Review

Promoting Sustainable Utilization and Genetic Improvement of Indonesian Local Beef Cattle Breeds: A Review

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Abstract: This paper reviews the literature relevant to the breeding of cattle grazed in tropical environments and particularly Indonesia. The aim is to identify new breeding opportunities for cattle owned by Indonesia's smallholder farmers, whilst also conserving unique local cattle beef breeds. Crossbreeding has been practiced extensively in Indonesia, but to date there have been no well-designed programs, resulting in many mixed-breed animals and no ability to determine their genetic composition, productive capabilities or adaptation to environmental stressors. An example of within-breed selection of Bali cattle based on measured live weight has similarly disregarded other productive and adaptive traits. It is unlikely that smallholder farmers could manage effective crossbreeding programs due to the complexities of management required. However, a tropically adapted composite breed(s) could perhaps be developed and improved using within-breed selection. Establishing reference population(s) of local breeds or composites and using within-breed selection to genetically improve those herds may be feasible, particularly if international collaborations can be established to allow data-pooling across countries. The use of genomic information and a strong focus on all economically important traits in practical breeding objectives is critical to enable genetic improvement and conservation of unique Indonesian cattle breeds.

Keywords: beef cattle; tropical environments; crossbreeding; within-breed selection; genomic selection; productive traits; resistance to environmental stressors; reference populations; breed conservation

1. Introduction

About 120 million Indonesians, or ~11% of the country's total population, live on less than USD2 per day, with another ~40% of Indonesia's population vulnerable to falling into poverty as their income hovers marginally above the national poverty line. The agricultural sector employs two thirds of Indonesia's poor and hence, it represents a vitally important component of Indonesia's economy.

Demand for beef in Indonesia has been increasing due to growth in population and household income. However, demand has been outstripping supply, and the self-sufficiency ratio at a national level has hovered around 65% over the past 10 years, requiring 30–40% of beef to be met by imports, mainly live cattle and frozen beef from overseas [1].

About 6.5 million smallholder farmers living in rural areas across Indonesia produce ~90% of the beef produced in Indonesia, while the remaining ~10% of beef production is delivered by a small number of commercial farmers (<1% of all beef farmers) and large beef cattle companies concentrated primarily in Java [2]. A very strong opportunity, therefore, exists to strengthen Indonesia's beef sector, to improve the productivity and profitability of smallholder beef farmers and to also improve the livelihoods of Indonesia's rural poor.

Beef cattle production in Indonesia is increasing through ongoing improvements of cattle health and growth and reproduction rates and reducing cattle death rates through improved cattle management (for example, the use of forage tree legumes in intensive and extensive cattle production systems) [3–9]. Genetic improvement of the existing cattle population would also be a very feasible opportunity if effective options to identify genetically superior breeding cattle could be developed and implemented [2].

This paper, therefore, undertakes a review of the scientific literature relevant to genetic improvement programs in tropical environments with a specific aim of identifying the best opportunity or opportunities to genetically improve beef cattle in Indonesia. It examines the value of existing crossbreeding and within-breed selection programs in Indonesia as well as the potential role of new genomic (DNA-based) tools to improve on-farm productivity and business profitability. An additional aim in designing new breeding programs for Indonesia must be the conservation of indigenous cattle genetic resources where their ongoing viability may be endangered. Hence, the review also considers their conservation, with the aim of making recommendations on the best option(s) available for smallholder cattle farmers in Indonesia in the foreseeable future.

2. Indonesian Beef Production and Marketing Systems

Knowledge of specific beef production and marketing systems is required for the design of relevant breeding objectives underpinning effective genetic improvement programs. In Indonesia, smallholder farmers use a wide range of crop residues and by-products to feed and manage cattle through intensive or extensive production systems. Intensive systems, typical of areas where availability of grazing land is scarce, use stalls to house the cattle and cut-and-carry feeding systems, primarily to fatten sale cattle. Under extensive systems, cattle are free-grazing. Extensive systems apply only where greater land areas exist (e.g., eastern Indonesia) and are generally used for breeding and growing young cattle prior to the sale for fattening.

Extensive research in eastern Indonesia shows that cattle numbers, beef production, reproduction and farm profitability can all be significantly increased for cow-calf systems and cattle fattening operations that are closely integrated with dryland farming systems [3,5–9]. In those regions, Bali cattle (*Bos javanicus*) are most often used by smallholder farmers, although some crossbred animals of unknown breed composition and bred using artificial insemination (AI) are used for fattening. In Central Java and other areas of Indonesia, where cattle grazing under palm oil plantations is strongly encouraged by the Government of Indonesia [10], crossbred cattle are preferred by the farmers although the economic yield is similar to that of local cattle. This is because crossbred cattle are taller and cattle traders buy cattle primarily on the basis of their visual appearance, with larger body-framed animals (regardless of weight) attracting higher prices [11,12].

Cattle purchased by traders across Indonesia are subsequently slaughtered at local butcher shops and abattoirs, for purchase by consumers through local wet markets. However, ongoing research in Indonesia shows that very strong potential exists to establish new beef markets for Indonesian cattle slaughtered in modern commercial abattoirs that will reward smallholder farmers for the value of the product they deliver to consumers through large supermarkets, hospitality venues and tourist hotels across Indonesia [Dahlanuddin et al., University of Mataram, unpublished].

Although the sale of cattle through local traders is currently the main outlet for cattle from smallholder farmers, it is suggested that in the future, well-designed genetic improvement programs should target the specifications provided by these potential new markets as part of their breeding objective.

3. The Need for Cattle That Are Well Adapted to Tropical Beef Production Systems

Indonesia is a tropical country with an innately harsh environment. This means that Indonesian cattle are routinely exposed to numerous environmental stressors such as ecto-parasites (cattle ticks; horn-, buffalo- and screw-worm flies; other biting insects),

endo-parasites (gastro-intestinal helminths or worms), seasonally poor nutrition, high heat and humidity and diseases that are often transmitted by the parasites, with such exposure likely to increase significantly due to climate change over coming years. Each of these stressors has the potential to seriously impact the survival, growth and reproduction of the cattle. The impact of each stressor on production and animal welfare is often multiplicative rather than additive, particularly when animals are already undergoing physiological stress such as lactation, e.g., [13–16]. Under Indonesia's cattle production systems, it is generally not possible to control these stressors through cattle management strategies due to lack of access to treatments (either due to their high cost and/or non-availability in Indonesia) or the unwillingness of the Indonesian farmers to use them, often for cultural reasons. Even if intervention strategies were feasible, the treatments per sé often cause their own problems. For example, chemical treatments to control parasites generate concern about residues in beef products. As well, the parasites acquire resistance to the chemical treatments, creating additional parasite-control problems [17]. In intensive feedlot systems, high heat and humidity, even in the absence of other stressors, can become critically important for both production and animal welfare reasons. In such cases, management interventions may be possible, but they are difficult and/or expensive to implement, particularly in poorly adapted cattle. Hence, the best method of reducing the impacts of these stressors to improve productivity and animal welfare is to breed cattle that are productive in their presence, without the need for managerial interventions. In Indonesia, this means using cattle that are very well adapted to the harsh tropical environments, usually because they or their ancestors have evolved in those climates.

Differences in the performance of cattle breeds reared in tropical climates are often masked by the effects of environmental stressors on productive attributes [18,19]. In particular, British and European breeds perform differently in both temperate and tropical environments, with the European breeds growing faster to a larger mature size than British breeds when the feed supply is unlimited, but because of their larger breed size, they also take longer to conceive and calve than the British breeds. In tropical environments when feed is limited or of poor quality, the European breeds perform more poorly than the British breeds.

Hence, as summarized by [18] and adapted by [20], for most purposes in tropical environments, cattle breeds can be categorized into general breed types or groupings including:

- *Bos taurus* (British/European breeds that evolved in cooler British and European climates, e.g., Angus, Hereford/Limousin, Simmental);
- *Bos indicus* (breeds that evolved on the Indian sub-continent, e.g., Ongole, Brahman, Nelore);
- Tropically adapted taurine breeds (southern African Sanga, e.g., Afrikaner, Mashona; West African humpless, e.g., N'dama; and Criollo breeds of Latin America and the Caribbean, e.g., Romosinuano);
- Tropically adapted *Bos indicus* × *Bos taurus* composite breeds (e.g., Santa Gertrudis, Braford, Charbray);
- Tropically adapted taurine × British/Continental composite breeds (e.g., Bonsmara, Belmont Red, Senepol);
- East African zebu breeds (e.g., Boran); and
- The first cross (F_1) between *Bos indicus* and *Bos taurus*, which has attributes that are different from other breed types, particularly in harsher environments.

