



***DETECTION OF POLYMORPHISMS AND FECUNDITY
DETERMINATION IN *Axis axis* Erxleben, *Rusa timorensis* Blainville AND
Rusa unicolor Kerr RAISED IN LENGGONG, PERAK, MALAYSIA***

MUHAMMAD SANUSI YAHAYA

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By

MUHAMMAD SANUSI YAHAYA

**Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia,
in Fulfilment of the Requirements for the Degree of Doctor of Philosophy**

May 2020

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Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirement for the degree of Doctor of Philosophy

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May 2020

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In animal breeding and conservation programmes selection is usually based on fecundity traits. Selection methods such as the traditional marker-assisted selection, which is based on observable phenotypes and genomic selection, which uses genomic features for selection and it can be genome-wide scanning or the candidate gene approach are employed. These candidate genes are polymorphic and their polymorphism is associated with traits of interest. Polymorphisms in form of SNPs and RFLPs have been employed to select animals for breeding and or conservation. This study is therefore, aimed at discovering polymorphisms in the protein-coding region of five fecundity genes: BMP15, FOXL2, GDF9, MHCDQA1 and MTNR1A in *Axis axis* Erxleben, *Rusa timorensis* Blainville and *Rusa unicolor* Kerr reared at PTH Lenggong.

This study applied cytogenetic methods to detect morphological and numeric chromosomal aberrations in three breeds of deer comprising 60 individuals. Following the discovery of chromosomal aberrations, DNA was obtained from 45 individuals to amplify the protein coding regions of the fecundity genes, through high fidelity PCR. The genes were confirmed by mapping on metaphase chromosomes through Fluorescent *in situ* Hybridization (FISH). The PCR products were thereafter sequenced by Sanger's method. Following sequencing, a combination of Bioinformatic tools were used to detect SNPs and RFLPs in the fecundity genes. The genes were translated into proteins and analyzed for structure and function. Prediction programs and phylogenetic analysis were used to generate wild type proteins, which were used as templates to predict protein structure and the effect of amino acid substitutions on protein function.

Fifteen of the 60 animals were found to carry chromosome aberrations. High fidelity PCR produced 225 sequences, which were confirmed by FISH and used in the downstream analysis. A total of 117 SNPs and 13 restriction sites with utility in animal selection were discovered in the protein coding regions of the fecundity genes through scan. After protein translation 19 variants were discovered; 3 in BMP15, 4 in FOXL2, 2 in GDF9, 3 in MHCDQA1 and 7 in MTNR1A. 11 of the variants carry neutral substitution and are therefore predicted to be functional. Based on the protein analysis 10 out of the 45 animals; TP27F, TF375, TP14F, TN60M, SJ4M, AX1, AX4F, AX3F, AX6F, AX7F were predicted to carry a combination of functional fecundity proteins.

A large number of animals within the study population carry chromosomal aberration. Significant genetic diversity exists in the study population and some animals carry defective fecundity protein variants. The presence of chromosomal anomaly and protein polymorphisms, with some variant predicted to carry deleterious amino acid substitutions, may be one of the reasons for fertility decline in the study population. There is evidence of hybridization between *R. timorensis* Blainville and *R. unicolor* Kerr. *Axis axis* Erxleben is likely to have undergone inbreeding and allele fixation. It is concluded that the type of husbandry practiced in PTH Lenggong, Perak, where animals of different breeds are kept together, and the absence of a well-designed breeding program for the deer, might be responsible for these fertility problems.

Keywords: Cytogenetics, Chromosomal aberration, Deer, Fecundity, Fertility decline, Protein prediction

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

**PENGESANAN KELAINAN KROMOSOM DAN POLIMORFISME DALAM
SEGMENT PENGKODAN PROTEIN DARIPADA LIMA GEN KESUBURAN
DALAM *Axis axis* Erxleben, *Rusa timorensis* Blainville dan *Rusa unicolor* Kerr
DI LENGGONG, PERAK, MALAYSIA**

Oleh

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Dalam program untuk pembiakan dan pemuliharaan haiwan, secara lazimnya pemilihan adalah berdasarkan ciri-ciri kesuburan. Kaedah pemilihan seperti pemilihan tradisi berbantu penanda berasaskan ciri fenotip dan pemilihan genomik berasaskan imbasan sebaran genom atau pendekatan gen calon telah digunakan. Calon gen ini adalah polimorfik dan polimorfismenya berkait dengan ciri yang berkepentingan. Polimorfisme dalam bentuk SNP dan RFLP telah digunakan untuk memilih haiwan untuk tujuan pembiakan dan pemuliharaan. Dari itu kajian ini menumpu kepada pencarian polimorfisme dalam bahagian pengkodan protein untuk 5 gen kesuburan: BMP15, FOXL2, GDF9, MHCDQA1 dan MTNR1A dalam kumpulan rusa baka-baka *Axis axis* Erxleben, *Rusa timorensis* Blainville dan *Rusa unicolor* Kerr yang dipelihara di PTH Lenggong.

