ Rusa marianna* (Philippine brown deer)

This species is native to the Philippines and inhabits areas from the sea level up to 2900 m in primary and secondary forest (Oliver et al. 2008). It is a medium size deer but smaller than the sambar. During rutting females might shape a small group up to eight. Males remain solitary and they are aggressive. Males have short antlers (20-40 cm in length) and a bodyweight of 40 to 60 kg (Wildscreen 2003).

- *Cervus nippon* (Sika deer)

The distribution of sika is from eastern Siberia, Japan, Manchuria, Formosa; in China-Chihili, Shansi, and the eastern Yangtze Basin from Chekiang and Kiangsu into northern Kwantung (Feldhamer 1980). They inhabit forest areas with dense understory. They feed on bushes and shrubs in the subalpine forest. The sika deer is a sedentary species but because of need of access to water they have some seasonal movements (Harris 2008, Feldhamer 1980).

The sika deer is a small to medium sized deer (4.5 to 80 kg) and body colour varies among subspecies. There are signs of sexual size dimorphism in which males are larger than females (8.7% larger). Antlers are about 30-66 cm long with 2-5 tines. The male start the breeding season with winter pelage, while female has summer pelage. Males have velvet antlers and older males shed their antler sooner than the younger. During rut, males lose up to 20-30% of their bodyweight. It is not a gregarious species and small herds or group size has been recorded. Males are solitary and they gather during the rutting time when antlers are cast. Males are territorial and they mark their territory by digging a hole with the forehead and antler followed by trashing the ground with their antlers. They urinate in those holes frequently. Males gather up to 12 females in their territories that they mate with, and fighting has often been recorded. The sika is known as one of the most vocal Cervidae. It has 10 different vocalizations. Males emit a sound approximately one month before the rut in which they prepare for roaring activity and physical motions (Feldhamer 1980, Landesman 1999). The growth rate of the male is higher than that of the female and young adults have higher length antler growth, which relates to the number of female held during breeding season. Therefore, early growth in the yearling is important for reproductive success (Koga and Ono 1994). A Study showed that the sika deer like other temperate Cervidae including red deer, fallow deer, white tailed deer, reindeer and wapiti, typically exhibits seasonal breeding (Chan et al. 2009). This species is phylogenetically close to the giant wapiti from North America and northern Asia (Geist 1998).

- *Cervus/Rusa timorensis* (Timor deer/Javan deer)

The Timor deer is distributed mostly in Southeast Asia; based on IUCN data it is a native species in Indonesia. Javan deer is a tropical and subtropical grassland species but the range of habitat is flexible. It prefers forest areas and grasslands. They are nocturnal and most activity included in rutting even in areas of low risk of hunting, occurs during night (Reyes 2002, Hedges et al. 2008). There is sexual size dimorphism between male and female (the male weighs about 152 kg and the female approximately 74 kg). Males have three-pined antlers (Figure 20) and it is categorized as a



Figure 20: Male Javan deer. Photographer: Gerald Cubitt. [www.arkive.org](http://www.arkive.org)

large deer with up to 1 m shoulder height (Goss 1983). Competition among males to access female in oestrous has been recorded during the rutting period. The Javan deer is gregarious and

during mating the male decorates its antler with grass to attract females. Males are extremely vocal and aggressive during breeding season (Reyes 2002). Studies show that a decrease in testosterone level is associated with decreasing aggressive behaviour and deactivation of velvet antlers (Van Mourik et al. 1986).

- *Cervus/Rusa unicolor* (Sambar)



Figure 21: Indian sambar (*Cervus unicolor*) male on edge of woodland, Ranthambore NP, Rajasthan, India. Photographer: Francois Savigny. [www.arkive.org](http://www.arkive.org)

The distribution of *Rusa unicolor* is from India and Sri Lanka to Nepal, Bhutan and China. There is a debate on the pattern of activity in this species. Some indicate that it is nocturnal, some studies showed no significant variation, and some mentioned that this species is cathemeral. This species is not social and a temporary group is formed in dry season with up to 30 individuals, but in wet season group size is

