ABSTRACT: Feed intake, reproductive performance, growth, and body composition were recorded on mating pairs and sampled offspring from mouse lines selected for high (MH), low (ML) heat loss as an indication of maintenance energy requirements, as well as an unselected control (MC). Survival rates recorded on mating pairs were used to determine parity distribution at equilibrium. Total input and output of parents and offspring at equilibrium were calculated to determine lifecycle biological efficiency. Offspring output was greatest in MC and lowest in ML mice. Parent output did not differ substantially. Input was greatest in MH and lowest for ML mice for offspring and parents. Lifecycle biological efficiency was similar in MC and ML, while lowest in MH mice. Superior output in MC outweighed lower inputs in ML mice. Avoiding negative response in output must be considered when selecting to reduce maintenance energy requirements.

Keywords: feed efficiency; heat loss; maintenance energy; selection

Introduction

Feed intake to meet maintenance energy requirements is the largest component of total intake and therefore represents the greatest input cost for all livestock species. Selection to reduce maintenance energy requirements should be independent of growth or other measures of production, thereby resulting in improved feed efficiency. Heat loss can be used to select for reduced maintenance energy requirements as energy that is consumed and not stored is released as heat, and this trait has previously been shown to exhibit genetic variation (Nielsen et al. (1997b); Williams and Jenkins (2003)).

Nielsen et al. (1997b) confirmed that maintenance energy requirements could be altered by selection for heat loss measured via direct calorimetry and established a high (MH) and low (ML) maintenance line, as well as an unselected control (MC) line in 3 independent replicates after a total of 25 generations of selection. However, ML mice have shown decreased lean content, litter size, and weaning weight, which would be undesirable traits in livestock species (McDonald and Nielsen, 2007; Nielsen et al. (1997a)). Additionally, while ML had greater survival rates up to 5 parities, MC mice were found to have superior survival rates, body weights, and reproductive performance than either selection line, particularly across an entire lifecycle (Bhatnagar and Nielsen (2014a,b)). Thus, benefits of selecting for reduced maintenance energy requirements could differ depending on how long mating animals are maintained.

The objective of this study was to utilize these unique mouse lines to imitate a livestock production system and determine if differences in reproductive performance, growth, survivability, and body composition outweigh improved individual feed efficiency observed in animals with lower maintenance energy requirements by calculating the lifecycle biological efficiency of these lines.

Materials and Methods

Experimental Animals. Animals used in this study were sampled from 3 replicates of lines of mice divergently selected for heat loss as an indicator of maintenance energy requirements (MH = high, ML = low, MC = control). Twenty-one mating pairs were sampled from each of 9 independent line by replicate combinations (189 total pairs) at 7 wk of age and maintained for the duration of the study. Offspring were sampled at weaning (21 d) and maintained until maturity (49 d) for data collection.

Data Collection. Complete description of collection and analysis of performance data has been reported by Bhatnagar and Nielsen (2014a,b). Number born, number weaned, litter weaning weight, and pup weaning weight were recorded for every parity produced by each mating pair while on study. Mating pairs were culled due to poor reproductive performance, death, or illness and survival analysis was performed using number of parities as the unit of time. Mating pairs were divided into 3 groups within each line by replicate combination for rotational measurements. Feed intake, growth, and body composition were recorded in group-1 animals from start of experiment to weaning of parity 1, then switched to group-2 animals from weaning of parity 1 to weaning of parity 2, etc. so that data were recorded at all stages of the experiment, but not continuously for an individual pair. Offspring were sampled in a similar rotational fashion (sampled from group-1 mating pairs at parity 1, group-2 at parity 2, etc.). Offspring were sampled in same sex pairs with both sexes equally represented for feed intake, growth and body composition measurements. Additional offspring were selected for recording growth data only. Feed intake and growth were measured from 21 to 49 d of age and body composition was measured at 49 d of age. Coefficients of
energy (kcal·BWkg\(^{-0.75}\)·d\(^{-1}\)) for maintenance were calculated by line for mating pairs, and line and sex for offspring, using regression.