Kajian ini menggunakan kaedah sitogenetik untuk mengesan kecacatan morfologi dan kromosom numerik dalam 3 jenis baka rusa yang terdiri daripada 60 individu. Berikutan terdapatnya kecacatan kromosom, DNA telah diperolehi daripada 45 individu untuk meluaskan bahagian pengkodan protein bagi gen kesuburan dengan menggunakan PCR berketepatan tinggi. Gen ditentukan secara pemetaan kromosom metafasa melalui *Fluorescent in situ Hybridization* (FISH). Produk PCR kemudiannya disusun mengikut kaedah Sanger. Dengan menggunakan sekumpulan peralatan Bioinformatik, SNP dan RFLP untuk gen kesuburan telah dikenal pasti. Gen kemudiannya diterjemahkan kepada protein untuk analisis struktur dan fungsi. Program ramalan dan analisis filogenetik digunakan untuk menghasilkan protein bentuk liar yang dijadikan templat untuk meramalkan struktur protein dan kesan penggantian asid amino terhadap fungsi protein.

Sebanyak 15 daripada 60 individu didapati membawa kecacatan kromosom. PCR berketepatan tinggi menghasilkan 225 susunan yang disahkan secara FISH dan digunakan dalam analisis aliran. Dengan menggunakan teknik imbasan, 117 SNP dan 13 tapak sekatan yang berguna untuk pemilihan haiwan dalam bahagian pengekodan protein bagi gen kesuburan telah ditemui. Selepas penterjemahan protein, 19 varian ditemui: 3 dalam BMP15, 4 dalam FOXL2, 2 dalam GDF9, 3 dalam MHCDQA1 dan 7 dalam MTNR1A. Sejumlah 11 varian membawa penggantian neutral, dari itu diramalkan berfungsi. Analisis protein mendapati 10 daripada 45 individu: TP27F, TF375, TP14F, TN60M, SJ4M, AX1, AX3F, AX4F, AX6F dan AX7F diramalkan membawa satu kombinasi protein kesuburan yang berfungsi.

Sejumlah besar individu dalam kumpulan yang dikaji membawa kecacatan kromosom. Terdapat wujudnya kepelbagaian genetik yang signifikan dalam kumpulan kajian ini dan sebahagian individu membawa varian terencat bagi protein kesuburan. Kehadiran anomali kromosom dan polimorfisme protein dengan beberapa varian diramalkan membawa penggantian asid amino mungkin menyebabkan penurunan tahap kesuburan dalam kumpulan kajian ini. Terdapat bukti berlakunya hibridisasi di antara *Rusa timorensis Blainville* dan *Rusa unicolor Kerr*. *Axis axis Erxleben* berkemungkinan juga telah melalui pembiakan dalaman dan pengekalan allele. Kesimpulannya, masalah kesuburan dalam kumpulan rusa di PTH Lenggong, Perak boleh dikaitkan dengan amalan menempatkan haiwan pelbagai baka dalam satu kumpulan dan tidak mengamalkan program pembiakan haiwan yang teratur.

Kata kunci: Sitogenetik, kecacatan kromosom, Rusa, kesuburan, masalah kesuburan, ramalan protein

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This thesis was submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfilment of the requirement for the degree of Doctor of Philosophy. The members of the Supervisory Committee were as follows:

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LIST OF ABBREVIATIONS

AF	Agitation Frequency
BCIP	5-bromo-4-chloro-3-indolyl-phosphate
BLAST	Basic Local Alignment Search Tool
BMP	Bone Morphogenetic Proteins
CCI	Calving-conception interval
CNV	Copy number variations
CCD	Charge-coupled Device
CGH	Comparative Genomic Hybridization
CM	Culture Medium
CI	Centromeric index
DOP-PCR	Degenerate Oligonucleotide Primed PCR
DKCL	Duration of cells in KCL
DAPI	4',6-diamidino-2-phenylindole
ExPASy	Expert Protein Analysis System
FISH	Fluorescent <i>in situ</i> hybridization
FPG	Fluorochrome-Photolysis Giemsa
FBS	Fetal Bovine Serum
GDF	Growth Differentiation Factors
ISH	<i>in situ</i> hybridization
KCl	Potassium chloride
MEGA	Molecular Evolutionary Genetics Analysis
MHCDQA	Major Histocompatibility Complex DQ Alpha
MTNR1A	Melatonin Receptor 1A