Additionally, and of direct relevance to Indonesia, *Bos javanicus* (Bali cattle) and *Bos banteng* (Banteng cattle) are believed to have each evolved from *Bos bibos* ancestors, but independently of these other breed types [21]. Bali cattle are hypothesized to have differences in their Y chromosomes relative to other species of cattle [22]. They can be crossed with *Bos taurus* and *Bos indicus*, though the male offspring are hypothesized to be infertile [23].

Comparative rankings of some of the different breed types for different characteristics in temperate and tropical environments based on [18] and adapted by [20] are shown in Table 1. Because of the paucity of direct breed-type comparisons from most tropical and

sub-tropical areas, the rankings in these regions are largely based on results from Belmont Research Station and from associated research programs in northern Australian beef industry herds [18,20]. Comparisons in temperate areas are largely derived from the Meat Animal Research Center in Nebraska, USA and related studies in warmer environments such as Florida, USA [18,20]. There are no known direct breed comparisons between *Bos javanicus* (Bali cattle) and the other breed types, so the rankings in Table 1 are inferred from breed performance summarized by [21].

Table 1. Comparative rankings of different breed types for productive traits in temperate and tropical environments and for adaptation to some stressors of tropical environments [18,20] (the higher the number, the better the performance for the trait, and the greater the resistance to environmental stressors).

Breed Type	*Bos taurus*		Adapted *Bos taurus*	*Bos indicus*		F_1 Brahman × British	*Bos javanicus* (Bali) [f]
	British [g]	European [e,g]	Sanga [g]	Indian [g]	African [g]		Indonesian
Temperate [a]							
Growth	4	5	3	3	2	4	3
Fertility	5	4	4	3	4	5	4
Tropical [a]							
Growth	2	2	3	4	2	4	3
Fertility	2	2	5	3	4	5	5
Mature size	4	5	3	4	3	4	3
Meat quality [b]	5	4	5	3	4	4	unknown
Resistance to environmental stressors							
Cattle ticks [c]	1	1	4	5	5	4	4
Worms [d]	3	3	3	5	4	4	unknown
Eye disease	2	3	3	5	4	4	unknown
Heat	2	2	5	5	5	5	5
Drought	2	1	5	5	5	4	5

[a] A temperate environment is assumed to be one free of environmental stressors, while tropical environment rankings apply where all environmental stressors are operating. Hence, while a score of, for example, 5 for fertility in a tropical environment indicates that breed type would have the highest fertility in that environment, the actual level of fertility may be less than the actual level of fertility for breeds reared in a temperate area, due to the effect of environmental stressors that reduce reproductive performance. [b] Principally meat tenderness. [c] *Rhipicephalus (boophilus) microplus*. [d] Specifically *Oesophagostomum*, *Haemonchus*, *Trichostrongylus* and *Cooperia* spp. [e] Data from purebred European breeds are not available in tropical environments and responses are predicted from the CSIRO Rockhampton crossbreeding data. [f] No direct comparisons available, so rankings should be regarded as indicative only. [g] British breeds include for example Hereford, Angus and Shorthorn; European breeds include for example Charolais, Simmental and Limousin; Sanga breeds include for example Afrikaner, Mashona and Ndama; *Bos indicus*—Indian breeds include for example Ongole, Brahman and Nelore; *Bos indicus*—African breeds include for example Boran.

The comparative rankings shown in Table 1 suggest that potentially the best breeds for use in Indonesian cattle production systems are likely to include the tropically adapted taurine breeds and *Bos javanicus* (as either pure breeds or composites that retain sufficient levels of resistance to environmental stressors) or crossbreeding programs that focus on combining both productive and adaptive traits.

4. Indonesian Cattle Breeds

As the second largest biodiversity, Indonesia possesses a collection of native and local cattle breeds. These types of cattle have in the past been considered to be less efficient [24] and less productive [25] relative to the imported genetically improved *Bos taurus* (taurine) breeds. However, the perceptions of those earlier studies are not based on scientifically valid breed comparisons under tropical production systems. Hence, recommendations about the use of imported genetically improved *Bos taurus* (other than in well-designed crossbreeding programs based on tropically adapted cow breeds) are unlikely to be valid under Indonesian beef production environments.

The most common local breeds farmed by beef producers in Indonesia are Bali (*Bos javanicus*), Peranakan Ongole Grade (PO, *Bos indicus*) and Madura cattle, an ancient stabilized cross possibly based on combinations of *Bos bibos*, *Bos indicus* and *Bos taurus*, but with the breeds of origin yet to be accurately determined.

To date, no well-designed studies have been undertaken to actually determine whether the perceived low productivity in local cattle is due to poor management and inadequate nutrition (that will impact to an even greater degree on the poorly adapted taurine breeds being introduced to Indonesia), or because they are yet to undergo any well-designed genetic improvement programs, or both.

4.1. Bali Cattle (Bos javanicus)

Bali cattle (*Bos javanicus*) are native Indonesian cattle, believed to have possibly originated from wild Banteng and domesticated on Bali island [26,27]. Based on archaeological data from Indonesia there is no evidence that cattle were introduced in Java or Bali before the advent of Hinduism, suggesting that Bali cattle have been domesticated for less than 2000 years [28]. This helps explain why the physical characteristics of domestic Bali cattle are so similar to those of the wild Banteng (Figure 1). Bali cattle are visibly smaller relative to *Bos indicus* or *Bos taurus* breeds, but they are inferred to be more robust than the *Bos taurus* breeds in coping with stressors of harsh tropical environments and poor-quality feed (Table 1). Several reports document their good reproductive performance [21,27,29], though it should also be noted these reports are not based on scientifically valid direct comparisons with other breeds of cattle. Bali cattle are also reportedly highly resistant to infections by ticks and tick-borne diseases, but highly susceptible to Jembrana disease [30,31]. Jembrana is a disease with symptoms similar to Malignant Catarrhal Fever (MCF), capable of infecting cattle, buffalo, swine and sheep. In Bali cattle, the most visible clinical symptoms include high fever and severe diarrhea, which can lead to death [32]. Unfortunately, none of these reports on the performance of Bali cattle is based on well-designed experimental comparisons of their performance relative to other breeds, so the need for genuine breed comparisons remains for future research.

Figure 1. Images of Bali (*Bos javanicus*) breed animals: (**A**) Bali bull at final weight prior to slaughter; and (**B**) Bali cow and calf.

Nowadays, Bali cattle populations are spread across the Indonesian archipelago, mainly in the islands of Bali, Sumatra, Kalimantan, Java and East and West Nusa Tenggara. In Bali, they are managed in intensive and semi-intensive systems, whilst in Sumatra and Kalimantan they mostly integrated with palm oil plantations. In East and West Nusa Tenggara they are reared on a mix of intensive (cut-and-carry, stall-based) and extensive pasture systems [29].

Although Bali cattle are smaller than other *Bos indicus* and *Bos taurus* breeds, and even though there are no results from well-designed breed comparisons yet available, it can be

interpreted that *Bos javanicus* cattle are well adapted and productive in Indonesia's tropical beef production systems. Additionally, because they are a unique species of cattle they warrant ongoing conservation. Ideally in the near future, the genome of these cattle will be sequenced for the first time, to allow a better understanding of their unique attributes relative to other *Bos* spp. (e.g., *Bos indicus, Bos taurus*), as well as to assist in the design of within-breed selection programs to enhance their conservation. We are currently exploring opportunities through Indonesian and international agencies to secure funding to sequence the unique Indonesian cattle breeds and enable this comparison.

4.2. Ongole Grade Cattle (PO)

Peranakan Ongole cattle (PO) are derived from Ongole or Sumba Ongole [33]. Towards the end of the 19th century, several Indian *Bos indicus* breeds were imported into Indonesia for use as dual-purpose, draught/beef animals, with the Ongole (known elsewhere as Nelore) deemed the most suitable [28]. Hence, around 1914 all purebred Ongole cattle in Indonesia were sent to the Island of Sumba, where they were managed as a purebred herd, with the herd gradually expanding and purebred Ongole bulls subsequently exported from Sumba to other Indonesian islands to be used for crossbreeding purposes [28]. Ongole cattle are a specific breed from within the *Bos indicus* species, though a recent study [34] found that *Bos javanicus* contributes about 6–7% of the average breed composition of PO cattle. PO cattle are now mainly found in the island of Java (90%), with the remainder located in Lampung, South Sumatra, North Sumatra, Central Sulawesi and North Sulawesi provinces [35]. PO cattle were developed for draught purposes. Hence, they are large with strong bodies (Figure 2) as well as being docile and tolerant to heat and other environmental stressors [27], though again there are no scientifically valid comparisons relative to other cattle breeds.

