Impacts of nutrition on reproduction in female red deer (*Cervus elaphus*)

Phenotypic flexibility within a photoperiod-mediated cycle

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Red deer genotypes/subspecies

Scottish red deer
\((C.\textit{e}.\textit{scoticus})\)

North American Wapiti
\((C.\textit{e}.\textit{nelsoni})\)

Eastern European red deer
\((C.\textit{e}.\textit{hippelaphus})\)

Composites (crossbreeds)
Taxonomy... damn Taxonomy!

- There is much debate about the taxonomic status of Red deer/Wapiti.
- While I have, throughout this talk, referred to them as sub-species of *Cervus elaphus* (after Whitehead 1993), current view seems to be that Red deer and Wapiti are separate species.
- It is not the purpose of this talk to engage into a big debate around this ... taxonomy is a ‘man-made’ construct that follows often contradictory rules.
- For the purposes of this talk, it is acknowledged that that the various geographical genotypes freely interbreed, and the resulting progeny are fully fertile...no amount of taxonomic debate changes that fact.
- But I am respectful of other peoples considerations around nomenclature.
Farming red deer in NZ

- Started in 1970s following on from over-harvest of feral herds
- Mainly based on ‘scoticus’ foundation stock from the wild
- Introgression of Wapiti (C.e.nelsoni, roosevelti, manitobensis) and Eastern European red deer (C.e. hippelaphus, pannonensis) (1980s and 1990s)
- Most animals are ‘composites’ (crossbreeds)
- Venison production (>50% of worlds traded production)
- Velvet antler (>30% of worlds traded production)
- 1-1.2 million farmed red deer in New Zealand
- Focus of considerable research investment over last 35 years
- Reproductive productivity of hinds has featured strongly in research
Seasonal breeding

- Red deer are strongly entrained by prevailing photoperiod to maintain synchronised conceptions in autumn and birth in summer
- Adaptation to cold temperate (continental) climates to ensure neonate survival and optimum growth before the onset of first winter
- Transference across the equator results in simple 6-month phase shift
- New Zealand climate is considerably more moderate but still highly variable weather patterns...some mal-adaptation to austral environment
- Principally a misalignment between lactation and peak feed supply in lowland environments
- Research to understand drivers of seasonality...as well as genetic and phenotypic variation in seasonal onsets of annual breeding
Photoperiodism and gestation length

- Photoperiod ‘entrains’ endogenous circannual cycles by synchronising the mating season (i.e. timing of conceptions) of red deer around the autumn equinox (often referred to as ‘The Rut’)
- Most cervid species perceive photoperiod cues, but respond according evolutionary pressures for optimum birth timing
- Even tropical species generally retain vestiges of photoperiodism, but maybe only expressed when translocated to non-tropical environments
- Gestation length varies between species according to the time required to produce a viable neonate...positively correlated with mature body-mass
- Combination of conception date + gestation length determines birth timing
- Current dogma: these traits are ‘genetically-fixed’ traits for each species

Question: what levels of genotypic and phenotypic variation exist and why?
Subtle genetic variation: conception date

- Because *Cervus elaphus* occupies a geographical cline from Western Europe to North America, it would be reasonable to expect some sub-species variation in breeding seasonality.

- Observed difference in conception date and birth date of about 2 weeks between *scoticus* and *hippelaphus* on NZ deer farms, largely driven by conception date.

- Genetic variation amongst composites (*scoticus x hippelaphus*):
  - Standard Deviation = 7.9 days
  - Repeatability between years = 0.29 +/- 0.03
  - Heritability = 0.20 +/- 0.03

- Genetic selection (DEERSelect) for earlier conception date
- Average genetic gain 1.5 days over 10 years

DEERSelect genetics gain graph
Non-genetic (environmental) effects on the phenotype

Focus of this talk is on environmental (mainly nutritional) influences on reproductive seasonality and annual reproductive success in female red deer.

