Review

Frequency of the prolificacy gene in flocks of Indonesian thin tail sheep: a review

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Abstract

Indonesian thin tail (ITT) sheep have a major prolificacy gene ($FecJ^F$), the frequency of which is higher in the new born lambs, than in the remainder of the flock when mating is random, because carrier ewes produce more progeny than do non carriers. The frequency of the gene may vary between flocks, but remains relatively stable in flocks with established husbandry procedures. The countermanding selection pressures maintaining the equilibrium value for the frequency of $FecJ^F$ are mainly those deriving from higher mortality rates of lambs in larger litters. Embryo survival is not significantly different across the range of ovulation rates in ITT ewes, in contrast to observations in other prolific breeds. Generation intervals and the incidences of metabolic and infectious diseases in ewes carrying larger litters can also affect the frequency of $FecJ^F$ in flocks. In turn, each of the factors affecting the frequency of $FecJ^F$ is modulated by the level of nutrition and management in each flock. The distribution of prolificacy genotypes in the ewes of a standard flock is calculated as $FecJ^F FecJ^F/12; FecJ^F FecJ^* /44; FecJ^* FecJ^* /44$ giving a frequency of 0.34 for $FecJ^F$. The frequency of $FecJ^F$ is then 0.43 in the lambs at birth, when their numbers have been amplified in the carrier ewes. There are heavier metabolic demands on ewes carrying larger litters and the foetuses constitute a higher proportion of weight gain during pregnancy. Consequently, more of the lambs of carrier ewes are smaller and weaker at birth, and the reserves of the ewes for colostrum and milk production are depleted. When low lamb survival rates in larger litters are considered, the frequency of $FecJ^F$ falls to 0.35 in the lambs at weaning in lean years and 0.38 in middling years. At a high level of husbandry, ewe weight gains during pregnancy and lamb survival rates improve substantially, and after 3 years, the frequency of $FecJ^F$ in the lambs at birth is estimated to have risen to 0.49; and 0.47 at weaning. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Indonesian thin tail sheep; Prolificacy; Gene frequency

1. Introduction

Indonesian thin tail (ITT) sheep are the predominant breed in the province of West Java where they are well adapted to the hot humid environment. Traditionally, they are maintained in family flocks of about three ewes, many families relying on neighbours for a ram. They are housed at night in small elevated pens with slatted floors, and are provided with feed cut and carried from roadsides, woodland and fallow land. In some areas family flocks are permanently housed, while in others they graze under supervision during part of the day. Small closely supervised flocks appear to provide the conditions necessary to maintain genes for prolificacy (Mason, 1980), and a prolificacy gene with major effect (Bradford et al., 1986, 1991), occurs...
in the ITT breed. On institutional farms, ewes are usually kept in group pens and nutrition and management vary widely. Like most prolific breeds of sheep (Bindon et al., 1996), ITT sheep reach puberty early (Sutama et al., 1988), resume ovarian activity shortly after parturition (Sutama et al., 1988) and are non seasonal breeders (Fletcher and Putu, 1985). With this combination of traits, the breed produces meat efficiently (Reese et al., 1990; Iniguez et al., 1991; Inounu et al., 1993), in spite of the small size of the ewes (17–30 kg). The prolificacy gene of ITT sheep is designated \( \text{Fec}^J \), with the standard allele \( \text{Fec}^J^+ \), (COG-NOSAG, 1989).

When mating is random, gene distributions of traits which do not affect reproduction remain relatively stable. However, for a prolificacy gene, the frequency in the zygotes is determined by the frequency in the parental generation amplified by the prolificacy of the ewes. That is, a homozygous normal ITT ewe, which produces mainly single lambs, will contribute genes to one zygote, whereas a homozygous carrier, which produces mainly twins and triplets, Table 1, will contribute genes to more than two zygotes. In the absence of countermanding selection pressures, the frequency of the fecundity gene would increase with each generation. Nevertheless, distributions of litter sizes in institutional and village flocks in West Java, Table 2, remain relatively stable. Bradford et al. (1986, 1996) have suggested that the prolificacy gene is in all populations of ITT sheep at a frequency of 0.05–0.25. Factors which may modulate the frequency of \( \text{Fec}^J \) in flocks of Indonesian sheep on institutional farms and in villages are assessed in this review, and distributions of genotypes and the corresponding frequencies of \( \text{Fec}^J \) under different husbandry conditions, are calculated. In addition, some of the characteristics of other prolific breeds are compared with those of ITT sheep.