bigger – up to 100 (Timmins et al. 2008j). This species inhabits near cultivated areas and gardens to access food, but the range of living is thick forest, swamp forest areas to open shrub. Sexual size dimorphism is significant in the sambar (larger male rather than female) (185-260 kg for the male and about 162 kg for the female). The antlers have three or four tines (Figure 21) and males have dense mane on their neck (shoulder height up to 100 cm); also, males are darker than the females (Geist 1998, Brown 2002). Stags are solitary and during breeding season they are aggressive defending territories by marking with scent glands (Brown 2002). The Male digs a hole and urinates in which fallows by wallowing antler to the rim of hole; they also mark bushes with pre-orbital glands and rub their antler to the trees; these kind of behaviour looks like that of the white-tailed deer except the pre-orbital gland marking, wallow and preach. Males have less vocal signalling than other cervids (Geist 1998). Studies have shown that the sambar deer, like other tropical species including rusa deer, chital deer, Père David's Deer and brown brocket deer, are indigenous to equatorial regions and are considered non-seasonal breeders (Chan et al. 2009). During the rutting season, adult males have been seen with hinds and fawns. The group size is small in sambar (up to five individuals). Compared to the chital, sambar deer males are vulnerable to predators; they are solitary therefore the sex ratio is biased towards females in this species (Ramesh et al. 2012).

- *Rucervus schomburgki* (Schomburgk's deer)

This is an extinct species, the last wild population died in 1932 and the last individual was killed in captivity in 1938. Their range of distribution was Thailand. This species preferred over-flooded swampy plains with high grass, cane and shrub lands but avoided forest areas (Duckworth et al. 2008). A study showed that there is a double channel in the pedicle which does not exist in other *Rucervus* species, and there is also a resemblance between *Rucervus*



Figure 22: Schomburgk's deer (*Cervus schomburgki*); Photo from West Berlin Zoo though Lothar Schlawe (1911)

*duvaucelii* and *Rucervus schomburgki* but no resemblance with *Rucervus eldii*; it means that *R. eldii* belonged to another evolutionary line (Meijaard and Groves 2004, Pitra et al. 2004). Geist also mentioned that this species was close to barasingha but the antler has radical branching and no evidence of neck mane has been found. It is now considered an extinct species and was categorized as a medium-sized deer (Figure 22). The Shoulder height was 100-110 cm with a body length of 88 cm and a 10 cm long tail; it weighed about 22 kg (Geist 1998, Siamensis.org 2001, Maas 2011).

- *Elaphurus davidianus* (Père David's deer)

This species was originally distributed in humid and warm regions in the east of China. In the 19<sup>th</sup> century, it became extinct in the wild and was reintroduced 200 years later to China. It



Figure 23: Père David's deer stag. Photographer: Ingrid Van den Berg. www.arkive.org

seems that this species prefer swampy and marshy area (Wildscreen 2003). The sex ratio is female biased (Jiang et al. 2000). It is a large deer with the larger and bulkier brow tine rather than beam tine in the antler (Figure 23) (55-80 cm). The natural habitat for Père David's deer was river valleys and low-laying plains. Rutting follows by calling, flehmen response and scattering grass with the antlers. Males design their antlers with grass to attract females. A male joins the harem of females and

defends it. Antagonistic behaviour consists of chasing and biting by dominant males (Walton and Hosey 1983, Jacobson 2003). Males have a two antlers dropping cycle, first in the summer and the second in January. Père David's deer is social species and they are together in large groups but in the rutting period. Females visit several groups and dominant males join them after fighting with other males; aggressive behaviours are antler butting, chasing, biting and foreleg kicking. There is sexual size dimorphism in which male is larger than female (214 kg male and females 159 kg) (Wildscreen 2003, Jacobson 2003).

- *Dama dama* (Fallow deer)



Figure 24: Fallow deer (*Dama dama*) stag resting, London, UK September. Photographer: Graham Eaton. www.naturepl.com

The original distribution of fallow deer is southern European regions along the Mediterranean Sea, Asia Minor, and possibly northern Africa and Ethiopia. They live in different habitats from cold- humid to warm and dry in forest, grassland, and savannah and so on, but they prefer a warm-humid environment (Feldhamer et al. 1988). Fallow deer has a seasonal reproductive cycle with cyclically casting and re-growth of antler (Asher et al. 1996). Both sexes of the fallow deer live separately most of the time during the year but close to the rutting period, they shape a mixed group. Some studies suggest that larger and mixed groups are set up in open lands; other researches indicate that in an enclosed area harem groups and mixed groups are probably shaped more than in open lands (Apollonio et al. 1998). Males

are mostly solitary, but after re-growth of the antlers (50 to 70 cm) may shape a small group (Figure 24). Before rutting, males spend more time on their territories and mark the territory by pawing, urinating and rubbing. They decorate their antlers by scattered grass and understory (Feldhamer et al. 1988, Massei and Bowyer 1999). Antagonistic behaviour has been recorded in this species amongst males but preferably they choose vocalization or parallel walk before physical combat which prohibits them any injury in the time that they are not sure about winning a physical conflict (same as *Cervus elaphus* but with more frequency in Fallow deer) (Bartoš et al 2007). Studies showed that the dominant lek male has high reproductive success in lower rank single territorial males and at last, sub-ordinate lek male has the lowest breeding success (Saltz 1996).