Figure 2. Images of Ongole grade (*Bos indicus*) breed animals: (**A**) Ongole bulls in a traditional Indonesian cattle market; and (**B**) Ongole cow and calf.

The characteristics of productive and reproductive traits of PO cattle are summarized in Table 2, but as with the performance of Bali cattle, the results are not based on scientifically valid comparisons of performance relative to other breeds managed under the same production conditions.

Table 2. Productive and reproductive characteristics of Ongole grade (PO) cattle (Note these figures are not based on scientifically valid breed comparisons, so such comparisons can only be inferred from the different studies).

Trait	Number of Animals	Mean ± sd	Production System [Reference]
Birth weight (kg)	59	30.91 ± 1.97	Govt. facility, Kendal, Central Java [36]
	309	31.09 ± 5.31	Farmers, Kebumen, Central Java [37]
Weaning weight (kg)	59	110.10 ± 11.20	Govt. facility, Kendal, Central Java [36]
	165	102.10 ± 12.19	Govt. facility, Grati, East Java [38]
	1819	98.87 ± 1.97	Farm, Tanjungsari, Lampung [39]
Yearling weight (kg)	165	127.30 ± 0.27	Govt facility, Grati, East Java [38]
First mating (month)	1407	23.06 ± 0.93	Farmers, Kebumen, Central Java [40]
	35	22–28	Govt facility, Ciamis, West Java [41]
First calving (month)	1407	32.46 ± 0.90	Farmers, Kebumen, Central Java [40]
Post-partum mating (month)	1407	4.37 ± 0.64	Farmers, Kebumen, Central Java [40]
	103	2.38 ± 0.86	Farmers, Tuban, East Java [42]
Service per conception	1407	1.97 ± 0.20	Farmers, Kebumen, Central Java [40]
	55	2.11	Govt facility, Ciamis, West Java [43]
	60	1.18 ± 0.39	Farmers, Lamongan, East Java [44]
Calving interval	103	16.94 ± 2.19	Farmers, Tuban, East Java [42]
	55	15.39 ± 2.43	Govt facility, Ciamis, West Java [43]

PO cattle are mostly kept by smallholder farmers in Java under low-input/low-output production systems, with low average daily gains of around 0.25 kg/day [45]. However, under a controlled research environment with fermented sorghum based feed, the average daily gain of PO cattle ranged from 0.8 to 0.9 kg/day [46], while Ongole cattle directly imported from Sumba and reared under grain-based feed in the same research centre based on a diet of 12.5% crude protein yielded an average daily gain of 0.94 kg/day [47].

Over recent decades the main genetic improvement strategy for PO cattle has focused on upgrading the breed to Brahman or Brahman cross [27], using Brahman semen to inseminate the existing PO females. As both PO and Brahman are *Bos indicus* breeds, the practice in Indonesia has been to name the resulting crossbred progeny as Brahman crosses. If the female crossbreds are subsequently inseminated again with Brahman semen, the progeny closely resemble the Brahman breed and hence, locally, they are known as Brahman.

Over the last two decades there has also been a marked change in the purpose of this breed, with an important use of the Ongole breed now being as dams in crossbreeding programs with exotic breeds such as Simmental and Limousin, using imported semen and AI. The F_1 crossbreds derived from this type of cross have proven to be highly productive in both tropical and temperate environments, because the very great genetic diversity between *Bos indicus* and *Bos taurus* ensures heterosis or hybrid vigour is maximized (Table 1). However, careful consideration needs to be given to how the F_1 crossbreds are subsequently used in breeding programs because of the strong possibility they will be joined with an inappropriate third breed, resulting in progeny that are poorly adapted to the stressors of tropical environments.

Based on the performance of PO cattle inferred from Table 2 (albeit in the absence of scientifically valid breed comparisons), their productive and reproductive characteristics suggest their performance does not differ markedly from other *Bos indicus* breeds. This in turn suggests that conservation of the PO as a pure breed may not be justified, particularly when it is considered the breed has been genetically improved through well-designed and commercially focused breeding programs in Brazil (where it is known as Nelore) over many generations. Rather, their best use may be as a dam breed in well-designed crossbreeding programs or in formation of composite breed(s) that specifically match the requirements of cattle production systems in Indonesia, as described in more detail in subsequent sections of this paper.

4.3. Madura Cattle

Madura cattle were initially believed to be derived from ancient crossbreeding of Bali and/or the wild ox *Bos bibos* and zebu cattle either in Madura or in Java, with the crossbreeding believed to have occurred ~1500 years ago when Indian culture was introduced to Indonesia [48]. In 1977, those authors [48] suggested that phenotypic evidence indicated Madura cattle could have been derived from three-way crosses between *Bos bibos* spp., *Bos indicus* and *Bos taurus* types. This theory has received substantial support from [49] based on the geographical distribution of bovine haemoglobin beta (Hbb) alleles in Southeast Asian cattle. That study on the genetic components of Indonesian cattle confirmed the mitochondrial DNA of Madura cattle was a mix of zebu (*Bos indicus*) and Banteng, while the Y chromosome contained traces of zebu and *Bos taurus* breeds [26]. A three-way cross that excluded Bali cattle may also explain why Madura bulls do not appear to suffer the same fertility problems as are believed to occur for crosses between Bali cattle and *Bos taurus* or *Bos indicus* [23].

Hence, Madura cattle are a unique, stabilized composite of different *Bos* spp., with the precise composition of *Bos* spp. still to be determined. Determination of the specific breed composition will best be achieved through use of genomic sequence information, as suggested in a later section of this paper.

Madura cattle are small- to medium-sized animals, with very homogenous but unique characteristics [28]. Full details of their characteristics are provided by [48,49]. They are reported to be one of the best draught cattle breeds and are very well adapted to the local conditions and traditional management systems of Indonesia [50], though again, the reports are not based on scientifically valid breed comparisons. Madura cattle are now distributed in East Java, Kalimantan, Sulawesi and East and West Nusa Tenggara Islands in Indonesia [51] and are popular for their perceived good beef quality and their ability to grow under harsh tropical environments [52], although another report suggests Madura cows only produce sufficient milk for their calves to grow slowly [28]. They are also reputed to be more resistant to Jembrana disease than Bali cattle [53]. Hence, they are very well accepted in Indonesia's dryland farming systems, particularly with regard to what are perceived to be higher growth and reproduction rates relative to Bali cattle [50].

Other than the common Madura cattle that have no cultural function (and where no sustained genetic improvement has occurred), there are two types of Madura cattle, namely Sonok and Karapan. Karapan is a bull racing event where Madura bulls are used. Sonok is also a cultural event, but where female Madura cattle are used in conformation contests (Figure 3).

Past selection within both the Sonok and Karapan lines has therefore been based on attributes that improve the ability of the animals to compete in these cultural events. Karapan cattle are characterized for their strength, agility and aggressiveness. By contrast, female Sonok cattle are judged by conformation traits, such as height at their withers, colour, body conformation, body condition, health and harmonious walking in a pair [50]. Bulls in the Sonok population must be descendants from cows that participate in Sonok contests. They are selected on phenotype, especially body conformation and some "beauty" standards (coat colour, horn shape, eye shape, etc.). Cows that perform well in Sonok contests and their male descendants are very popular for breeding purposes.

Hence, these two traditional festivals became the means for traditional selection and conservation of Madura cattle, and that may continue into the future unless the farmers are encouraged to change their breeding objectives to focus on profitability traits to service commercial beef markets. Caution should be taken though regarding these traditional breeding practices. As animal records are non-existent and the demand for superior males for breeding purposes is very high, there are reasons to be suspicious that the inbreeding level may be high. An unpublished study by Prastowo and Widyas in 2018 on the SRY genes of 18 Sonok bulls showed those genes can be narrowed down to just three haplotype groups. The productive and reproductive characteristics of Madura cattle are shown in Table 3.

Table 3. Productive and reproductive characteristics of Madura cattle (note these studies are not based on scientifically valid breed comparisons).