2. Modulation of the frequency of \( \text{Fec}^J \)

The frequency of \( \text{Fec}^J \) in flocks is modulated by nutrition and husbandry practices which are reflected in ovulation rates, survival and growth of lambs in larger litters, generation intervals, and metabolic diseases of ewes carrying large litters.

2.1. Ovulation rate

High levels of supplementary feeding over several months increased ovulation rates. The diet was free access to freshly cut grass, plus concentrate, 10 MJ/kg dry matter and 15% crude protein, either ad lib., or 700 g/day, and was compared with a maintenance diet of the same ingredients. In the study of Henniawati and Fletcher (1986), the mean body weights of the supplemented 2 and 4 tooth ewes increased from 19.5 kg to 24.5 kg over 22 weeks and the mean ovulation rate increased to a maximum of 2.65 at the sixth oestus after the beginning of the feeding regime, compared with 1.69 at the maintenance level. Nevertheless, mean litter size was only 1.78 compared with 1.50 at the maintenance level. At the same level of supplementation young ewes had a mean ovulation rate of 2.1 and a litter size of 1.8 compared with control ewes with 1.6 and 1.5 respectively (Sutama et al., 1988). So with prolonged supplementation at a high level, there was a higher ovulation rate, lower embryo survival and a small increase in litter size.
Reese et al. (1990) provided energy supplementation up to 826 kcal ME/day to ewes grazing on a rubber plantation. Litter size at the highest level of supplementation was 1.49 compared with 1.26 at lower levels, in ITT sheep from Sumatra, which have a relatively low frequency of the prolificacy gene. Lamb birth weights, survival rates and growth rates all improved. On the other hand, in the Research Institute for Animal Production (RIAP) flock (Inounu et al., 1993), mean litter sizes produced by each of the prolificacy genotypes during years of good nutrition (Subandriyo and Inounu, 1994), did not differ from those of the lean and middling years (Inounu et al., 1993), Table 2. Lower levels of supplementation, provided strategically, did not affect ovulation rates (Inounu et al., 1985; Chaniago et al., 1988).

If supplementation does increase litter sizes, and the three prolificacy genotypes respond in proportion to their ovulation rates, then the frequency of $F_{ecJ}F_{ecJ}$ would increase in lambs from supplemented ewes.

### 2.2. Conception rate and embryo survival

Conception rates, embryo survival rates and net rates of survival of ova in ITT ewes were high, and embryo survival rates did not differ significantly over the range of litter sizes, Tables 3 and 4, and prolificacy genotypes (Bradford et al., 1991). Nevertheless, the trend of decreasing embryo survival rates with increasing ovulation rates in ITT ewes, was similar to that of other prolific breeds, Table 4, reflecting decreasing marginal response of uterine efficiency with increasing numbers of embryos (Meyer, 1985).

Thus, on the basis of the available data, conception rate and embryo survival will not have significant effects on the frequency of $F_{ecJ}F_{ecJ}$ in the progeny of...
ITT sheep; but would reduce the frequencies in other prolific breeds.

2.3. Survival from birth to weaning

In the study of Obst et al. (1982), 31% of lambs died. Of those lambs, 32% were stillborn, 5% died at birth and 49% between birth and 3 days, and 60% of the total deaths were from litters of triplets and above. About 40% of the total deaths were attributed to lambs being small, weak or immature, and 11% to mis-mothering. Inoumu et al. (1993) found that stillbirths constituted 52% of mortality to weaning.