**Lifecycle Biological Efficiency.** Results from the survival analysis were used to estimate the parity distribution of a population of mice within each line at equilibrium using Markov-chain methods (Azzam et al. (1990)). This distribution was used to produce a vector (PD) specifying the number of mating pairs at each parity in a hypothetical population of 100 total mating pairs when enforcing a maximum of 4, 8, or 12 parities. Offspring and parent inputs and outputs were then calculated for each line and parity situation.

Offspring output was defined as lean content of offspring at 49 d and was calculated by multiplying PD elementwise by the number weaned (minus animals retained as replacements), body weight of 49-d-old animals, and percentage lean of those animals. Separate values for each sex were used for body weight and percent lean.

Offspring input was defined as energy intake for maintenance, lean growth, and fat growth from 21 to 49 d and was calculated by multiplying PD elementwise by energy intake of an individual animal and number weaned. Individual energy intake was calculated by summing the sum of the metabolic body weights (ΣBW\(^{0.75}\)) times the coefficient of energy for maintenance, lean gain times 2.9 kcal/g, and fat gain times 12.8 kcal/g. The energy coefficients for lean and fat gain were obtained from the literature (Pullar and Webster, (1977)). Sum of metabolic body weights was defined as the integral of daily metabolic body weight of an individual of the 28-d feeding period, which is calculated as follows:

\[
\Sigma BW^{0.75} = [(1.75*ADG)^{-1}] \\
*[(PWW+28*ADG)^{1.75} - PWW^{1.75}]
\]

where ADG is average daily gain and PWW is the weaning weight of an individual pup.

Parent output was defined as the lean content of culled parents and was calculated by multiplying PD elementwise by percentage of culled parents (excluding those that died of natural causes), body weight of a mature male and female, and percent lean of mature male and female.

**Table 2. Maintenance energy coefficients (kcal·BWkg\(^{-0.75}\)·d\(^{-1}\)) for offspring and parents by line\(^1\)**

<table>
<thead>
<tr>
<th>Line</th>
<th>MH</th>
<th>MC</th>
<th>ML</th>
</tr>
</thead>
<tbody>
<tr>
<td>Offspring(^2)</td>
<td>261.9</td>
<td>229.0</td>
<td>225.8</td>
</tr>
<tr>
<td>Parents(^3)</td>
<td>270.7</td>
<td>233.3</td>
<td>225.6</td>
</tr>
</tbody>
</table>

\(^1\)MH = high and ML = low heat loss selection; MC = unselected control

\(^2\)Average of coefficients for males and females

\(^3\)Average of coefficients across 4 feeding periods

Parent input was defined as energy intake for mating pairs and was calculated by multiplying PD elementwise by energy intake of a mating pair for maintenance and weaning weight. Energy intake was calculated my multiplying body weight of a pair times the maintenance energy coefficient by days on feed plus litter weaning weight times 5.28 (energy coefficient of lactation and feed intake of litter prior to weaning).

Calculations resulted in vectors specifying input or output at each parity, which were then summed down the row to obtain totals for each at equilibrium. Lifecycle efficiency was then calculated for each line and maximum parity scenario by dividing the sum of offspring and parent output by the sum of offspring and parent input.

**Results and Discussion**

**Offspring Output and Input.** Control mice produced the greatest output, while ML mice produced the least, and MH were intermediate. Reduced output in ML mice was due to slightly smaller litter sizes, body weights, and lean content (Bhatnagar and Nielsen (2014a,b)). Output was greatest when allowing a maximum of 8 parities for all lines, and similar at a maximum of 4 and 12 parities. Output decreased due to smaller litter sizes in later parities as shown in Table 1 (Bhatnagar and Nielsen (2014a)).