Trait	Mean ± s.d.	Number of Animals	Breed (Type)	Reference
Birth weight (kg)	16.89 ± 2.86	60	Madura	[53]
	16.25 ± 2.37	77	Madura male	[54]
	17.08 ± 2.40	60	Madura female	[54]
Weaning weight (kg)	90.32 ± 3.42	186	Madura	[55]
	97 ± 13.77	84	Madura	[56]
	151.58 ± 36.98	24	Madura (Sonok) female	[57]
Yearling weight (kg)	122.17 ± 6.15	186	Madura	[55]
	120 ± 10.86	84	Madura	[56]
	247.55 ± 40.48	11	Madura (Sonok) female	[57]
Mature weight (kg)	294.3 ± 43.0	30	Madura (Karapan) female	[54]
	279.1 ± 89.0	30	Madura female	[54]
	392.3 ± 60.4	37	Madura (Sonok) female	[54]
First mating (month)	198.5 ± 0.81	59	Madura	[52]
	22.63	39	Madura (Karapan)	[58]
	23.40 ± 4.17	291	Madura (Sonok)	[59]
First calving (month)	29.96 ± 0.81	59	Madura	[52]
	33.92 ± 3.88	291	Madura (Sonok)	[59]
Post partum mating (month)	3.44 ± 0.17	59	Madura	[52]
	2.57	39	Madura (Karapan)	[58]
	3.40	25	Madura (Sonok)	[58]
	1.48 ± 0.09	59	Madura	[52]
	1.47	39	Madura (Karapan)	[58]
	1.59 ± 0.3	291	Madura (Sonok)	[59]
Open Days (day)	5.53 ± 0.65	291	Madura (Sonok)	[59]

Currently there is insufficient information to determine whether conservation of the Madura breed as a pure breed is warranted because, depending on the genomic composition of the breed, it may be possible to regenerate the breed through crossbreeding. However, if the breed can be demonstrated scientifically to be more resistant to Jembrana disease [51], and have better growth and reproductive performance than Bali cattle [48], then conservation and selection of the breed based on existing populations would be much more useful than attempting to regenerate the breed.

Ongoing use of the breed also depends on whether future uses of the Madura breed are primarily commercially market-driven (where objectively measured traits in the breeding objectives are important and hence, their performance relative to other cattle breeds must be a strong consideration) or whether future breeding programs remain focused on traditional or cultural uses of the breed. The breeding objectives for these different uses of the cattle differ substantially, so if future breeding programs remain focused on cultural uses, then conservation of the breed would be justified due to the lengthy history of genetic improvement within the breed based on selection for cultural attributes, with perhaps a 'desired gains' approach being used to derive economic weightings for these cultural attributes in future (see Section 6.1 for further discussion of different types of breeding objectives).
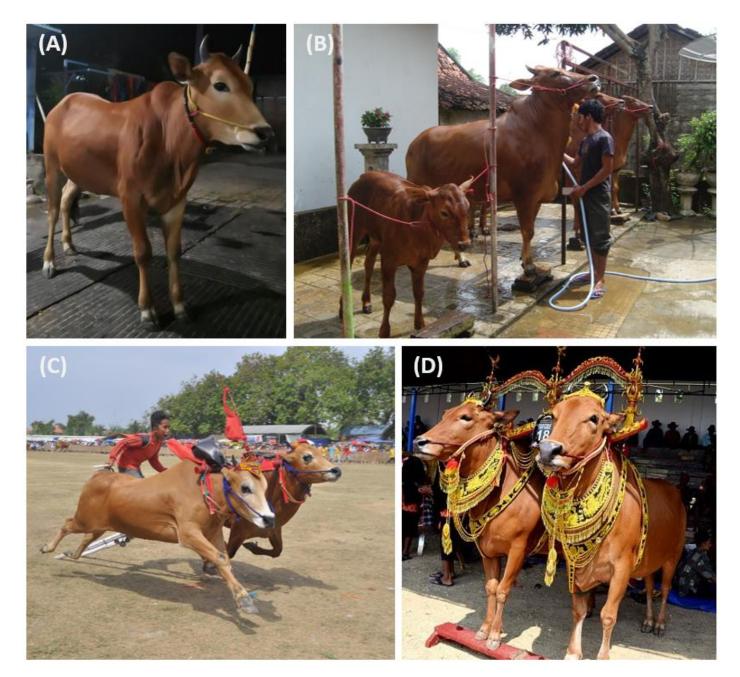
Figure 3. Images of Madura breed animals: (**A**) Madura bull–these bulls are typically selected for their strength, agility and aggressiveness to participate in Karapan cultural events; (**B**) Madura cows and calf; (**C**) Madura bulls participating in a Karapan contest; and (**D**) Madura cows used in Sonok cultural events, where they are traditionally selected on their conformation traits as well as their ability to walk harmoniously as a pair in these Sonok events.

Additional information about the Madura's breed composition through genomic analyses and ideally, additional phenotypic information of the Madura relative to the performance of other cattle breeds in well designed, controlled experiments would assist in decisions about the need to conserve the breed.

4.4. Challenges to Improving These Indonesian Cattle Breeds

Indonesia has established initiatives aimed at conservation and genetic improvement of Indonesian local cattle but those initiatives are unable to operate as needed to ensure genetic improvement is focused on both cattle productivity and adaptation. By way of

example, the Bali cattle breeding centre located on the island of Bali conducts progeny tests to identify the "best" sires within the population [60]. Proven bulls from the breeding centres are then sold to AI centres, with semen from the bulls sold to farms across Indonesia. However, such progeny tests only rank the bull candidates based on the growth performance of their offspring, completely ignoring other economically important attributes in the offspring such as reproductive performance, beef quality and resistance or tolerance to environmental stressors. Together with an Indonesian law that forbids the importation of any cattle to Bali to ensure "pure" Bali cattle are conserved on Bali Island, the export of the best genetic resources from Bali each year (via semen sales from the AI centre to all areas of Indonesia) may have actually decreased the genetic merit of Bali cattle. By contrast, in the extensive production systems of Indonesia's palm oil plantations, Bali cattle are allowed to roam and mate naturally, with no formal breeding program applied and mating amongst relatives being common, potentially resulting in high levels of inbreeding.

The island of Madura is also subjected to the same law that forbids the importation of cattle to the island. However, unlike Bali, there is no facility responsible for breeding Madura cattle. Rather, cultural events have been primarily responsible for stimulating smallholder farmers to select female cattle based on body conformation, appearance and behavior and bulls on their strength and aggressiveness. Such selection was undertaken traditionally with no formal knowledge of animal breeding, though farmers are aware of the drawbacks of inbreeding even though that cannot be avoided completely due to limited population size. The use of visual appraisal to select breeding cattle has improved the cultural value of cattle, particularly in the Sonok population [61], with their productive performance generally regarded as comparable to their respective crossbred populations [50].

Hence, to improve the productivity and adaptation of cattle herds across Indonesia, well designed genetic improvement programs (crossbreeding and/or within-breed selection) need to be implemented, with a strong focus on economically important productive, adaptive and fitness traits and consideration also given to conservation of unique cattle breeds through development of practical breeding objectives, as suggested by [62] Nielsen et al. (2014).

5. Achieving Genetic Improvement by Crossbreeding

Crossbreeding has been widely used to improve livestock productivity in many countries to capture the advantages of heterosis or hybrid vigour resulting from crossing genetically diverse breeds [2,25]. Key reasons for crossbreeding include [63]:

- Generation of direct heterosis or hybrid vigor, measured as the extra performance of the crossbreds relative to their parental breeds. The percentage increase in performance ranges from 0–10% for growth traits and 5–25% for fertility traits [64], but the effect of heterosis on the total production system can be greater than this, as effects accumulate over traits e.g., [65]:
- The averaging of breed effects, to breed an animal of intermediate size to fit a particular management cycle or market demand and could involve either regular systems of crossing or the creation of composite breeds e.g., [65];
- Maternal heterosis where crossbred cows exhibit considerable heterosis in their ability to rear fast-growing, viable offspring;
- Sire-dam complementation, where the crossbreeding system aims to use breeding cows of small to intermediate mature size (though not so small for dystocia to be a problem) as well as being fertile. When a large terminal sire breed is used over a smaller dam, the proportion of available feed directed to growing animals is increased for the benefit of the entire production system, particularly where breeding occurs through AI; and
- Breed complementarity whereby breeds used for the crossbreeding program are specifically selected so the strengths of one breed are used to complement or mask the weaknesses of another breed.