Survival from birth to weaning is directly related to the weights of individual lambs at birth, and there is a strong inverse relationship between survival to weaning, and litter size, Table 5. Larger litters comprise a larger proportion of ewe weight gain during gestation than do singles (Inoumu et al., 1993), Table 6, so after parturition ewes with larger litters have lower body reserves and are less able to provide colostrum and milk for the small lambs in those litters. This leads to lower survival rates of lambs to weaning, Table 7, and lower litter weights at weaning, Table 6.

Moreover, the low survival rates in larger litters are exacerbated when the level of nutrition is low, Tables 6 and 7.

The quality and quantity of milk produced by ITT ewes is in the low range of sheep breeds (Sutama et al., 1988), but the requirement of the small lambs is also low. Level of nutrition and litter size affected weight changes of ewes, Table 6, and milk production, but not milk composition (Sitorus et al., 1985b). During 12 weeks from lambing, average milk production was 26 kg on a low level of nutrition and 31 kg on a higher level (Sitorus et al., 1985b), similarly 25 and 37 kg respectively (Sutama et al., 1988), and an average of 30 kg (Atmadilaga, 1958). Milk production was higher during the second lactation on both levels of nutrition (Sutama et al., 1988). Suckling of twins increased milk production by 28% on a low level of nutrition and 5% on a high level. Maximum production occurred 3–4 weeks after lambing (Atmadilaga, 1958; Sitorus et al., 1985b; Sutama et al., 1988).

Table 3
Conception rates and survival of embryos to lambing, for ewes producing different numbers of corpora lutea. Most ewes were served once when oestrus was first detected. Data of Javanese and Semarang strains of ITT sheep in Bradford et al. (1986)

<table>
<thead>
<tr>
<th>Number of corpora lutea</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4–5</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of ewes mated</td>
<td>79</td>
<td>79</td>
<td>29</td>
<td>14</td>
<td>201</td>
</tr>
<tr>
<td>Number of ewes lambed</td>
<td>57</td>
<td>65</td>
<td>19</td>
<td>12</td>
<td>153</td>
</tr>
<tr>
<td>Fertility (%)</td>
<td>72</td>
<td>82</td>
<td>66</td>
<td>71</td>
<td>76</td>
</tr>
<tr>
<td>Embryo survival/ewe lambing (%)</td>
<td>100</td>
<td>92</td>
<td>89</td>
<td>80</td>
<td>91</td>
</tr>
<tr>
<td>Net survival of ova (%)</td>
<td>72</td>
<td>75</td>
<td>59</td>
<td>57</td>
<td>69</td>
</tr>
</tbody>
</table>

Table 4
Distributions of the mean litter sizes, and survival rates, which correspond to each ovulation rate in lambing ewes of some prolific breeds

<table>
<thead>
<tr>
<th>Mean litter sizes (embryo survival %) at different ovulation rates</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breed</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td>ITT&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.83 (92%)</td>
</tr>
<tr>
<td>Romanov</td>
<td>1.90 (95%)</td>
</tr>
<tr>
<td>Finn, sheep</td>
<td>1.72 (86%)</td>
</tr>
<tr>
<td>D’man</td>
<td>1.80 (90%)</td>
</tr>
<tr>
<td>Icelandic</td>
<td>1.76 (88%)</td>
</tr>
</tbody>
</table>

<sup>a</sup> Javanese and Semarang strains of ITT sheep.

<sup>b</sup> Including five.
Survival of lambs, particularly those in larger litters, is dependent on the levels of nutrition and management in a flock. In turn, low survival rates of the small lambs in large litters is the major pressure countermanding amplification of the frequency of $\text{FecJ}^F$ in the zygotes of prolific ewes. The survival rates of lambs in larger litters would increase from the commencement of better husbandry in a flock, and continue to improve over a full reproductive cycle. Survival of lambs is inversely related to litter size regardless of the level of husbandry, Table 7, so the frequency of $\text{FecJ}^F$ in the flock would continue to rise as more large litters were produced and more lambs survived. Ultimately, a new equilibrium will be established between the distribution of litter sizes and lamb survival at the new level of husbandry. At very high levels of nutrition, the increased incidence of metabolic diseases in ewes (Obst et al., 1980, 1982; Fletcher et al., 1982; Aitkin, 1996) would reduce the increase in the frequency of $\text{FecJ}^F$. Lambs in larger litters have lower survival rates in all prolific breeds of sheep (Aitkin, 1996).