- *Dama mesopotamica* (Persian Fallow deer)

The Persian fallow deer was originally distributed in the western parts of Asia (Iran, Iraq, Israel, Jordan, Lebanon, Palestine, Syria and eastern Turkey). The last wild population was recorded in Iran 1974, which were captured and reared in a zoo in Berlin (Saltz 1996, Rabiei and Saltz 2011). It is supposed to prefer dense thickets (wild population inhabits in riparian forest tickets) along river and prevent to be close to roads or settlements. This is a medium to large deer with the weight of 50–70 kg for females and 80–100 kg for males. Most of the time they move alone but sometimes shape a group of 2-8 individuals (Zidon et al. 2008). There is no significant result of shaping herd, or living in small groups or being solitary in this species. The bucks have bulky antlers (Figure 25) which lack the palm in the upper part of that of the European fallow deer, and the Persian fallow deer is larger (Wildscreen 2003, Rabiei and Saltz 2011).



Figure 25: Persian fallow deer buck with fawn.  
Photographer: Eva Bartov. [www.arkive.org](http://www.arkive.org)

Males are territorial and after establishing the territory, they tolerate males of smaller size but not similar sized in their area (Dolev et al. 2002).

- *Elaphodus cephalophus* (Tufted deer)

The distribution of the tufted deer is Myanmar and China. This species chooses habitats close to water, forest and rainforest in high altitudes. A tufted deer is larger than a muntjac (17-50 kg). Males are larger than females and they have small and spiky antlers, which sometimes are covered by tuft hair from the forehead. The male uses barking to attract mates as well as for alarm. They are observed in pairs but are usually solitary. Males are territorial and fight for territories during breeding season; during fighting they use their canines (2.5 cm long) rather than the antlers. The tufted deer is usually nocturnal (Lundrigan and Oas 2003, Wildscreen 2003). This species seems to be basal in the muntjac group because antlers are rudimentary and never cast, also they have short slender pedicles, and the size of the two sexes is equal (Rabinowitz et al. 1999).

- *Muntiacus atherodes* (Bornean yellow muntjac)

The Bornean yellow muntjac is a native species in Malaysia and Indonesia and found only in

Borneo. They choose a variety of habitats to live in, from low to dense vegetation and forest. They normally choose a habitat close to water bodies. The male has thin and long simple horns (16 - 42 mm; body weight 13-18 kg) without burr, and there is a lack of tuft of hair covering antlers. The canines in males are long and curved outward from the lips, which shapes a tusk. Females have a knob in the place of antler and tufts of hair covering it. The reproductive strategy seems to be similar to that of other muntjacs and females are polyestrous. *Muntjac atherodes* is diurnal and usually observed alone, but has often been recorded in pairs within small territories (adult male and adult female). This species barks for alarm and also use secretion to mark the territory, reproductive states and social communication (Jetzer 2007, Timmins et al. 2008a).

- *Muntiacus crinifrons* (Black muntjac)

The distribution of the black muntjac is in the western provinces of China and northern part of Myanmar. It lives in forests between 800 and 1000 m above sea level that cover deciduous forests, dense understory, evergreen trees and bamboo patches. Females are on average larger than the male (female 24.1-25.5 kg, recorded by Schaller and Vrba 1996, and male 23.1 kg). The male has antlers, which at the pedicel is covered by hair (not exceeding 60 mm; 20-60 cm) (Messick 2006, Wood 2006, Geist 1998). Some authors have indicated that the black muntjac has no annual shedding. They have found some similarities in antler size and morphology with *M. atherodes*. Males mark their small territory and defend it aggressively especially during the mating period; this territory could overlap with other females as well. There is no significant breeding season recorded, but they are polyestrous. This species is solitary, sometimes found in small groups (Wildscreen 2003, Wood 2006). To mark territories, they use pre-orbital and frontal glands. The male uses their upper canines that look like a tusk to defend territories. Studies show that because of small antler relative to body size, there is a lack of social hierarchy among males, and the small body size is suited for fighting but not social dominance and sparring. Males use scent marketing to define the territory and also barking, visual contact such as raising tuft and showing of the white part of tail has been recorded as an alarm signal (Wood 2006). They have a non-seasonal reproductive cycle (Harris 2008).