The advantages of crossbreeding are greatest in tropical beef production systems because of the need to use breed types with greater diversity (e.g., *B. indicus* × *B. taurus*)

to achieve adaptation in the offspring. This in turn maximizes the amount of heterosis in the cross [15,16,51,66,67]. However well-designed crossbreeding programs that reliably deliver improvements in productivity (other than the first crosses between unrelated breeds) are also very difficult to implement by most farmers globally due to the need to avoid reductions of heterosis (also known as recombination loss) in second and subsequent generation crossbreeds. This is particularly true in Indonesia, where sustainability of crossbreeding programs is frequently challenged by constraints such as poor adaptation of the crossbred progeny to the local environment or lack of logistical support [25]. Even in advanced countries with very large herds and sophisticated infrastructure, cattle breeders find it difficult to ensure segregation of bulls of one breed from cows of another to ensure appropriate crossbreeding. Hence, in those cases they have often preferred to develop stabilized composite breeds comprising appropriate admixtures of the different breed types.

In the following discussions on options for crossbreeding using Indonesia's cattle breeds, we acknowledge a considerable wealth of crossbreeding knowledge exists from other tropical areas of the world such as South and Central America, southern USA and northern Australia. However, we have elected not to present data from those studies because of the vastly different production systems, the significantly greater expertise and skills of the farmers in those different regions and their increased access to technologies for measurement and data capture relative to those of smallholder farmers in Indonesia.

To examine the feasibility of various crossbreeding programs in Indonesia's smallholder farming systems, Table 4 provides a brief examination of some selected crossbreeding designs and makes recommendations around which types of programs might be successful in Indonesia. In crossbreeding theory, there are many additional combinations of different cattle breeds, but at a practical level, none of the more complex systems is feasible for smallholder farmers in Indonesia and hence, they are deliberately excluded from Table 4.

Table 4. Examples of simple crossbreeding designs and the feasibility (as assessed by the authors) of managing them by Indonesia's smallholder beef farmers [25].

Crossbreeding System and Key Features	Feasibility of Implementation in Indonesia
F₁ cross: bulls of Breed A (e.g., *Bos indicus*) are joined to cows of unrelated Breed B (e.g., *Bos taurus*) to generate F_1 progeny (AB). F_1 AB progeny are then either sold or joined to a third unrelated breed as described in the next cross	Generating F_1 crosses between unrelated breeds using AI is feasible (see discussion below) but selling all F_1 females will cause problems for smallholder farmers unless they can purchase new purebred Breed B heifers to retain sufficient, productive females in their herds. If the F_1 females are used for breeding, then it is essential they be joined to a well-adapted, unrelated third breed of bull to ensure their progeny are sufficiently well adapted to environmental stressors
Backcross: F_1 AB females are backcrossed to a bull of either Breed A or breed B, generating progeny that are 25% Breed A, 75% Breed B or vice versa. In subsequent joinings, 75% Breed B females are joined to purebred Breed A bulls, generating progeny that are 62.5% Breed A, 37.5% Breed B or vice versa	The major problem with a backcross program in Indonesia is that, in addition to some loss of heterosis in the F_2 *et seq.* progeny, almost inevitably some progeny in F_2 *et seq.* generations (i.e. those comprising 62.5% *Bos taurus*) will lack the resistance to environmental stressors required to ensure their productivity in smallholder farming systems
Terminal three-breed cross: bulls of an unrelated Breed C (e.g., *Bos javanicus*) are joined with F_1 female AB progeny to generate progeny comprising 25% Breed A, 25% Breed B and 50% Breed C	If issues associated with retaining a productive breeding herd described above can be overcome, then a 3-breed cross is expected to be as productive as the F_1 AB cross, However all 3-breed cross progeny would need to be sold or used to form a composite breed. This means that, as with the F_1 cross above, smallholder farmers would need to purchase replacement females to maintain the size of their breeding herds. Such a system is unlikely to be feasible amongst smallholder farmers in Indonesia
Formation of composites or stabilized crossbreeds: an alternative to the 3-breed cross described above could be to inter-se mate bulls and females having the same (or additional) breeds in their genetic composition e.g., join F_1 Breed A × B bulls with F_1 Breed C × Breed D females to produce F_2 progeny with 25% of each of Breeds A, B, C and D and then continue to inter-sé join the 25% A × B × C × D progeny over subsequent generations	Providing the progeny of these crosses were sufficiently resistant to the stressors of tropical climate, development and maintenance of a composite breed in this type of design would capture the benefits of heterosis and the system could be managed in a relatively straightforward way by smallholder farmers. Ideally, a progeny test program could be introduced in Indonesia to identify genetically superior animals in such a stabilized composite breed (see later section in this paper). And if the third unrelated breed type included a representative breed(s) from the tropically adapted taurine breeds (Table 1), then expected recombination losses due to epistasis would be significantly reduced relative to F_2 *et seq.* crosses between *Bos indicus* × *Bos taurus*

The Indonesian government initiated crossbreeding programs based on AI and imported semen in the early 1980s [51]. Although those programs have continued to be supported by a number of government incentives since then, significant improvements in the productivity of beef herds in the country are yet to be demonstrated [2], probably because F_2 *et seq.* generation crossbred progeny experienced recombination losses due to the difficulties in maintaining appropriate crosses of the different parental breeds in smallholder farmer herds. Some successes in improving individual animal productivity were achieved, but there has been no widespread impact on increasing cattle growth rates or the national cattle population through the improved reproductive performance of crossbred females [51], with no economic benefits at the farm level and no observable improvement in the adaptation of the crossbred offspring to the environmental stressors [51].

The lack of control of these Indonesian crossbreeding programs at the farm level has led to the emergence of unidentified mixed breeds of cattle [65]. Without good knowledge of the composition of these cattle in terms of 'adapted' versus 'productive' genetics, it has not been possible to achieve the primary aim of crossbreeding in Indonesia i.e., to maximize animal productivity without compromising cattle adaptation to the tropical environment [19]. Furthermore, these poorly designed crossbreeding programs may have jeopardized the ongoing conservation of unique local cattle genetic resources, which need to be retained to maintain biodiversity.

Some examples of simple crossbreeding systems based on Bali and Madura cattle in Indonesia are summarized below to allow recommendations to be made on the future directions of genetic improvement of cattle herds in Indonesia (either through crossbreeding and/or within-breed selection–see later sections of this paper.)

Crossbreeding has occurred between *Bos javanicus* (Bali) and *Bos taurus* or *Bos indicus* breeds outside Bali Island. The crossbred progeny had improved growth performance relative to pure Bali cattle [68–71], but field observations reported the male progeny had reproductive problems. Another problem was related to high mortality rate of calves under extensive production systems [29]. Causes of these high mortality rates have not been identified but field reports from oil palm plantations suggest that female Bali cattle have poor mothering abilities as they often left their new-born calves under those extensive production systems, thereby contributing to the high calf mortality rates. Previous studies also showed a decline of population size and genetic quality of Bali cattle represented by a decrease of growth-related traits (such as body size and weight) over generations [27,72].

Table 5 reports results of crossbreeding experiments based on progeny of Bali females and F_1 crosses with Simmental, Limousin, Brahman and PO bulls. The crossbreeding results are derived from independent experiments in AI centres in Papua and Nusa Tenggara provinces, while the exotic breed purebred data are derived from other AI centres. Hence the results are not directly comparable across experiments and should therefore be interpreted with care. The F_1 crossbred progeny were heavier at weaning (standardized to 205 days) and yearling ages, had higher average daily gains from the age of 7 to 12 months and they had larger body measurements compared to purebred Bali progeny. Table 5 was derived from [71] and compares economically important traits in beef cattle from different studies. It was aimed to give an initial awareness that crossbreeding using Bali cattle as dams to genetically improve their productivity requires greater consideration. It was concluded that the benefits of hybrid vigor or heterosis just for these growth traits were maximized due to the genetic diversity of the parental breeds [71].

Table 5. Growth performance of the progeny of purebred Bali cows and F_1 crosses with unrelated sire breeds.

Breed	Weaning Weight (Kg)	Yearling Weight (Kg)	Average Daily Gain [1] (Kg/day)	Body Measurement (cm) [2]		
				Wither Height	Body Length	Chest Girth
Bali (in Bali)	85.61 ± 14.30 [1]	135.09 ± 24.22 [1]	0.36 ± 0.24	107 ± 7.58	112.6 ± 11.67	149.2 ± 8.64
Simmental	235.50	430.00	-	-	-	-
Limousin	225.00	394.50	-	-	-	-
Brahman	223.50	372.00	-	-	-	-
PO	102.13	134.30	-	-	-	-
F_1 Simmental × Bali	131.61	179.21	0.26 ± 0.12	119.8 ± 4.76	123 ± 2.55	155.2 ± 14.15
	105.65 ± 5.27 [3]	200.43 ± 21.52 [3]				
	121.67 ± 16.18 [4]	230.98 ± 30.23 [4]				
F_1 Limousin × Bali	128.75	176.80	0.38 ± 0.06	119.2 ± 2.95	120.4 ± 10.04	153.6 ± 3.85
F_1 Brahman × Bali	115.90	157.60	0.45 ± 0.21	120.71 ± 4.31	127.43 ± 13.21	163 ± 12.9
F_1 PO × Bali	111.66	148.25	0.41 ± 0.25	120.4 ± 3.36	124 ± 7.04	339.2 ± 43.61

[1] [71]; [2] [70]; [3] [68] in lowland; [4] [68] in highland.