### 2.4. Breeding life of ewes

Age, weight and parity are generally inseparable in the data available; but they have important effects on ovulation rates and litter sizes, which were higher in older, heavier, multiparous ewes. Mean ovulation rates increased from 1.43 to 2.93 for ewe body weights from 17.1 to 29.6 kg (Bradford et al., 1986). Mean numbers of lambs per litter increased from 1.54 for primipara ewes to 2.47 for third and later parities (Bradford et al., 1986), Table 2. Ewes carrying the prolificacy gene would be differentially affected to the extent that average life span is reduced by the metabolic and infectious diseases to which ewes with larger litters are

### Table 5
Survival rates of individual ITT lambs from birth to weaning at 90 days, in relation to birth weight and litter size. Data from Chaniago et al. (1988)*

<table>
<thead>
<tr>
<th>Litter size</th>
<th>Survival rates (%) of individual lambs by birth weights and litter sizes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;1.0 kg</td>
</tr>
<tr>
<td>Single</td>
<td>(2)</td>
</tr>
<tr>
<td>Twin</td>
<td>25 (4)</td>
</tr>
<tr>
<td>Triplet</td>
<td>0 (12)</td>
</tr>
<tr>
<td>Quadruplet</td>
<td>0 (2)</td>
</tr>
<tr>
<td>All litter sizes</td>
<td>5</td>
</tr>
</tbody>
</table>

* ( )=Number of lambs per class.

### Table 6
Weight gains of ewes during gestation, and weaning weights of litters, related to the prolificacy genotypes and litter sizes in the RIAP flock of ITT sheep, in years with different levels of husbandry

<table>
<thead>
<tr>
<th>Level of husbandry</th>
<th>Lambs in litter</th>
<th>Prolificacy genotype</th>
<th>Litter size at birth</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>FF</td>
<td>F+</td>
<td>++</td>
</tr>
<tr>
<td><em>Ewe weight gain during gestation (kg)</em></td>
<td></td>
<td>0.5</td>
<td>1.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Lean</td>
<td></td>
<td>1.8</td>
<td>2.3</td>
<td>2.9</td>
</tr>
<tr>
<td>Middling</td>
<td></td>
<td>3.8</td>
<td>4.0</td>
<td>3.8</td>
</tr>
<tr>
<td>Good</td>
<td></td>
<td>6.7</td>
<td>7.4</td>
<td>7.7</td>
</tr>
<tr>
<td><em>Weaning weight of litter (kg)</em></td>
<td></td>
<td>12.2</td>
<td>11.9</td>
<td>10.9</td>
</tr>
<tr>
<td>Lean</td>
<td></td>
<td>13.7</td>
<td>12.7</td>
<td>14.2</td>
</tr>
<tr>
<td>Middling</td>
<td></td>
<td>20.2</td>
<td>19.0</td>
<td>23.0</td>
</tr>
<tr>
<td>Good</td>
<td></td>
<td>22.8</td>
<td>18.2</td>
<td>-</td>
</tr>
</tbody>
</table>

* Including quadruplets.
more prone (Aitkin, 1996). In the Ciawi flocks with a continuous high level of nutrition, 11% of breeding ewes in one flock died per lambing interval (Obst et al., 1980), the main causes being vaginal prolapse and pregnancy toxaemia (Obst et al., 1982), and dystocia (Fletcher et al., 1982). In the same flock, the mortality of ewes was halved when strategic supplementation replaced continuous high level feeding (Chaniago et al., 1988).