- **Conception date** (proxy for onset of ovulatory activity)
- **Gestation length** (interval from conception to birth)
- **Onset of puberty** (first conception as a proxy for pubertal ovulation)

It is my contention that environmentally-mediated variation in the expression of these traits hints at the adaptability of this species when confronted with seasonal but climatically variable environments.
The Toolkit....part 1

Body mass (live-weight)
- Most deer farms have facilities for weighing deer
- Principally used when assessing growth performance and as a predictor of pubertal success for rising-2-year-old (R2) hinds

Body Condition Score (BCS)
- Visual and palpation score (1-5 in half-score increments) to assess changes in muscularity (1-2) and subcutaneous body fatness (2.5-5) in mature hinds
- Not particularly useful in R2 hinds (body mass a more sensitive tool)
- Observer bias +/- 0.5 BCS units, but calibration between observers commonly applied
- Wide adoption by sheep, beef and deer farmers in NZ
- A change in 1.0 BCS units = 10kg body mass for adult hinds

Feed intake and lactation outputs
- Some studies have utilised individually-penned deer to measure daily DMI
- More often have utilised either group pasture DM allocation or the ‘alkane’ method at pasture
- Milk yield studies undertaken to assess energy inputs/calf outputs
The Toolkit...part 2

Ultrasonographic pregnancy diagnosis and fetal ageing

- Pregnancy diagnosis by ultrasound is one of the most widely adopted technologies by deer farmers
- Fetal ageing is a proxy for conception date, based on back-calculation of fetal age from date of scan
- Real-time ultrasonography to visualise fetal morphology and dimensions to establish fetal age +/- 5 days
- Applicable between Days 25 and 80 from conception...easily calibrated
- Routinely used by stud breeders on DEERSelect to assign conception date/birth date

X-ray computed tomography (CT-Scan)

- For detailed assessment of tissue accretion in young (muscle) and adult (fat) red deer, as well as fetal growth

DNA- based parentage and composite breed-type assessment

- Genotyping by Sequencing (GBS) platform has a suite of 75-80K SNPs used for parentage and breed type in red deer
- Very high level of adoption by stud breeders (greater than for sheep and cattle breeders in NZ)
Conception date phenotype

- Lactation is of high nutritional cost to the hind
- Energy expenditure over summer influences body mass and body fat reserves by the start of the breeding season
- Many principles of the influence of nutrition on reproductive success in Scottish red deer established from classical studies on the Isle of Rhum (Clutton-Brock et al. 1982)
- Rhum represents a fairly extreme environment for Red deer
- Excessive energy demands of lactation can ablate or modify the timing of ovulation and conception
- Even calf sex can influence reproductive performance of their dams
- Male calves born heavier, suckle longer and more frequently...dams more likely to fail to produce a calf the following year
The NZ context

- Calves generally weaned from their dams in late Feb/early March (pre-rut)
- Post-lactation/pre-mating BCS of the hind is very strongly influenced by the nutritional environment over the summer lactation
- Very low BCS (i.e. < 1.5) represents extreme cachexia involving muscle catabolism...usually associated with complete reproductive failure (anovulation).
- BCS 1.5-2.5 represents extreme leanness (low body fat), with a high probability of either anovulation or delayed conception
- Thereafter, between BCS 3.0-4.5+, incremental increases in BCS are associated with increasingly earlier onset of ovulation and conception.
- Effects of lactation seem to be invariably mediated via BCS (evidence for a direct hormonal effect is equivocal)
Lactating vs non-lactating

- Effects of pre-rut vs. post-rut weaning of calves on hind conception date profiles studied by Pollard et al. (2002)
- 10 farms across two years in which hind-calf pairs were weaned in either early March (pre-rut) or late June (post-rut)
- Calves weaned early gained less weight over autumn
- But mean conception dates of their dams were earlier by 12 days in Year 1 and 7 days in Year 2
- This effect could be fully accounted for in differences in hind BCS between the two groups by late March/early April (main period of matings)
- Early weaned hinds had gained an average of 0.5 BCS units between weaning and mating (a period of about 2-3 weeks)
- This result has been repeated many times across deer farms in NZ
Pre-calving BCS phenotype...influence of lactation outputs