In contrast to growth traits for male progeny in Table 5, the female F_1 Bali crossbreds had poorer reproductive performance than their purebred Bali contemporaries. A similar occurrence of infertility was reported in other groups of male crossbred offspring [73]. The reproductive performance of F1 Bali × Simmental and F1 Bali × Limousin females is worse compared to similar groups of purebred Bali female cattle that were reared by smallholder farmers with similar production systems but not in the same contemporary group as the crossbred females (Table 6). The crossbreds had longer days open and increased calving intervals, lower pregnancy and calving rates, and higher pre-weaning mortality rates, resulting in the crossbreds having lower overall reproductive efficiency compared to purebred Bali females reared by smallholder farmers with similar production systems. These results are atypical of most crossbreeding studies elsewhere, where generally the greatest heterosis is achieved in traits with the lowest heritabilities, such as female reproductive performance, meaning that F_1 crossbreds usually out-perform either of the parental breeds. Reasons for these results in Indonesia could be due to the need for significantly greater feed inputs in the much larger crossbred females. In beef cattle production systems, female reproductive performance is a key trait and considered to be the most important factor economically [74], especially for smallholder farmer cow-calf production systems. Poor reproductive performance of breeding cows results in major economic losses, due to the additional expenses needed for feed, labor, breeding and animal health costs as well as the costs of calf losses [74].

It is possible that chromosome number imbalance from crossing of Bali cattle (*Bos javanicus*) with *Bos taurus* and *Bos indicus* species may have resulted in infertility of the female crosses, not only in males as suggested by [23]. However, it should also be noted that the reproductive performance of all breeds in this table are higher than the reproductive performance reported by most studies undertaken in extensive tropical pastoral production systems elsewhere in the world, suggesting that genetic aberrations are unlikely to be the reason for this lower performance of the crossbreds. It is possible the high reproduction rates simply reflect the low numbers of animals owned by smallholder farmers and hence, improved management of individual breeding cows is not only feasible but also very likely. Although the studies are not directly comparable, based on these results and the high economic weighting of reproductive performance in most cow-calf breeding objectives, smallholder farmers would likely improve the productivity and profitability of their herds by continuing to breed purebred cattle rather than trying to manage complex crossbreeding programs with exotic large European bull breeds.

Table 6. Reproductive data performance of Bali and F_1 crossbred females, where the purebred cows were reared by smallholder farmers in similar production environments [a].

Reproductive Performance	Bali	F_1 Bali $\times$ Simmental	F_1 Bali $\times$ Limousin
Days open (days)	81 $\pm$ 10	125 $\pm$ 23	-
Calving interval (days)	363 $\pm$ 20	412 $\pm$ 36	387
Pregnancy rate (%)	94.2 $\pm$ 3.8	78.9 $\pm$ 5.3	-
Calving rate (%)	88.5 $\pm$ 4.1	76.3 $\pm$ 6.3	75
Pre-weaning mortality (%)	8.7 $\pm$ 0.4	17.2 $\pm$ 1.2	5.6
Observation year	2015	2015	2019
Reference	[69]	[68]	[75]

[a] It should be noted that the purebred cows were not managed in the same contemporary groups as the crossbred cows, which in turn were recorded in independent studies. The numbers of progeny per sire are not available due to the lack of calving records across all three studies. Females ranged in age from 4 to 8 years but the study did not differentiate performance across the different ages and nor was age at first calving recorded (an important variable that may favour purebred Bali cattle because the F_1 crossbreds would have greater nutritional requirements than Bali cattle over their lifetime and those needs are unlikely to be achieved under smallholder farmer systems. A lack of sufficient nutrition during the dry season is also believed to be responsible for the high pre-weaning calf mortality rates of F_1 Bali $\times$ Simmental cows.

In a different study, several genes such as GH, FSHR, BMP15 were reportedly involved with reproductive function in Bali cattle, but the correlations between those genetic variations and reproductive performance were low [76] suggesting they are unlikely to be having a major impact on female reproductive performance. It is not known whether those variations may also be associated with reproductive performance in Bali crossbred cattle. Further studies based on genomic information from *Bos javanicus* and other cattle species is warranted to determine the role of genetics in reproductive performance of these types of cattle.

With regards to Madura cattle, the Government of Indonesia also recommended genetic improvement by crossbreeding with *Bos taurus* breeds such as Limousin [11]. The aim of such crossbreeding was to produce offspring with larger and heavier body sizes with higher selling prices, but which retained the preferred Maduranese traits such as dark red coat color. Table 7 shows the physical characteristics of F_1 Madura $\times$ Limousin females. However, the crossbreeding study was poorly designed and uncontrolled in practice [27] and hence, there is concern the uncontrolled crossbreeding will threaten the conservation of Madura cattle genetic resources due to the lack of adaptation of the crossbred animals [11].

Table 7. Physical characteristics of Madura $\times$ Limousin cows based on different observational studies from Madura Island comparing sub-populations of Madura cattle (Sonok, Karapan, non-selected Madura and Limousin $\times$ Madura). Results from the different studies reported in this table are not directly comparable and hence, caution should be taken when interpreting the results.

Physical Characteristics	Mean $\pm$ sd	Reference
Age (year)	4.5 $\pm$ 0.2	[50]
	>4.0	[52]
Body weight (kg)	400.1 $\pm$ 92.6	[50]
	406.6 $\pm$ 28.8	[52]
Height at the withers (cm)	125.7 $\pm$ 6.2	[50]
	126.0 $\pm$ 1.9	[52]
Body condition score	3.8 $\pm$ 0.7	[50]

The Value of Crossbreeding to Genetically Improve Indonesia's Cattle Herds

Based on this review of crossbreeding studies using Indonesia's cattle breeds, it is clear there are no comprehensive and well-designed crossbreeding studies undertaken to enable valid comparisons of different cattle breeds and crossbreeds and to measure the extent of heterosis and recombination loss under Indonesian beef production systems. Well-

designed crossbreeding studies are still required to enable scientifically valid conclusions to be drawn about the role of crossbreeding in Indonesia, although it is unlikely that Indonesia's smallholder cattle farmers would be able to effectively manage the complexities of those types of studies. Additionally, in crossbreeding studies undertaken in Indonesia to date, there has been no distinction between different generations of crossbreeds, other than where progeny are known to be F_1 generation because they are bred using AI over cows of known pure breeds. The distinction between crossbred generations is critically important because of differences in the amount of heterosis and recombination loss in the different generations and crosses between different species, where the amount of both heterosis and recombination loss varies significantly depending on the generation and parental breeds used to generate the crosses.

Since the introduction of crossbreeding programs based on imported semen, it appears that most semen used in Indonesia has been derived from large European breeds such as Simmental and Limousin. Based on what is known of species performance (Table 1), these European sire breeds are not a logical choice for use in Indonesia's tropical production systems, firstly because of their known calving difficulties even when joined to the same cow breeds (meaning that dystocia can be anticipated as a problem if they are joined to the smaller Indonesian cow breeds) and secondly, because of their need for larger quantities of feed and poorer adaptation to tropical environments than other potential sire breeds.

It is therefore recommended that future crossbreeding programs be specifically designed around breeding objectives focused on high productivity and high adaptation to environmental stressors, to meet emerging commercial market requirements for high quality beef, unless cultural factors are expected to continue to be important as is likely in the case of Madura cattle. Under that scenario, the best option for the Madura breed would be to concentrate on within-breed selection, specifically focusing on the important cultural attributes.

6. Achieving Genetic Improvement by Within-Breed Selection

As described previously, the main beef cattle genetic improvement strategy implemented by smallholder cattle farmers in Indonesia to date has been crossbreeding. However, that strategy has not delivered the expected results, partly due to lack of consideration of appropriate breeding objectives that indicate cattle in Indonesia need to be both highly productive and very well adapted to the stressors of tropical environments. In the absence of well-defined breeding objectives, poor choices were made about the use of sire breeds in those programs, resulting in the generally poor performance of the crossbred progeny. Even with the development of appropriate breeding objectives and improved breed choices, it is not clear from the previous section that smallholder cattle farmers in Indonesia would be able to manage the many complexities of designed crossbreeding programs to enable them to achieve effective genetic improvement of their herds.