### 2.5. Generation intervals

ITT ewe lambs attained puberty when their body weights averaged 17–18 kg, so the slower growing lambs reared in larger litters, were up to 80 days older when they produced their first litters (Sutama et al., 1988). Similarly ewe lambs on high and low levels of nutrition, reaching puberty at similar body weights, were 221 days old on the high level, and 297 days on a low level (Sutama et al., 1988).

ITT ewes on a higher level of nutrition conceived about 60 days after lambing intervals were directly related to the postpartum body condition of the ewes (Sutama, 1992), and so were prolonged by about 9 days for ewes with previous larger litters (Sitorus et al., 1985a).

Low nutrition of lambs, and the draining effects on ewes bearing large litters, would increase generation intervals for carriers of the prolificacy gene, with the main effect being on the time taken for ewe lambs to reach puberty. There would be minor, long term selection against carriers of $\text{FecJ}^F$.

### 2.6. Husbandry procedures

The management procedures which can improve survival of ITT lambs are seldom recorded. At Ciawi, ewes were joined continuously with rams except for 2 weeks after parturition when ewes were in individual pens with their lambs. Dystocia cases were assisted, pregnancy toxaemia was treated and weak lambs were assisted to suckle (Obst et al., 1982). Nevertheless, there was a husbandry problem in that flock because no quadruplets survived over a number of years, Table 7 (Obst et al., 1982; Chaniago et al., 1988). Ewes and

---

**Table 7**

<table>
<thead>
<tr>
<th>Level of husbandry</th>
<th>Lambs in litter</th>
<th>Survival rates (%)</th>
<th>Litter size</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Genotype</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>FF F+ ++</td>
<td>Single Twin Triplet Quadruplet</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Institutional farms</td>
<td>Lean</td>
<td>41 58 74</td>
<td>81 55 30 21</td>
<td>Cicadas</td>
<td>Inounu et al., 1993</td>
</tr>
<tr>
<td></td>
<td>Middling</td>
<td>59 75 89</td>
<td>91 78 52 35</td>
<td>Cicadas</td>
<td>Inounu et al., 1993</td>
</tr>
<tr>
<td></td>
<td>Good One</td>
<td>88 80 90</td>
<td>94 84 83 73</td>
<td>Bogor</td>
<td>Inounu et al., 1993</td>
</tr>
<tr>
<td></td>
<td>Good Two</td>
<td>90 93 93</td>
<td></td>
<td>Bogor</td>
<td>Subandriyo and Inounu, 1994</td>
</tr>
<tr>
<td></td>
<td>Three and above</td>
<td>88 84 97</td>
<td>93 86 65a</td>
<td>Bogor</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>71 60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High nutrition/mixed management</td>
<td>94 73 46 0</td>
<td>Ciawi</td>
<td>Obst et al., 1982</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategic supplementation/ unknown management</td>
<td>85 66 27 0</td>
<td>Ciawi</td>
<td>Chaniago et al., 1988</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Levels of supplementation/ good management</td>
<td>92 77 67 55</td>
<td>Sumatra</td>
<td>Iniguez et al., 1991</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Village Unknown nutrition/ management</td>
<td>97 88 70</td>
<td>Village</td>
<td>Inounu et al., 1993</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a Including quad.
lambs need space, time and quiet to promote mothering and bonding (Gatenby et al., 1994; Poindron et al., 1996). Most mature ITT ewes lambed within 30 min, and licked the newborn lamb. Lambs stood within 30 min and ewes encouraged them to suckle by nuzzling the rump. There were no differences between lambs from single and multiple births (Sutama and Inounu, 1993; Gatenby et al., 1994). Assisting weak lambs to suckle, hand feeding and fostering can improve survival of weak lambs if suitable carers are available (Tiesnamurti, 1992a,b). Some village families supplement weak lambs with milk substitutes (Bell and Inounu, 1982), but fostering and hand rearing are rare on institutional farms. Self weaning of lambs from large litters at about 5 weeks probably occurs (Sutama et al., 1988), as it does in other prolific breeds (Poindron et al., 1996). Again, the frequency of FecJF is raised when lambs in larger litters survive.