- *Muntiacus feae* (Fea's muntjac)

Fea's muntjac inhabits Thailand and Myanmar. They live below 1500 m of sea level. This species prefers woodland and humid forest with dense vegetation. Females are taller than the

male (unlike Indian muntjac) by six to seven centimetres (average weight is 25 kg). The antler is longer than that of *M. crinifrons* and the pedicle is long and has a black line that continues to the centre. This long pedicle could be an adaptation to living in a low-nutrition area; they need less energy to re-grow antlers after shedding. In addition, the male has a pair of one to two cm tusks. Males are supposed to be territorial and fight for the territory with antlers and tusks. This territory may include several females. Males and females may fight over resources and males mark their territory with pheromones. A thin pedicle seems not created for fighting and intra-sexual conflict is less than among other muntjacs. Breeding has been recorded all year around. *Muntiacus feae* is solitary and nocturnal (Messick 2006).

- *Muntiacus gongshanensis* (Gongshan muntjac)

The Gongshan muntjac inhabits Tibet, Myanmar, southern China and the north of Thailand. Lowland forest and evergreen area is favourable among this species. It is similar to the Fea's muntjac but different in karyotype (Thompson 2006, Timmins et al. 2008b, Giest 1998). Males have small dagger shaped antlers covered in tuft of hair. Females are taller than the male (female: 57-61cm and male: 47-52 cm). The average body weight is 18 to 20 kg in both sexes. No evidence of seasonal breeding has been recorded and males seem to defend their small territories against other males. They are supposed to be solitary and they are active early in the morning and late in the evening. Males use scent marking for signalling reproductive status (Thompson 2006).

- *Muntiacus muntjak* (Southern red muntjac, Indian muntjac)

The range of the southern red muntjac is from Pakistan to India and Nepal throughout Southeast Asia and southern China. This species prefers hilly areas, dense vegetation and monsoon forests. Males have short antlers with long burrs (16 cm beam with 3.9 cm brow tine; maximum size 24-27 cm (Schaller and Vrba 1996)) also they have tusks (1 inch long); females have knobs covered by tuft of hair. Males and females are almost the same size (body height 89-135 cm) with a body weight of 14-35 kg (female 24.5 kg and male 30-35kg, based on Schaller and Vrba 1996). Breeding has not been specified to one season. During rutting, their home range overlaps and males are not aggressive even during rutting period. They are solitary and are both diurnal and nocturnal. They breed all year around (Jackson 2002, Geist 1998). The small group consists of pairs or a female with young. Some studies showed no evidence of female territoriality or male exclusive range (Timmins et al. 2008c).

- *Muntiacus reevesi* (Reeves' muntjac, Chinese muntjac)

The Reeves' muntjac is distributed in temperate and tropical forests in the southwest of China and Taiwan. McCullough et al. (2000) mentioned that the average body weight in the male is 12 kg and 8 kg for the female (11.1 kg according to Schaller and Vrba 1996; 9.0–18.3 kg by Hemami et al. 2004). Females tend to be lighter in colour than males. Sexual dimorphism is significant in this species and they have antlers (12.5 to 15 cm; larger than 11 cm, Timmins et al. 1998) and also tusk-formed canines (1-2 inches long). They use their tusks for fighting instead of their antlers. They breed all year around so they have fast antler growth after shedding (Deuling 2004). The muntjac generally has large facial scent gland and it is mostly a diurnal solitary species (sometimes it has been seen in pairs or small groups), which chooses forest areas; therefore, no long visual signal or marking is beneficial in this species. The Reeves' muntjac uses olfactory marking for dominance and aggression, and scent marking is important in social communication but mutual conflicts are rare (Barrette 1977, Leason et al. 2008). The female is not territorial and home ranges are not overlapping with other females. But for the male, home range overlaps and they are territorial; at the centre of the home range overlapping is minimized (home range size is 17 hectares and 15 hectares for male and female, respectively, but in the McCullough study it was 14.3 and 6.2 ha) (McCullough et al. 2000).

- *Muntiacus putaoensis* (Leaf muntjac)

This species is reported from northern Myanmar and adjacent India. The Leaf muntjac probably chooses forest areas as other muntjacs do (Timmins et al. 2008d). This species is the smallest one among three sympatric species in Myanmar (*M. muntjak* and *M. crinifrons*). DNA sequencing showed that the leaf muntjac is a sister taxon to *M. truongsonensis* but they differ in colour of coat and tail. *Muntiacus putaoensis* as two other species, *M. truongsonensis* and *M. rooseveltorum* prefers old growth forests in mountain areas (Amato et al. 1999). The average antler tine of the male is 3.2 cm and there is no dimorphism in size and appearance among males and females (12.1 kg for males and 11.8 kg for females). Tusks exist in both sexes and the female in this species is more aggressive than other females in other muntjac species (Rabinowitz et al. 1999, Lovin the outdoors 2009).

