Selection limits in dairy cattle

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Dairy cattle is a unique example of genetic selection

• Long-time data accumulation in U.S. dairy cattle
  – Data collection started in 1895
  – National genetic evaluation started in 1936
  – Over 87 million observations for current genetic evaluation

• Large sample increases accuracy of genetic selection

• Long-term selection provides practical understanding of selection limits
Selection limit

• Definition

Selection response ceased or reached a plateau
(Falconer and Mackay, 1996; Hartl and Clark, 1997)

• Reasons for selection limit
  – Gene fixation: good allele fixed, or bad allele eliminated
  – Genetic variation exhausted
  – Genetic variation still exists but plateau reached
    (reverse selection still has response)
Objective

• Explore dairy selection limits through analyzing USDA long-term dairy selection data
  – Observed and predicted milk yield increases
  – Observed and predicted maximum milk yields

• Genetic potential for future improvements
  – Observed frequencies of alleles with milk effects as indirect evidence of distance from gene fixation or selection limits
  – Multi-trait selection for profitability
Methods

• USDA long-term dairy selection data: 1957-2015
  – 87,729,358 Holstein observations milk yield
  – Unadjusted average milk yield:
    Average across ages and lactations
  – Adjusted milk yield:
    305-day lactation, 2X milking, 36 months of age

• Genetic potential for future selection response
  – GWAS estimates of positive allelic effects for milk yield using 294,079 first lactation cows
  – Allele frequencies of the positive alleles to estimate departure from fixation
Observed average milk yield of 58 years, 1957-2015
Predicted average milk yield of 60 years, 2018-2077

\[ y = 122.91x - 235136 \]
\[ R^2 = 0.989 \]

Average milk yield (kg, y)
Year (x)

- Observed average milk yield of 58 years, 1957-2015
- Predicted average milk yield of 60 years, 2018-2077
- 1957-2015: +7.1 tons in 58 years
- 2018-2077: +7.4 tons in 60 years

University of Minnesota
Adjusted milk yield for 305 day, 2X milking, 36 months old

\[ y = 111.46x - 213232 \]

\[ R^2 = 0.9888 \]

Average adjusted milk yield (kg, y)

Year (x)

5000 7000 9000 11000 13000 15000 17000 19000

1957 1977 1997 2017 2037 2057 2077

6988 9865 11150 18270

11582

13812

16041

18270

1957-2015 +6.1 tons in 58 years

2018-2077 +6.5 tons in 60 years
Summary of average milk yields

• 58 years of genetic selection during 1957-2015
  – Average 11.1-12.5 tons in 2015 per cow
  – 7.1 tons increase in unadjusted average milk yield
  – 122kg increase per year in unadjusted average
  – 6.1 tons increase in adjusted average milk yield
  – 112kg increase per year per cow in adjusted average

• 60 years of predicted annual average milk yield by 2077
  – 20 tons per cow, unadjusted average (+7.4 tons)
    • 5091 observations already reached or exceeded this level
  – 18 tons per cow, adjusted average (+6.5 tons)
    • 2260 observations already reached or exceeded this level
Maximum annual milk yields

- **Internet info**
  - 35 tons
  - 25 tons
  - 20 tons in 60 years

- **University of Minnesota**
  - 35 tons
  - 25 tons
  - 20 tons

- Maximum in 1957 took 60 years to become average
  - 12773
  - 12724

- Average milk yield (kg) vs. Year
Prediction of maximum milk yield in 60 years by 2077 (unadjusted)

y = 122.62x - 234560
R² = 0.9894

y = 223.53x - 421919
R² = 0.761

- **Maximum:** 42 tons by 2077 (42352 kg)
- **Average:** 20 tons by 2077 (20148 kg)
Prediction of maximum milk yield in 60 years by 2077 (adjusted)

Maximum in 1957 took 60 years to become average

\[ y = 111.46x - 213232 \]
\[ R^2 = 0.9888 \]

\[ y = 156.38x - 292758 \]
\[ R^2 = 0.8879 \]
Summary of maximum milk yields

• Observed maximum milk yield in USDA data
  – 28,614 kg or 28.6 tons in 2007, unadjusted
  – 22,499 kg or 22.5 tons in 2000, adjusted

• Current record
  – 35,114 kg or 35.1 tons in 2016 (4-year old cow, 365 days)

• Predicted maximum milk yield by 2077
  – 42 tons unadjusted, 7 tons above the current record
    • Physical limitations unknown
  – 32 tons adjusted
    • Optimistic, given the 35-ton unadjusted record
Can a cow’s body produce 42 tons of milk a year?