Only a few rams are required for breeding and the remainder must be culled, so, if the best ram lambs are kept they will probably have been singles, and there will have been selection reducing the frequency of FecJF. Weight was the main selection criterion for rams and ewes for the flocks of village families (Bell and Inounu, 1982).

2.7. Frequencies of FecJF and distributions of litter sizes

The reported distributions of litter sizes in the RIAP flock from 1981 to 1989 are relatively consistent, Table 2, probably because fluctuations in the level of husbandry were random at Cicadas, where there were lean years (1982, 1985, 1986, 1988) and middling years (1981, 1983, 1984, 1987, 1989), (Bradford et al., 1991; Inounu et al., 1993). The frequency of FecJF would be around that corresponding to the average level of husbandry over the period, being buffered as the maiden ewes from each lambing, entered a flock containing older ewes reared under differing husbandry regimes. In 1990, the flock was moved to Bogor and the husbandry was good from 1991 to 1993 (Inounu et al., 1993; Subandriyo and Inounu, 1994). Ewe weight gains during gestation, survival rates of individual lambs to weaning, and litter weaning weights, are presented as indicators of the respective levels of husbandry, Tables 6 and 7.

<table>
<thead>
<tr>
<th>Frequency of F</th>
<th>Single</th>
<th>Twin</th>
<th>Triplet</th>
<th>Quadruplet</th>
<th>Quintuplet</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>76</td>
<td>24</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.1</td>
<td>66</td>
<td>30</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.2</td>
<td>57</td>
<td>35</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.3</td>
<td>49</td>
<td>38</td>
<td>11</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>0.35</td>
<td>45</td>
<td>40</td>
<td>13</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>0.4</td>
<td>41</td>
<td>41</td>
<td>14</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>0.5</td>
<td>35</td>
<td>42</td>
<td>19</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>0.6</td>
<td>29</td>
<td>43</td>
<td>22</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>24</td>
<td>42</td>
<td>25</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>0.8</td>
<td>20</td>
<td>40</td>
<td>28</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>0.9</td>
<td>16</td>
<td>37</td>
<td>31</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>1.0</td>
<td>14</td>
<td>33</td>
<td>34</td>
<td>17</td>
<td>2</td>
</tr>
</tbody>
</table>

The distribution of litter sizes at birth in a flock, reflects the distribution of prolificacy genotypes of the ewes, as each genotype produces a distribution of litter sizes, Table 1. Empirically, each of the distributions of litter sizes in flocks, Table 2, approximates the distribution of litter sizes which would result from a Hardy Weinberg distribution of prolificacy genotypes in the breeders, Table 8. The reason for this relationship will be discussed when survival rates of lambs in different litter sizes are considered below. The distribution of litter sizes in the RIAP flock during lean and middling husbandry periods (Inounu et al., 1993), Table 2, approximates that for a frequency of 0.35 for the prolificacy gene, Table 8. At that frequency of the prolificacy gene, the distribution of litter sizes for each genotype, Table 1, can be transposed to provide the distribution of prolificacy genotypes for each litter size, Table 9. Application of those values to the observed distribution of litter sizes from Inounu et al. (1993), Table 2, gives the actual distribution of prolificacy genotypes in the ewes as FecJF/FecJF/12; FecJF/FecJF/44; FecJF/FecJF/44, compared with the Hardy Weinberg approximation of FecJF/FecJF/12; FecJF/FecJF/46; FecJF/FecJF/42. The actual distribution of genotypes in the ewes is then used to calculate the number of lambs of each genotype in each litter size, being the product of the frequency of the proli-
The frequency distribution of prolificacy genotypes of ITT sheep in each litter size, on the basis of a frequency of 0.35 for the gene, as discussed in the text. Data transposed from Inouu et al. (1993)