- The impacts of lactation on hind BCS is not only determined by nutrition during lactation, but also ‘entry level’ BCS (i.e. fat reserves in late pregnancy)

- Stevens et. al.(2017) used 2x2 crossover design to investigate High vs. Low BCS pre-calving relative to High vs. Low pasture covers (e.i. level of nutrition) over lactation

- High BCS entering into lactation can buffer against severe impacts of low nutritional status during lactation by up to 6 weeks

- High nutritional status over lactation can be associated with improved hind BCS despite the energetic demands of raising calves
Gestation length phenotype

- Cervid species have gestation lengths (GLs) ranging from 200-280 days; loosely correlated with mature body mass
- Often considered to be genetically programmed and inflexible
  - European Red deer......233-234 days average
  - North American Wapiti...245-250 days average
- Fetal genotype exerts some effect (e.g. Wapiti x European Red deer fetus in Red deer hind)
- However, it is now apparent that GL within red deer subspecies is more variable than previously considered
- Strongly influenced by environmental factors occurring before and during pregnancy
Impacts of late gestational feeding....

Asher et al. (2005) observed a marked effect of level of dam nutrition between Days 150 and 220 of pregnancy (‘third trimester’)
- Overall variation: range of 27 days
- Low nutrition to hinds resulted in longer gestations
- High nutrition to hinds resulted in shorter gestations
- No effect on calf birth weight

Garcia et al. (2006) also noted extremely wide variation of GL related to timing of conception
- Early conceiving hinds (artificially induced by 68 days) had longer GLs
- Later conceiving hinds (naturally mated) had shorter GLs
- However, early conceiving hinds exhibited lower body mass gains over late pregnancy...indicating a possible nutritional effect
Impacts of late gestational feeding...

- Scott et al. (2008) showed that for every 10 days difference in conception date there was a change in GL of 1.9-4.9 days.

- Initially described as a putative ‘push/pull’ control of gestation length to promote within herd birthing synchrony in the face of phenotypic variation in conception date.

- Later studies by Scott et al. (2015) tested the hypothesis that the negative association between GL and conception date is mediated by late gestational nutrition.

- Early and Late mated hinds on High or Low nutrition in later half of pregnancy.

- CT-Scans of conceptus (fetus and uterus) on Days 120, 150, 180 and 210 of gestation.

- Over-riding conclusion: GL negatively associated with hind feed intake and hind live-weight gain during final trimester of pregnancy. Nutrition influences rates of fetal development...this may be the key to GL variability.
Hypotheses

(1) Under conditions of modest feed imbalance during the later half of pregnancy, variation in gestation length compensates for variation in fetal growth trajectory to ensure optimisation of birth weight

- Some contradictions: Severe nutritional restrictions in Red deer (Rhum) and Wapiti (Oregon) resulted in low birth weight...there may be limits to the compensatory mechanisms

- Fallow deer show very little variation in GL, and under-nutrition of the pregnant doe invariably leads to low birth weights and high fawn mortality...hypothesis is not universal to all deer species

- However, GL variability has been observed for reindeer and sika deer

(2) Induction of parturition is driven by the fetus, being dependant on attainment of a specific fetal mass/maturity to initiate parturition

- This is supported by the measured variance in fetal growth trajectory (CT-Scan) and the low variance in birth weight in Red deer...but not necessarily supported from studies on Fallow deer
Puberty in Red deer hinds