Due to the complex management requirements of crossbreeding systems, the opportunity to achieve genetic improvement using within-breed selection needs to be evaluated because genetic improvement has very significant potential to improve the productivity, profitability and adaptability of Indonesia's cattle herds.

To date, two substantially different approaches have been taken to genetically improve Indonesian cattle herds using within-breed selection. The most successful approach has been the improvement of the Madura breed for cultural purposes, where use of visual selection successfully improved cows' body conformation, appearance and behaviour and bulls' strength and aggressiveness. However, it is not clear whether there is an ongoing need to continue visually improving these cattle for cultural reasons or whether more commercially-oriented breeding objectives are likely to become more relevant in future. The second within-breed selection approach used in Indonesia is the ongoing use of progeny tests to select Bali bulls, but based only on the growth performance of their offspring while completely ignoring other economically important traits such as reproductive performance,

beef quality and adaptation to environmental stressors [60], some of which are known to be negatively genetically correlated in other breeds of cattle.

It therefore appears that commercially-relevant, market-driven breeding objectives and effective within-breed selection services to enable selection of cattle based on those breeding objectives will need to be evaluated, and their feasibility determined, prior to establishing new systems from the beginning, if within-breed genetic improvement is to effectively achieve ongoing genetic improvement of cattle herds in Indonesia.

As described by [77], traditional genetic improvement programs based on measuring large numbers of pedigree-recorded animals in well-defined cohort groups for the full range of economically important productive and adaptive traits is generally impossible for smallholder farmers and particularly those in tropical environments such as in Indonesia, where environmental stressors encountered by the cattle significantly compound the difficulties of implementation. Even the Bali breed progeny test program described earlier in this paper can only obtain accurate pedigrees for, at most, 3 generations because the program is not undertaken in a sustainable way. The system used by that program evaluates 3–5 bull candidates in one year, with the candidates identified based on mass selection of growth traits. The bulls are then mated to multiple females to produce multiple offspring, with the progeny test then being used to rank the bulls on the growth performance of the offspring. For subsequent years, the same system is applied but without any genetic linkages created across the different years.

However, the opportunity now exists to use genomic data in conjunction with the use of digital information and communication technologies to develop new opportunities to improve the rates of cattle genetic gains by characterizing indigenous and crossbred animals for use in conservation, crossbreeding and within-breed selection programs, to improve economically important traits. Use of genomic information is costly, but keeping large numbers of animals over many generations to obtain accurate pedigrees and genetic parameters is also very costly with regards to both financial and time investments and is also generally not feasible for smallholder cattle farmers in Indonesia.

6.1. Developing Breeding Objectives for Indonesia's Cattle Smallholder Farmers

Breeding objectives define the "ideal" animals that a farmer wants to breed, with breeding objectives applying to both crossbreeding and within-breed selection programs. Generally, breeding objectives are defined by identifying the traits affecting the profit of the cattle business, as well as the importance of each trait to that profit. A breeding objective is specific to a particular market or group of similar markets, meaning it is important to understand the market requirements. Depending on the target market, some traits have greater importance than others (for example, live weights early in life as an indication of live weight at sale). However, the breeding objective also needs to consider factors that might promote or detract from achieving those important goals (for example, if cattle in Indonesia are not well adapted to the environmental stressors that are endemic in Indonesia, they will not grow to market weights as expected, a case in point being the overall failure of crossbreeding programs in Indonesia to achieve their potential highlighted in an earlier section of this paper).

In terms of the genetics of the traits, some traits are highly heritable or readily passed on from one generation to another and so greater progress towards breeding objectives can be achieved by targeting traits that are highly heritable (although there is also good evidence that strong genetic progress can be made by focusing on traits such as cow annual weaning rates that are lowly heritable). Greatest progress towards achieving the breeding objective will be achieved by focusing on traits of economic importance rather than traits associated with the personal preference of the breeder.

In the case of Madura cattle used for Sonok and Karapan festivals, where cultural or traditional attributes are important, an economic weighting could be derived based on the value of those cultural or traditional attributes to the sale price of the cattle, as well as potentially to the value of the cattle to the communities based on income from the

festivals. Regardless of the traits included in the breeding objective, it will be important for the farmer to record the desired animal traits impacting on enterprise profitability and to estimate the relevant importance of each of those traits. From there, the economic impact of changing each important trait can be calculated from both financial and production data.

A sequential procedure to enable development of beef cattle breeding objectives is presented by [78] and includes four phases: (1) specify the breeding, production and marketing system; (2) identify the sources of business income and expenses; (3) determine the biological traits influencing the income and expenses; and (4) derive the economic value of each trait, which those authors recommended be based on discounted gene flow method. However, there are a number of alternative approaches such as simple profit equations, bio-economic models simulating the whole production system or use of desired gains approaches (for example with cultural or traditional attributes in Madura cattle) in combination with profit equations or bio-economic models (to adjust for undesirable genetic changes) that could be used [62]. Additional studies provide examples of the different applications of breeding objectives in both beef cattle cross- and straight-breeding programs [62,78–80].

Amongst smallholder cattle farmers in Indonesia, it will therefore be important that they not only focus on optimizing cattle productivity, but their production systems should also account for all traits related to productivity (growth, reproduction, product quality), adaptability (resistance or tolerance to environmental stressors), sustainability (animal health and welfare) [19,25,81–83] and even cultural and traditional attributes where they are economically important.

6.2. Requirements for Within-Breed Selection Programs for Indonesia's Smallholder Beef Farmers

Conducting a within-breed genetic improvement program for smallholder farmers in Indonesia is not straightforward. However, there is clear evidence from many countries that within-breed selection for a range of economically important productive and adaptive traits in the breeding objective has resulted in permanent genetic improvement of those traits, directly benefiting not only the pure breeds under selection, but also animals in crossbreeding and composite development programs. This is particularly true with the use of genomic (DNA based) information [84,85] in the breeding programs.

Although many successes have been reported in the past, conventional genetic improvement programs that rely on measurement of large numbers of pedigree-recorded animals in well-defined and controlled cohort groups is time consuming, laborious, financially costly and in Indonesia, probably too complex for smallholder cattle farmers to manage. However, recent major advances in genomic technology (summarized by [77]), in conjunction with the use of new digital information and communication technologies that allow automated or semi-automated data collection, are now enabling very significant new opportunities to improve the productivity of livestock industries in countries like Indonesia through the use of genomic selection, which uses genome-wide genetic markers to estimate the genetic merit of individual animals [86–88].

Within Indonesia, there is a consortium of researchers from several universities and Indonesian government agencies with interests in conserving and genetically improving Indonesia's unique livestock breeds. Strong support and willingness to engage have also been expressed by potential international collaborators and funding agencies. Hence, a primary purpose of this paper is to demonstrate that possible solutions to implementing genetic improvement programs for smallholder cattle farmers do exist. The major requirements for setting up new within-breed selection program(s) in Indonesia are therefore briefly summarized below.

- *Accurately recorded phenotypes*: The main limitation to genomic and traditional within-breed selection in extensively managed livestock such as beef cattle is the difficulty and expense of measuring animals in appropriately sized contemporary groups for the full range of economically important productive and adaptive traits. Unless the genetic improvement programs are adequate in terms of contemporary group size

and structure, the measurements will not enable useful predictions of genetic merit. A related paper [77] provides a detailed description of the phenotypes that should ideally be included in cattle breeding objectives and the feasibility of recording them in smallholder farmer herds in low-middle income countries. As indicated by [77], measurement of most phenotypes required for genetic improvement programs in smallholder herds is generally not feasible. Hence, those authors recommended establishing reference populations that are genetically linked, but managed separately, to smallholder cattle herds. The feasibility of setting up reference populations for this purpose in Indonesia is explored further below.

- *Genetic parameters for all traits in breeding objectives:* As indicated in an earlier section of this review, the only known within-breed selection program to focus on improvement of an objective trait in Indonesia is that undertaken for Bali cattle and based only on cattle growth. Heritabilities for live weights at different ages and genetic correlations between them are reported by [89–91]. However, there are no known genetic parameters for other traits for beef cattle reared under Indonesian production systems. There are, though, many reports from the scientific literature providing heritabilities and genetic correlations between most economically important traits, though the estimates based on adaptive traits and new traits (e.g., carcass and beef quality, efficiency of feed utilization, methane emissions) are more limited than those derived for growth and reproductive performance. Hence, the best approach to establish within-breed selection programs for use in Indonesia would be to initially use published estimates from other tropical and sub-tropical environments, with the aim of ultimately estimating relevant parameters from Indonesia's cattle herds in future. This approach would enable within-breed selection programs for the full range of economically important traits to commence, once the other challenges to establishing such programs have been overcome. A positive aspect of such an approach is that benefits would accrue not only to within-breed genetic improvement, but also to crossbred populations, as reported by [84].