Table 9
Calculated frequency distributions (%) of each of the prolificacy genotypes of ITT sheep in each litter size, on the basis of a frequency of 0.35 for the gene, as discussed in the text. Data transposed from Inouu et al. (1993)

<table>
<thead>
<tr>
<th>Litter size</th>
<th>FF</th>
<th>F+</th>
<th>++</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single</td>
<td>4</td>
<td>26</td>
<td>70</td>
</tr>
<tr>
<td>Twin</td>
<td>11</td>
<td>65</td>
<td>24</td>
</tr>
<tr>
<td>Triplet</td>
<td>33</td>
<td>67</td>
<td>0</td>
</tr>
<tr>
<td>Quadruplet</td>
<td>100</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Quintuplet</td>
<td>100</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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murti et al., 1984), survival of lambs from birth to weaning can be better than on institutional farms, Table 7 (Inounu et al., 1993), and there is a high proportion of larger litters, Table 2 (Inounu et al., 1984; Subandriyo, 1986). There are other factors which may influence the results of village studies. Whereas record keeping can be reliable on institutional farms where a responsible person can check the animals daily, in villages, data may be collected intermittently by an outsider who can only obtain that information which can be recalled by those who are willing to cooperate. Moreover, culturally, villagers may provide information which they believe will please a guest, and village people may have different perceptions, such as farmers generally not counting lambs which die within 3 days of birth (Bell and Inounu, 1982).

3. Comparisons with other prolific breeds

As described above, the frequency of the prolificacy gene in ITT sheep is, in the main, an equilibrium between the amplifying effect of the higher ovulation rates of carrier ewes, balanced by lower survival rates of the smaller lambs from litters with multiple lambs. The equilibrium point is set by the level of husbandry in the flock which affects survival rates of lambs, and perhaps litter sizes. A similar equilibrium might be expected when prolificacy is controlled by many genes. In that case the frequencies of minor prolificacy genes would be in equilibrium with the survival rates of lambs in larger litters, the equilibrium level being modulated by the level of husbandry.

Of the prolificacy genes with large effect in sheep, none are known to be alleles, the Booroola gene is linked to markers from a region of the human chromosome 4q (Montgomery et al., 1993), the Inverdale gene of Romney sheep is on the X chromosome (Fahmy and Davis, 1996) and the locations of the Thoka gene of Icelandic sheep, the Olkuska gene and FecJ\(^F\) of ITT sheep are not known. Ovulation rates are a more direct measure of the effects of a prolificacy gene than are litter sizes, which are affected by embryo wastage, which varies between breeds, Table 4. Breeds and synthetics into which a major prolificacy gene has been incorporated recently (Booroola, Cambridge and Belclare), tend to have wide ranges (1–14) of ovulation rates (Bindon et al., 1996), whereas those prolific breeds which have evolved in small flocks in traditional societies, Romanov (Ricordeau et al., 1990), D’man (Lahlou-Kassi and Marie, 1985), ITT (Bradford et al., 1986) and Icelandic (Eythorsdottir et al., 1991), regardless of whether prolificacy is the product of one or many genes, have compact ranges (1–7) of ovulation rates, which may have evolved with prolificacy. Nevertheless, all of the prolific breeds have litter size ranges from 1 to \(\leq 7\), probably reflecting the common constraint of uterine efficiency (Meyer, 1985). Ovulation rates and litter sizes of different major prolificacy genes are best compared when the frequencies of the genes are known, or like genotypes are available. Piper and Bindon (1996) have selected for the prolificacy gene within their Booroola flock until the vast majority are homozygous carriers. In the RIAP flock of ITT sheep the ewes have been retrospectively separated into genotypes on the basis of their lifetime breeding records (Bradford et al., 1991; Inounu et al., 1993; Subandriyo and Inounu, 1994). The mean litter sizes of the homozygous carriers are comparable, Booroola 2.59 (Piper and Bindon, 1996) and ITT 2.83 (Bradford et al., 1991). However, there is a large difference between the corresponding ovulation rates, Booroola 5.65 and ITT 2.92, which reflects the means and variances of ovulation rates discussed above.