- Physical limitations are unknown
- Genetic selection has changed the cow’s body

Record-breaking cow, 2017


UMN control line unselected since 1964

Photo by Yang Da
## Changes of body measurements since 1964

<table>
<thead>
<tr>
<th>Trait (PTA)</th>
<th>1964</th>
<th>1975-1985</th>
<th>Contemporary</th>
<th>Direction</th>
</tr>
</thead>
<tbody>
<tr>
<td>STA</td>
<td>-1.840±1.357</td>
<td>-1.146±0.775</td>
<td>0.413±0.990</td>
<td>↑↑</td>
</tr>
<tr>
<td>STR</td>
<td>-0.875±0.871</td>
<td>-0.629±0.853</td>
<td>0.198±0.872</td>
<td>↑↑</td>
</tr>
<tr>
<td>BD</td>
<td>-1.508±1.225</td>
<td>-0.855±0.866</td>
<td>0.271±0.876</td>
<td>↑↑</td>
</tr>
<tr>
<td>DF</td>
<td>-3.232±2.482</td>
<td>-1.638±0.957</td>
<td>0.703±0.906</td>
<td>↑↑</td>
</tr>
<tr>
<td>RA</td>
<td>0.474±0.622</td>
<td>0.143±0.688</td>
<td>0.069±0.792</td>
<td>↓↓</td>
</tr>
<tr>
<td>RW</td>
<td>-1.705±1.220</td>
<td>-0.918±0.837</td>
<td>0.276±0.903</td>
<td>↑↑</td>
</tr>
<tr>
<td>FUA</td>
<td>-1.754±1.278</td>
<td>-1.479±0.825</td>
<td>0.641±1.110</td>
<td>↑↑</td>
</tr>
<tr>
<td>RUH</td>
<td>-2.749±2.013</td>
<td>-1.704±0.954</td>
<td>0.942±1.171</td>
<td>↑↑</td>
</tr>
<tr>
<td>UD</td>
<td>-0.782±0.730</td>
<td>-0.857±0.738</td>
<td>0.316±0.962</td>
<td>↓↑</td>
</tr>
<tr>
<td>UC</td>
<td>-2.114±1.538</td>
<td>-1.607±0.887</td>
<td>0.470±1.013</td>
<td>↑↑</td>
</tr>
<tr>
<td>FTP</td>
<td>-1.665±1.307</td>
<td>-1.447±0.906</td>
<td>0.564±0.916</td>
<td>↑↑</td>
</tr>
<tr>
<td>RTP</td>
<td>-1.797±1.461</td>
<td>-1.607±0.908</td>
<td>0.477±0.929</td>
<td>↑↑</td>
</tr>
<tr>
<td>TL</td>
<td>0.063±0.555</td>
<td>0.251±0.783</td>
<td>-0.076±0.758</td>
<td>↑↓</td>
</tr>
<tr>
<td>FA</td>
<td>-0.893±0.866</td>
<td>-0.867±0.964</td>
<td>0.622±1.052</td>
<td>↑↑</td>
</tr>
<tr>
<td>RLS</td>
<td>-0.447±0.616</td>
<td>-0.249±0.811</td>
<td>-0.163±0.769</td>
<td>↑↑</td>
</tr>
<tr>
<td>RLR</td>
<td>-1.241±1.134</td>
<td>-0.980±0.911</td>
<td>0.611±0.974</td>
<td>↑↑</td>
</tr>
<tr>
<td>FL</td>
<td>-1.176±1.033</td>
<td>-1.045±0.916</td>
<td>0.677±0.919</td>
<td>↑↑</td>
</tr>
<tr>
<td>FS</td>
<td>-2.173±1.607</td>
<td>-1.378±0.766</td>
<td>0.695±0.910</td>
<td>↑↑</td>
</tr>
</tbody>
</table>

Are there sufficient genetic variation for continued increases in milk yield?

- Selection caused genome-wide changes but lacked allele fixation

Allele frequency differences between selected and unselected Holsteins

Genome changes from unselected Holsteins to selected Holsteins
Milk alleles far from fixation (294,079 cows)

- Top 1000 positive milk alleles had frequencies 0.05–0.77
- 80% of the alleles had frequencies ≤ 0.3
- Fat alleles had similar range of frequencies
- Sufficient genetic variation exists for further genetic improvement

Positive allelic effects for milk yield
- ‘A’ allele of \(DGAT1\): 0.77
- GC: 0.66

Positive allelic effects for fat yield
- ‘G’ allele of \(DGAT1\): 0.23
- \(LY6D\): 0.73
Will selection for milk yield cause other problems?

- Fertility had serious declines since 1957
- SNP effects with high milk yield tend to have low fertility, low livability, and high somatic cell score
- Current selection index has a negative weight for milk yield

https://www.uscdcb.com/eval/summary/trend.cfm

<table>
<thead>
<tr>
<th></th>
<th>FY</th>
<th>PY</th>
<th>SCS</th>
<th>DPR</th>
<th>LV</th>
</tr>
</thead>
<tbody>
<tr>
<td>MY</td>
<td>0.29</td>
<td>0.80</td>
<td>0.09</td>
<td>-0.26</td>
<td>-0.08</td>
</tr>
<tr>
<td>FY</td>
<td>0.53</td>
<td>-0.04</td>
<td>-0.22</td>
<td>-0.03</td>
<td></td>
</tr>
<tr>
<td>PY</td>
<td>0.08</td>
<td>-0.25</td>
<td>-0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCS</td>
<td></td>
<td></td>
<td>-0.16</td>
<td>-0.17</td>
<td></td>
</tr>
<tr>
<td>DPR</td>
<td></td>
<td></td>
<td></td>
<td>0.33</td>
<td></td>
</tr>
</tbody>
</table>
Multi-trait selection to reduce negative indirect selection response