NOR	Nucleolar Organizer Region
NBT	Nitro Blue Tetrazolium
OECD	Organization for Economic Co-operation and Development
PBMC	Peripheral Blood Mononuclear Cells
PGD	Preimplantation genetic diagnosis
QTL	Quantitative Trait Loci
PRINS	Primed <i>in situ</i> DNA
ProtParam	Protein Parameters tool
PROVEAN	Protein Variation Effect Analyzer
RFLP	Restriction Fragment Length Polymorphisms
SNP	Single Nucleotide Polymorphisms
STELA	Single Telomere Lengths
SMS	Sequence Manipulation Suite
SIFT	Sorting the intolerant from tolerant
TGF-beta	Transforming Growth Factor Beta
TL	Total Chromosome Length

CHAPTER 1

INTRODUCTION

1.1 Background of the study

Fecundity traits are an important selection requirement for animal breeding and conservation programmes. Animals, which are prolific and adaptive to environmental conditions, are desirable, as they fit the objective of many of such production systems. To select animals for breeding a number of selection methods are employed; these methods include the traditional marker-assisted selection, which is based on observable phenotypes and genomic selection, which uses genomic features for selection (Meuwissen, Hayes, & Goddard, 2016) and it can either be genome-wide scanning or the candidate gene approach. The latter is largely considered today because of its reliability and shorter time requirement. Selection based on candidate genes is a molecular-marker-assisted selection that has gained acceptance and is widely used among breeders and researchers (Meuwissen *et al.*, 2016)

Loss of fecundity is a serious issue that must be addressed immediately whenever it is reported in livestock production centers. It often results in immeasurable economic losses to the livestock industry (Lee & Kim, 2007). To address loss of fecundity in livestock, adequate supporting tools such as fertility and fitness data are used. Fertility data include non-return rate, calving-conception interval (CCI), calving-to-first service interval, conception (pregnancy) rate, heat detection assessment, In-calf rate. Other composite measures include; fertility factor, FERTEX score and fertility index and data on fitness such as disease resistance and so on (Buaban *et al.*, 2015). The application of these data to propagate animals has played a pivotal role in the animal industry through both traditional and molecular animal selection methods (Matoušek, 1986). The advancement in molecular methods along with phenotypic records has contributed to genomic data for more accurate and rapid propagation of animal genetic resources. Currently, without fertility data it is almost impossible to attempt fertility assessment and its improvement (Nani *et al.*, 2019).

Generally, genetic evaluation starts by the analysis of phenotypes to identify genetic influences, while molecular genetics usually begins with known alleles or DNA sequences and later analyze their influence on phenotypes (Rexroad *et al.*, 2019).

The identification of genome regions and genes related to important phenotypic traits allows for selecting animals based on genetic markers that are linked with such traits. These genetic markers include genes or DNA sequences with observable variations, known as polymorphisms, among members of animal groups (Rexroad *et al.*, 2019).

Genetic polymorphisms in the form of Chromosomal polymorphisms, Copy number variations (CNVs), mini and microsatellites, Restriction Fragment Length Polymorphisms (RFLPs), Single Nucleotide Polymorphisms (SNPs), and other forms of variations within DNA sequences have been used as markers in population and evolutionary genetics (Bauduer et al, 2009), systematics, molecular phylogeny and agricultural genetics (Spiridonova et al, 2017). They have afforded scientists the ability to tag genes and other pieces of DNA through multiple alleles at individual loci. Polymorphisms have been used in areas from genotype investigations; mapping of quantitative loci affecting economic traits in animals and plants; mapping of disease genes; and evolutionary comparisons of DNA sequences to chromosome organizations between related species (Borowski *et al.*, 2016; Carranza *et al.*, 2016). Genes with such variations are known as candidate genes.