4. Other small ruminants on Java

ITT sheep are the predominant breed of the wet province of West Java, and Javanese fat tail (JFT) sheep predominate in the drier province of East Java. Both breeds of sheep have been on Java for centuries, both are prolific, and they have similar distributions of litter size, Tables 2 and 10. The RIAP sheep are referred to as a thin tail flock, but approximately 20% of the genetic material came from JFT ewes (Inounu et al., 1993). The ranges of the breeds overlap in Central Java, and it is probable, but not certain, that both breeds carry the same gene. There are two main breeds of goat on Java, one a crossbred bean goat (kambing kacang) which has been there for centuries, and the other predominantly Jamnapari (Ettawah), a more recent importation. Both are prolific (Obst et al., 1980), Table 10. So the animal husbandry environment on Java favours prolificacy in small ruminants.
5. Utility of ITT sheep

In a hot humid environment, ITT sheep are highly productive (Reese et al., 1990; Iniguez et al., 1991; Inounu et al., 1993). In a managed production program, it would be necessary to select the appropriate mix of prolificacy genotypes to optimise production on the available feed (Bradford et al., 1991). Given the lability of the frequency of $FecJ^P$, the equilibrium mix of genotypes will respond to the level of husbandry provided. If that mix is not that which is desired, then the frequency could be maintained at a different level by using rams of an appropriate carrier status. All breeds in which a major gene for prolificacy is segregating have the problem of rearing the large litters produced by homozygous carrier ewes, and it unlikely that a solution can be found in any realistic intensive production system in a developing country. If a breed is required for production of meat in a semi-intensive system in the humid tropics, the ITT sheep offer adaptation to hot wet climates, prolificacy, 1.8 lambings per year and parasite resistance. Resistance of ITT sheep against gastrointestinal nematodes is comparable with that of other resistant breeds (Romjali et al., 1997), but there are still situations where chemical control is beneficial (Handayani and Gatenby, 1988). ITT sheep have very high resistance against *Fasciola gigantica* (Roberts et al., 1997a), possibly controlled by a major gene (Roberts et al., 1997b), which may be unique.

Acknowledgements

Opportunities to work for several years with Indonesian colleagues in livestock industries on ADAB, CIDA and ACIAR projects are greatly appreciated.

References


Table 10

Distributions of litter sizes in institutional flocks of Javanese fat tail sheep and Javanese goats

<table>
<thead>
<tr>
<th>Breed/species</th>
<th>Parity</th>
<th>Frequency distributions of litter sizes (%)</th>
<th>Mean litter size</th>
<th>Founding stock</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Single Twin Triplet Quadruplet</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>JFT sheep</td>
<td></td>
<td>51 43 5 1</td>
<td>1.56</td>
<td>E. Java</td>
<td>Wardojo and Adinata, 1956*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>51 33 14 2</td>
<td>1.87</td>
<td>Madura</td>
<td>Obst et al., 1980</td>
</tr>
<tr>
<td>First</td>
<td></td>
<td>52 42 6 0</td>
<td>1.54</td>
<td>E. Java</td>
<td>Bradford et al., 1986</td>
</tr>
<tr>
<td>Second</td>
<td></td>
<td>46 33 20 0</td>
<td>1.72</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bean goat X</td>
<td></td>
<td>50 35 12 3</td>
<td>1.68</td>
<td>Not stated</td>
<td>Iniguez and Gunawan, 1990</td>
</tr>
<tr>
<td>Jamnapari goat</td>
<td></td>
<td>25 46 24 5</td>
<td>2.08</td>
<td>W. Java</td>
<td>Obst et al., 1980</td>
</tr>
<tr>
<td></td>
<td></td>
<td>32 55 13 0</td>
<td>1.81</td>
<td>C. Java</td>
<td>Obst et al., 1980</td>
</tr>
</tbody>
</table>

* Data cited by Mason (1980).