- Selection index of multiple traits
  - Negative weights for unfavorable phenotypes
- Measuring more traits offers better control of negative selection responses

Declining fertility had a reversal

Somatic cell score reduced

https://www.uscdcb.com/eval/summary/trend.cfm
## Multi-trait selection using ‘Net Merit’


<table>
<thead>
<tr>
<th>Trait</th>
<th>Units</th>
<th>SD</th>
<th>Value ($/PTA unit)</th>
<th>Relative value (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>NM$</td>
<td>CM$</td>
</tr>
<tr>
<td>Protein</td>
<td>Pounds</td>
<td>18</td>
<td>3.81</td>
<td>5.42</td>
</tr>
<tr>
<td>Fat</td>
<td>Pounds</td>
<td>25</td>
<td>3.56</td>
<td>3.56</td>
</tr>
<tr>
<td>Milk</td>
<td>Pounds</td>
<td>672</td>
<td>-0.004</td>
<td>-0.052</td>
</tr>
<tr>
<td>PL</td>
<td>Months</td>
<td>2.4</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>SCS</td>
<td>Log</td>
<td>0.21</td>
<td>-117</td>
<td>-148</td>
</tr>
<tr>
<td>Udder</td>
<td>Composite</td>
<td>0.90</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td>Feet/legs</td>
<td>Composite</td>
<td>1.03</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Body weight</td>
<td>Composite</td>
<td>1.03</td>
<td>-20</td>
<td>-20</td>
</tr>
<tr>
<td>DPR</td>
<td>Percent</td>
<td>2.3</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>HCR</td>
<td>Percent</td>
<td>2.4</td>
<td>2.2</td>
<td>2.2</td>
</tr>
<tr>
<td>CCR</td>
<td>Percent</td>
<td>2.8</td>
<td>2.2</td>
<td>2.2</td>
</tr>
<tr>
<td>CA$</td>
<td>Dollars</td>
<td>18</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>LIV</td>
<td>Percent</td>
<td>2.3</td>
<td>12</td>
<td>12</td>
</tr>
</tbody>
</table>
Table 4. Forecast genetic progress for 50 years of selection on 2017 net merit. (Cole and VanRaden, 2017)

<table>
<thead>
<tr>
<th>Trait</th>
<th>2010 base</th>
<th>Base + genetic progress</th>
<th>Genetic progress</th>
<th>Progress / base (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk (kg)</td>
<td>12,270</td>
<td>16,501</td>
<td>4,231</td>
<td>34%</td>
</tr>
<tr>
<td>Fat (kg)</td>
<td>457</td>
<td>698</td>
<td>241</td>
<td>53%</td>
</tr>
<tr>
<td>Protein (kg)</td>
<td>374</td>
<td>529</td>
<td>155</td>
<td>41%</td>
</tr>
<tr>
<td>PL (mo)</td>
<td>25.6</td>
<td>91</td>
<td>65.0</td>
<td>254%</td>
</tr>
<tr>
<td>SCS (log₂)</td>
<td>2.37</td>
<td>0.27</td>
<td>-2.10</td>
<td>N/A</td>
</tr>
<tr>
<td>UC</td>
<td>0</td>
<td>2.65</td>
<td>2.65</td>
<td>N/A</td>
</tr>
<tr>
<td>FLC</td>
<td>0</td>
<td>1.25</td>
<td>1.25</td>
<td>N/A</td>
</tr>
<tr>
<td>BWC</td>
<td>0</td>
<td>-6.75</td>
<td>-6.75</td>
<td>N/A</td>
</tr>
<tr>
<td>DPR (%)</td>
<td>28.5</td>
<td>54.5</td>
<td>26.0</td>
<td>91%</td>
</tr>
<tr>
<td>CA$ ($ )</td>
<td>0</td>
<td>360</td>
<td>360</td>
<td>N/A</td>
</tr>
<tr>
<td>HCR (%)</td>
<td>57.2</td>
<td>77.7</td>
<td>20.5</td>
<td>36%</td>
</tr>
<tr>
<td>CCR (%)</td>
<td>35.1</td>
<td>77.1</td>
<td>42.0</td>
<td>120%</td>
</tr>
<tr>
<td>LIV (%)</td>
<td>84.8</td>
<td>121.8</td>
<td>37.0</td>
<td>44%</td>
</tr>
</tbody>
</table>
Genomic selection of multiple traits increases profitability

- ‘Net merit’ based on genomic evaluation improves profitability
- Promising approach: multi-trait selection, measuring more phenotypes, genomic selection

Conclusion

- 58 years of genetic selection in Holstein cattle achieved continued increases in milk production with no sign of nearing selection limits

- Multi-trait selection based on genomic selection can be effective for continued improvements of productivity and profitability
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  ➢ Consultation and discussion

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  ➢ Analysis of the 1957-2015 Holstein milk yields

Li Ma and Jicai Jiang
  ➢ GWAS analysis using 294,079 Holstein cows