- *Megamuntiacus vuquangensis* (Giant muntjac, Large-antlered muntjac)

The large-antlered muntjac is recorded from the Annamite mountain chain and associated hill ranges of Laos, Vietnam and, marginally, in eastern Cambodia. This species prefers evergreen and semi-evergreen forests but not hilly areas in recorded regions, and mostly lives under 1000 m of sea level (Timmins et al. 2008e). This species is larger than the Leaf muntjac, with more complex and larger antlers (about 17-28.5 cm long and brow tine 9.8 cm (Figure 26), larger than 18 cm mentioned by Timmins et al. 1998e) and lives in a wider area (the form of antler is curved up and out, and then gradually inward and slightly backward) (Rabinowitz et al. 1999, Dong 2007). It chooses old forests before secondary forests chosen by the red muntjac. Males have 3.4 cm long tusk-like canines. The average weight in females is 34 kg (Schaller and Vrba 1996). Males are larger than females (30 to 50 kg) with larger canine teeth and darker coat during the rutting time (Mico 2004, Schaller and Vrba 1996).



Figure 26: Adult giant muntjac with fawn antlers in velvet in captivity in Laksao, Laos (20 December 1994) Photographer: G.B Schaller

- *Muntiacus truongsoneis* (Annamite muntjac)

The range of the Annamite muntjac is Laos and Vietnam. Their habitat preference is evergreen forests above 1000 m sea level, and even forest-free areas. However, in Vietnam it has been observed beneath this level as well. This species is solitary and territorial and the ecology seems to be similar to that of other muntjac species (Timmins et al. 2008f). This species is smaller than *Muntjac muntjac* (15 kg). Pedicle and antlers are shorter and it lacks a brow tine (tine 20mm, pedicle 36.5 mm, 10.6 mm beam). Canines in the male are longer than in the female and is well developed (left canine is 31 mm in male and 23mm in female). The distribution of this species is restricted to old growth mountain wet evergreen forest in Annamite (Giao et al. 1998, Breitenbach 2011). Aseasonal breeding is recorded as in other species of this group (Breitenbach 2011).

- *Muntiacus rooseveltorum* (Roosevelt's barking deer)

This species is native to Laos but the distribution is unknown. In 1929, a few sub-adult males were collected for Kelley-Roosevelts Asiatic Expedition, which later on caused this specimen called to be Roosevelt's barking deer as a new species of muntjac (Amato et al. 1999,

Timmins et al. 2008g). Roosevelt's barking deer inhabits above 1000 m of sea level in evergreen forests. It seems to be solitary and territorial as other muntjacs (Timmins et al. 2008g).

- *Muntiacus puhoatensis* (Puhoat muntjac)

The range of this species is limited to the Pu Hoat area in the Que Phong District, Nghe An Province in Vietnam. The local habitat consists of evergreen forest with close canopy and specimens were found higher than 900 m (Timmins and Duckworth 2008b).

- *Muntiacus vaginalis* (Northern red muntjac)

This species is distributed widely from Sri Lanka, most of India, northern Pakistan, Nepal, Bhutan, Bangladesh and southern China, including Hainan and southern Tibet, and into Southeast Asia. It inhabits a variety of habitats, from grassland to dense evergreen forests, deciduous forests, from sea level to high-level mountains. The northern red muntjac can breed all around the year and in seasonal habitats, seasonality in breeding has been recorded. It is



Figure 27: *Muntiacus vaginalis* (Boddaert, 1785) - Northern red muntjac, male. Photographer: Klaus Rudloff . Germany, Tierpark Berlin  
<http://www.biolib.cz/IMG/GAL/BIG/174855.jpg>

solitary but has sometimes been observed in small groups consisting of pairs or females and fawns. It is nocturnal and diurnal depending on the area; and antler cyclic formation and shedding is still strong (Figure 27). They have a distinguished home range but are not territorial (Timmins et al. 2008h).

- *Muntiacus montanus* (Sumatran muntjac)

All specimens have been collected from above 1400 m and the local people distinguished two sympatric species, *M. muntjac* and *M. montanus*. One is smaller and darker with shorter antler than the other one. The ecology of this species seems to be similar to that of other muntjacs. There is no record of hunting for medical purpose or antler marketing (Timmins et al. 2008i).