Candidate genes are sequenced genes and genetic variations with known biological pathway that are involved in the physiology or development of traits of interest. Biological understanding of the role of the product of the wild-type of these genes forms the basis for their selection as candidate gene (Katzeff *et al.*, 2019). Those candidate genes with distinct role in reproduction and survival are referred to as fecundity genes (Abdoli *et al.*, 2016). Mutation in these genes can sometimes affect the intensity of their effects. This could be lower or higher than the effects of the wild-type version of the genes (Slota *et al.*, 2016). The FecX gene, for example, was found to increase ovulation rate by up to 1.0 in some heterozygous animals but homozygous ones were found to be sterile (Nicol *et al.*, 2009). Other genes related to fecundity, which have the same implications, are members of the Transforming Growth Factor Beta (TGF-beta) superfamily, particularly Bone Morphogenetic Proteins (BMPs), Growth Differentiation Factors (GDFs) (Nicol *et al.*, 2009) and most of these work was done on cattle, sheep, goat and swine (Han *et al.*, 2015a). Others are the melatonin receptor1 A (Yang *et al.*, 2014) and forkhead box (FOXL2) genes (Krepelova *et al.*, 2016). Identification and utilization of these genes is well described in the animal industry (Davis, 2004).

However, some animals suffer from a paucity of genetic and fertility data such as genome wide sequences and polymorphism data, and breeding record which severely limits the implementation of genomic approaches for addressing biological question in these species (Sabury *et al.*, 2011). One of the understudied species in this regard is the deer, which is a widely distributed ruminant species of the order *Artiodactyla* and family *Cervidae* (Solari & Baker, 2007). The *R. timorensis* Blainville, *R. unicolor* Kerr and *Axis axis* Erxleben fall within the category of understudied deer breeds (Zakaria *et al.*, 2016)

In the last few decades Malaysia has witnessed changes in deer farming, where the species has become popular as a source of protein in the livestock industry with immense potential for both local consumption and export capacity (Fitri *et al.*, 2017). To maintain this capacity, deer has been imported into the country from a number of different countries (El-Jaafari, Panandam, Idris, & Siraj, 2008) and kept together, breeding freely, exposing the animals to the risk of genetic mixture, introgression and

possible loss of some desirable, adaptive traits (Berthouly-Salazar *et al.*, 2012; El-Jaafari *et al.*, 2008). The conflict between the desire to use wild animals both as sources of animal protein and conserve them as wild game animals limits the ability of some deer farms to maintain useful fertility record, thereby affecting the development of the deer industry in the country. Consequently, the deer in Malaysia receives less attention, regarding research interest, compared to cattle, buffaloes and small ruminants in terms of efforts geared towards fertility improvement and genetic conservation. There are reports of dramatic and progressive loss of fertility in the Malaysian deer, particularly the *Axis axis Erxleben*, *Cervus nippon*, *Rusa timorensis Blainville* and *Rusa. unicolor*. Although some of these reports have been (El-Jaafari *et al.*, 2008; Zakaria *et al.*, 2016), most of them remain with farmers who keep grappling with the problems (Lee, 2014). The aim of any breeding program is to improve the potential of animals for maximum fecundity, which can be achieved by improving the genetic worth of the stock through methods that ensure proper selection (Rauw & Gomez-Raya, 2015). As it is difficult to measure fecundity because of paucity of adequate supporting tools, such as genomic and fertility data, in these farms, indirect methods through cytogenetics and molecular characterization of their fecundity genes may generate useful information for the improvement of animals in this category.

1.2 Statement of research problem

As the world's population continues to grow exponentially, the demand for animal protein has become more intense. This requires 1) efforts to improve strategies in livestock breeding by exploring faster and more efficient ways of propagating animals. 2) breeding of nonconventional livestock (Thornton, 2010). Deer is one of such animals currently farmed in many countries including Malaysia. Several farms were set up to serve as nucleus for the production and distribution of deer stock to smallholder farms across the country (El-Jaafari *et al.*, 2008). One of such farms is the Pusat Ternakan Haiwan (PTH) Lenggong. Many of these nucleus farms are grappling with fertility issues in the deer. Ordinarily with the current advancement in the area of animal breeding, especially the molecular genetics component, increasing such animal resources through existing selection methods should be rapid to address such fertility problems. For example, Restriction Length Fragment Polymorphisms (RFLPs) and Single nucleotide polymorphisms (SNPs) are important genetic markers, which in combination with onsite fecundity record can be used for animal improvement (Rexroad *et al.*, 2019). The utilization of SNPs as genetic makers for selection is quite mature in animals with abundant genomic data (model animals). Development of SNP panel, for identification of polymorphic sites, requires the comparison of large amount of DNA sequence data across multiple individuals (Haynes & Latch, 2012a). In model animals such as cattle, the availability of such data through genomic sequencing programmes has made possible the production and application of large SNP chip containing more than 50,000 markers. Unfortunately, other non-model animals do not possess large amount of genomic data to facilitate such development (BIXLEY, 2009). Another important issue is that of lack of comprehensive fertility record on some animal facilities (Zakaria *et al.*, 2016). Therefore, even when polymorphisms data become available there is need for