- *Data analyses and estimation of genomic breeding values*: The previously-mentioned related paper [77] also provides a detailed description of optimal models for predicting genomic estimated breeding values (GEBVs) and the value of genomic data in replacing recorded pedigree information. It additionally compares the positive and negative aspects of different approaches (BayesR, GBLUP) to estimating GEBVs, as applied specifically to genetic improvement programs for low-middle income countries, as well as describing the benefits of imputing full sequence information from lower density Single Nucleotide Polymorphism (SNP) panels.

- *Establishing infrastructure and human capacity building*: As outlined by [77], two problems of major significance to genetic evaluation systems for smallholder farmers in low-middle income countries are: (i) the lack of infrastructure required to undertake on-farm management and phenotyping of animals, laboratory testing of animal samples, data capture and storage and lack of computing facilities and appropriate software programs; and (ii) lack of human capacity, particularly in areas of technological capability and data analysis and interpretation. As those authors describe, new developments in the use of information and communication technologies are starting to address the issues of on-farm management and phenotyping of animals, whilst the development of livestock reference populations and formation of international collaborations currently hold greatest promise of addressing the remainder of these challenges.

- *Possibility of establishing cattle reference populations in Indonesia*: The related paper [77] also provides detailed descriptions of the role and value of livestock reference populations that have been established in multiple developed and developing countries globally, specifically to overcome the difficulty and expense of obtaining accurate phenotypes in large and well-designed cohort groups. The value of forming such reference populations in Indonesia would be increased considerably if they could

also be combined with international collaborations to enable sharing of computing platforms, data storage, analytical software, joint data analyses and human capacity development in all aspects of genetic improvement programs as also described by [77]. To date though, there are currently no known reference populations for smallholder beef cattle in any low-middle income country, primarily due to lack of the significant funding required for their establishment and the significant length of time required to achieve genetic improvement in those herds, which have an average generation interval of 4–6 years [77]. For Indonesia to establish such populations, this would mean not only identifying new sources of funding to support establishment of such populations, but potentially an even greater challenge in securing sufficiently large areas of suitable cattle grazing land in such a highly urbanized country to enable adequate numbers of beef cattle to be managed and recorded within well-designed cohort groups. The land area challenge and potential solutions will be examined in greater detail as part of a design phase, assuming the new sources of funding can be achieved.

- *Could international collaborations help overcome these challenges?*: As described in detail by [77] and summarized previously in this paper, international collaborations with genetic evaluation providers servicing smallholder farmers in other countries in tropical areas would help Indonesia overcome most of the challenges currently facing Indonesia. Additional benefits from international collaborations would include the need for fewer animals with recorded phenotypes and for less common cattle breeds (e.g., Bali and Madura cattle) where data are very limited, as evidenced by recent cross-country studies where pooled data were used to accurately estimate GEBVs for tick resistance in African and Australian breeds of cattle with limited data. The exceptional challenges that would remain for Indonesia are perhaps the most challenging though, as they are based on the need for new funding to help establish and maintain the resource populations over perhaps 10–20 years and access to the areas of land on which those populations would need to be managed. However, if the resource populations were able to be established, it is anticipated that, after the initial 10–20 years of operation, new business models would be implemented to allow farmers and other beef value chain participants who benefit directly from the genetic improvement to assume control and ongoing funding of the populations, as is now starting to occur in other countries.

7. The Critical Role of Genomic Information in Designing and Implementing New Beef Cattle Genetic Improvement Programs in Indonesia

As summarized by [77], potentially the greatest opportunity to significantly improve the productivity of all livestock industries in low-middle income countries in tropical environments is through the use of genomic information, with recent significant advances in genomic technologies greatly improving that potential. However, we also note that the value of genomic information for livestock breeding depends on the availability and quality of essential phenotypes for the full range of economically important productive and adaptive traits important in tropical environments.

Given the relatively poor success of earlier cattle breeding programs in Indonesia as summarized in this review, it is suggested the best way to design new cattle breeding programs (within-breed selection, formation of composites, crossbreeding programs and/or conservation of unique cattle breeds) would be for Indonesian researchers to establish international collaborations and work with those collaborators to develop the opportunities provided by genomic technologies and to simultaneously develop the capacity of Indonesian researchers in the use of those technologies.

In our view, this would best begin with sequencing the genomes of Bali (*Bos javanicus*), Madura and PO breeds, and comparing their sequences directly with the genomic sequence of *Bos taurus* and *Bos indicus* breeds. This would ideally be undertaken in collaboration with researchers involved in the 1000 Bull Genomes project [92]. Thereafter, lower density

SNP panels would be used for ongoing genotyping of animals recorded in those breeding programs. Results from such comparisons would:

- Determine whether the Indonesian breeds are unique and hence, require conservation as pure breeds;
- Definitively confirm the breed composition of Madura and PO cattle, thereby assisting in decisions about how best to use those cattle in future genetic improvement programs targeting productivity of Indonesian cattle herds;
- Confirm whether chromosome imbalance will potentially cause problems with crossbreeding of *Bos javanicus* with *Bos indicus* or *Bos taurus*;
- Assist in the design of within-breed selection, crossbreeding and conservation programs for these breeds; and
- Provide the basic information needed for ongoing studies to identify genes or genomic regions in those cattle breeds that account for large proportions of genetic variation in economically important traits.

Thereafter, the international collaborations established by Indonesian researchers would potentially also assist in the design and implementation of new breeding programs, particularly if it was possible to establish the proposed reference populations to measure and manage the cattle herds required to achieve the targeted genetic improvement (with smallholder beef farmers using AI and semen from proven genetically superior sire to achieve improvement in their own herds).

Once established, those reference populations would routinely use low-density, low-cost SNP panels and imputation to full sequence to provide genomic data (including pedigree information) for all animals in the reference populations. The genomic information, combined with measured phenotypes, would then be used to estimate GEBVs for every animal in the population and allow the effective design of within-breed selection programs that also prevent the rapid and large increases in inbreeding that are occurring in some cattle populations in Indonesia due to small population sizes.

Genomic information would also allow the design of crossbreeding programs based on precise knowledge of the breed composition of all animals to be used in the programs, thereby ensuring breeding females are joined to appropriate bulls in order to generate well adapted and productive crossbred progeny. This approach has been successfully used in controlled crossbreeding programs by smallholder dairy farmers in Africa and India [93–96].

In the relatively short-term future, the use of genomic (and other "-omics") information also has the potential to reduce and possibly replace the requirements for some difficult- or expensive-to-record phenotypes that currently represent a major constraint to effective implementation of genetic improvement programs in low-middle income countries. The greatest limitation to achieving this is the current lack of accurately-recorded phenotypes for those difficult- or expensive-to-record traits, against which the genomic information can be tested.

8. Conclusions

To respond to Indonesia's increasing need for greater supplies of beef, as well as to improve the productivity and profitability of Indonesia's smallholder cattle farmers, sustainable utilization and genetic improvement of Indonesia's local cattle are vitally important.

Based on this review of the literature relevant to Indonesia's smallholder beef breeding programs, it appears that to date, all crossbreeding and within-breed selection programs implemented in Indonesia (except for the visual selection for cultural attributes amongst Madura cattle) have not achieved the levels of genetic improvement that were initially targeted. Previous crossbreeding programs appear to have failed primarily through poor design of the programs as well as the complexity of management required for such programs, beyond the skill levels of smallholder farmers. The sole within-breed selection program based on objective measurements was restricted just to selection of bulls based

on live weights, whilst ignoring other productive and adaptive traits known from the published literature to be genetically correlated (sometimes negatively).

Hence, to achieve the permanent genetic improvement required to improve the productivity and profitability of Indonesia's smallholder farmer cattle herds, and to achieve conservation of Indonesia's unique cattle breeds, the opportunity now exists to develop and implement entirely new breeding programs.

Regardless of how the local cattle breeds are utilized, genetic improvement programs with well-formulated breeding goals should be designed and implemented to improve the ongoing productivity and profitability of smallholder farmer herds, as well as to conserve unique Indonesian genetic resources.

Conflicts of Interest: The authors declare they have no conflict of interest.

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