**Table 1: Number weaned by line\(^1\) and parity used to calculate offspring input and output.**

<table>
<thead>
<tr>
<th>Parity</th>
<th>MH</th>
<th>MC</th>
<th>ML</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11.37</td>
<td>10.93</td>
<td>9.63</td>
</tr>
<tr>
<td>2</td>
<td>11.40</td>
<td>12.26</td>
<td>10.96</td>
</tr>
<tr>
<td>3</td>
<td>10.87</td>
<td>11.00</td>
<td>9.57</td>
</tr>
<tr>
<td>4</td>
<td>10.88</td>
<td>11.02</td>
<td>9.73</td>
</tr>
<tr>
<td>5</td>
<td>9.96</td>
<td>10.14</td>
<td>9.21</td>
</tr>
<tr>
<td>6</td>
<td>10.07</td>
<td>9.37</td>
<td>6.87</td>
</tr>
<tr>
<td>7</td>
<td>8.22</td>
<td>9.03</td>
<td>6.54</td>
</tr>
<tr>
<td>8</td>
<td>7.18</td>
<td>7.26</td>
<td>6.42</td>
</tr>
<tr>
<td>9</td>
<td>5.96</td>
<td>6.81</td>
<td>6.67</td>
</tr>
<tr>
<td>10</td>
<td>5.52</td>
<td>5.82</td>
<td>6.15</td>
</tr>
<tr>
<td>11</td>
<td>5.08</td>
<td>4.82</td>
<td>2.01</td>
</tr>
<tr>
<td>12</td>
<td>5.00</td>
<td>3.80</td>
<td>2.00</td>
</tr>
</tbody>
</table>

\(^1\)MH = high and ML = low heat loss selection; MC = unselected control

MH from the MH line had the largest input, while offspring from the MH line had the largest input, while control mice produced the highest output.
Parent Output and Input. There was no large difference in parent output across lines, but MH mice produced the greatest output due to poorer survival rates at early parities (Bhatnagar and Nielsen (2014a)). Output dropped as maximum number of parities increased, though the drop was much steeper between 4 and 8 maximum parities. This steep drop was due to more pairs available for culling when only 4 parities were allowed since survival rates are higher at earlier parities and all remaining pairs would be culled after 4 parities (Bhatnagar and Nielsen (2014a)). As expected, inputs were greatest for MH mating pairs and lowest for ML (Bhatnagar and Nielsen (2014b); McDonald and Nielsen (2007); Nielsen et al. (1997a)). For MH and ML pairs, inputs decreased slightly from 4 to 8 maximum parities and then increased at a maximum of 12 parities. However, inputs for MC mating pairs increased as maximum number of parities increased.

Lifecycle Biological Efficiency. Control mice were shown to be the most efficient across all maximum parity scenarios, due to greater output, but MC mice were not appreciably more efficient than ML mice (Figure 1). Substantially greater intake by MH mice resulted in decreased efficiency compared to both MC and ML mice. Increased offspring output had the largest effect on efficiency, accounting for 95% of the total output of the system. Litter size and body weight were mostly responsible for differences in offspring output, and the effect of litter and weight traits on efficiency have been reported in other studies in rodents (Newman et al. (1985); Wang and Dickerson (1984)). Similar results have been observed in a swine study (Tess et al. (1983)), but reducing inputs is more important to beef cattle systems (Davis et al. (1983); Naazie et al. (1999)). Efficiency increased as maximum number of parities increased. This increase was due to the large decrease in offspring input with a smaller decrease in offspring output which is a result of smaller numbers weaned, but similar total litter weaning weight so individual pup weaning weight was greater in later parities.

Conclusion

Selection to reduce maintenance energy requirements in mice has been proven successful and is correlated with a reduction in feed intake that is maintained when modeled in a lifecycle production system. However, small detrimental changes in reproductive performance, body composition, and survival rates were found in low maintenance animals. In this study, authors show that reduced output offsets the benefit of reduced feed intake in terms of lifecycle biological efficiency. While low maintenance animals had a more desirable efficiency than high maintenance animals, improved outputs resulted in similar efficiency between control and low maintenance animals. Therefore, selection to reduce maintenance energy requirements should be considered with some reservation. Reduction in maintenance energy could be a useful selection goal in terminal sire lines where reproductive performance and survival rates are less important, or it could be useful as part of a selection index. Ultimately, the best strategy for improving lifecycle efficiency remains an important issue for livestock species.

Literature Cited


Figure 1. Lifecycle biological efficiency (total offspring and mating pair output divided by total offspring and mating pair input) of mice selected for high (MH) or low heat loss (ML) or unselected control (MC) when held to a maximum of 4, 8, or 12 allowed parities.