phenotype data to associate with the polymorphisms. Determination of fecundity status through candidate gene analysis, using computational methods will reduce this bottleneck and provide a viable alternative in reproduction studies.

1.3 Justification

Loss of fertility in the deer across Malaysia is militating against the deer industry by causing immeasurable economic losses. The husbandry practice of allowing semi domesticated animals of different breeds, or even species living together that were allowed to interbreed complicates the problem. The problem resulted in lack of proper farm record, such as fertility record on these farms. These coupled with the general lack sufficient genomic data in *A. axis Erxleben*, *R. timorensis Blainville* and *R. unicolor Kerr* in the public domain limit the application of high-end genomic method such as SNP chips for genotyping to investigate fecundity issues in these breeds. Additionally, *A. axis Erxleben*, *R. timorensis Blainville* and *R. unicolor Kerr* are currently designated as vulnerable by the IUCN (Hedges, Duckworth, Timmins, Semiadi, & Dryden, 2015). Bone Morphogenetic Protein 15 (BMP15) gene, Growth Differentiation Factor 9 (GDF9) gene, Forkhead protein (FOXL2) gene, Major Histocompatibility Complex DQ Alpha (MHCDQA) and Melatonin Receptor 1A (MTNR1A) gene are fecundity genes that are well characterized in animals (Abdolahi & Shokrollahi, 2019) (Snibson *et al.*, 1998). They are known to be directly involved in fecundity. Polymorphisms in these genes in the form of both Single Nucleotide Polymorphisms (SNPs) and Restriction Fragment Length (RFLPs) have been associated with fecundity in animals. Likewise, protein variations within them have been associated with fecundity; such that individuals who carry defective variants of the proteins were infertile. Cytogenetic investigation coupled with the study of these fecundity genes can provide insight into the fecundity problems involving these animals.

Molecular computational methods can scan these genes for polymorphisms and their proteins for variations as well as predict the effects of the variants on the fecundity of individuals. Combining cytogenetic and molecular computational resources to determine the fecundity status of these animals will shed light into future reproduction studies as well as make available a wealth of polymorphism data for future use in animal selection.

1.4 Research hypotheses

Cytogenetics and computational analysis of five fecundity genes; Bone Morphogenetic Protein 15 (BMP15), Growth Differentiation Factor 9 (GDF9), Forkhead Box L 2 (FOXL2), Melatonin Receptor 1A (MTNR1A) and Major Histocompatibility complex- DQAlpha (MHC-DQA) can be used to determine the fecundity status of three breeds of deer that are currently housed at PTH Lenggong.

1.5 Aim of the study

To determine the chromosomal and genetic polymorphisms, utilize the data to determine the fecundity status and to predict which animals are suitable for use in breeding in *Axis axis Erxleben*, *Rusa timorensis Blainville* and *Rusa unicolor Kerr* reared in Perak, Malaysia

1.6 Research objectives

The specific objective of this research are:

- i. To determine the karyotypes of three breeds of deer (*R. timorensis Blainville*, *R. unicolor Kerr* and *Axis axis Erxleben*) in Lenggong, Perak
- ii. To identify five fecundity genes (*BMP15*, *FOXL2*, *GDF9*, *MHCDQA* and *MTNRIA*) in deer through PCR
- iii. To confirm congruence and complementarity between the PCR products and the in situ genes through FISH in three breeds of deer in Lenggong, Perak
- iv. To determine Single Nucleotide Polymorphisms (SNPs) and Restriction Fragment Length Polymorphisms (RFLPs) in the fecundity genes of three breeds of deer in Lenggong,, Perak
- v. To predict the proteins encoded by (*BMP15*, *FOXL2*, *GDF9*, *MHCDQA* and *MTNRIA*) genes, their variants and functional status in three breeds of deer in Lenggong, Perak

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