- Puberty in hinds is defined as the time of their first viable ovulation.
- Normally occurs during second autumn of life (~16 months of age).
- However, entry into puberty is constrained by photoperiod and by body mass.
- Hinds in nutritionally deprived environments often delay puberty until their third or fourth autumn (e.g. Rhum).
- Reproductive performance of rising-2-year-old (R2) Red deer hinds on NZ deer farms has often fallen below expectations.
- Observed as highly variable pregnancy rates at Ultrasound scanning at 18-20 months of age...but clearly relates to anovulation.
- Pregnancy attainment is a proxy for anovulation.
- Low pubertal performance has incentivised considerable research investment over the last 15 years.
Permissive Body Mass Threshold (PBMT) for onset of puberty in hinds
Genotype influences on PBMT

(a) 100% Scottish
(b) 50:50 % Scottish x Eastern
(c) 100% Eastern
(d) 30% Wapiti
(e) 50% Wapiti
(f) 100% Wapiti
Early-growth influences on PBMT

- Monitoring of reproductive outcomes of >24,000 R2 hinds has reveal substantial year and farm variation in PBMT for given genotypes
- Example shown is a single large deer farm...Stud herd always showed a lower PBMT than the Commercial herd
- Genetic influence not likely to be main contributor...only one generation removed from Commercial herd
- Most likely explanation was the higher nutritional investment in more valuable Stud stock
- Considerable annual variation in PBMT in Commercial herd
- This hints at an early-life effect on the PBMT set-point
Hypothesis

The nutritional environment in early life influences the PBMT set-point, favouring a lower set-point for nutritionally advantaged individuals

- Investigated the cohort datasets (total of 6158 individuals) using weaning (3-month) live-weight as an indicator of early-life growth/nutrition
- Significant regressions between weaning weight and % pregnant at specified pre-joining live-weights of 60, 70 and 80 kg...but no effect >90kg.
- Higher cohort average weaning weight was associated with lower PBMT set-point
- Early-life environment is a predictor of the life-time environment
The ‘Environmental Stressor’ hypothesis

- Study supports the central hypothesis of early-life influences on the PBMT
- Conceptual model of an ‘environmental stressor’ effect
- Early-life somatic growth is very influential on reproductive processes and/or success in Red deer
- Mechanism behind this remain to be elucidated but our current hypothesis is the PBMT set-points are determined by rates of body lipid accumulation relative to overall body mass
- Adaptive strategy for favouring life-time performance over early puberty under adverse environmental conditions
Social facilitation effects

- ‘Social facilitation’ refers to environmental influences on reproductive phenotypes mediated by pheromonal, visual and auditory stimuli between conspecific individuals.
- Classic examples are ‘The Ram Effect’ in sheep...or...the ‘Boarding House Effect’ in humans.
- Limited, and contestable, demonstration of such effects in red deer.
- Moore & Cowie (1986) report on an oestrus induction effect of joining hinds with stags before the normal onset of ovulatory cycles... ’The Stag Effect’.
- McComb (1987) showed that hinds exposed to ‘roaring’ vocalisations of stags calved earlier than a control group.
- ‘The Stag Effect’ has seldom been replicated, possibly because of multiple uncontrollable and confounding variables.
Conclusions

For Red deer and Wapiti, the annual seasonal reproductive cycle is undeniably entrained by endogenous responses to prevailing photoperiod, with a small but heritable genetic variation.

However, for this species, environmentally mediated variation of the phenotype for certain reproductive traits can influence the actual birthing season by 2-4 weeks.

Arguably, the two most variable expressions of phenotype centre around conception date (reflecting onset of ovulatory activity) and gestation length, both of which appear to reflect the nutritional environment encountered by the hind at various points of the annual breeding cycle.

There is also the intriguing likelihood the early-life nutritional environments can determine set-points for attainment of reproductive events (e.g. hind puberty)...influencing survival and lifetime reproductive outputs.

Such phenotypic variation hints at a strong adaptive mechanism in a species that has successfully colonised new environments far removed from their ancestral range (e.g. NZ, Argentina, Australia).
Thank you