final report

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Strategic and novel approaches to reducing flystrike in sheep

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Executive summary

Flystrike is well recognised as a continuing issue for sheep in every environment in which they are farmed. The prevention of flystrike has received a lot of attention and investment in the modern era of sheep production, yet it still ranks as the fifth highest economic limitation to farming sheep in Australia. In addition to the large economic cost, flystrike is a serious animal welfare issue for the industry. Many of the welfare concerns that are likely to become the focus of consumer and activist pressure are directly related to flystrike. Reducing flystrike by non-chemical, non-surgical means has the triple impact of improving welfare, reducing chemical use and ensuring sustainable and ethical production. The goals are likely to be rewarded if not demanded by consumers. Whilst reducing the impact of flystrike has been the focus in industry, we believe that the target should be to prevent flystrike from occurring at all. We believe that with the appropriate application of current knowledge, combined with the deployment of new technologies in the pipeline, this is a realistic and attainable goal.

A thorough review of the current state of knowledge around flystrike was conducted including a review of developing technologies that may assist in the fight against flystrike. The review clearly demonstrates that significant investment has been made in understanding the sheep genetic factors that are important in reducing the susceptibility of sheep to flystrike. However, to date very little of this information has made it through to mainstream breeding programs. The industry is largely breeding sheep assuming that surgical and chemical means of reducing the risk of flystrike will always be available. This review has highlighted that a lot of the knowledge around flystrike is limited to Merino sheep with very little information on non-Merino breeds available. Furthermore, there are also very few tools available to industry to breed towards lower flystrike in non-Merino breeds. It is essential for Meat and Livestock Australia to obtain better knowledge in this area.

We see enormous potential in deploying the latest artificial intelligence (AI) techniques to many of the problems and opportunities around flystrike susceptibility, detection and prevention. The complexity and variability in the parasite-host-climate matrix is perfectly suited to deep learning techniques. We caution against significant investment in the short-term in further understanding of the biology involved in the host-parasite interaction or heavy investment in the high-risk and high-cost areas of vaccines, genomics and gene-editing. We favour a pragmatic approach of fully utilising the information that has been gained from the last century of research and super-charging its application by the latest relevant technologies. We are highly in favour of the utilisation of quantitative genetics to achieve a phase shift in flystrike susceptibility in the Australian sheep population. We feel that this goal can be achieved quite rapidly with the identification and exploitation of resistant genotypes already available in industry.

The recommendations from this review focus on moving towards an industry outcome where flystrike is reduced to zero. An integrated portfolio of work is suggested and prioritised. This portfolio will bring new tools to the fore for farmers as well as providing them with the tools and information necessary to reduce the incidence and prevalence of flystrike. The three pillars of investment that underpin the portfolio are:

1. **Non-susceptible sheep** – A series of projects about making a serious effort to breed genotypes that become less prone to flystrike over time. It is focussed on approaches that will get these genotypes widely used in the industry in a short to medium time horizon;
2. **Resilient management systems** – Providing farmers with the necessary information and knowledge to reduce flystrike to zero on their properties. It is centred around developing and delivering highly relevant information to producers and providing accurate and up to date information to sheep managers to ensure pre-emptive action in a timely way

3. **Reliable insect control methods** - This pillar is about gathering a complete understanding of the usefulness of current chemicals, farmer application methods and ensuring that chemicals remain effective whilst reducing excessive reliance on such chemicals.

The combination of the most effective control systems represented by these three pillars is envisaged to be used in integrated pest management (IPM) systems for long-term control of this serious parasite.

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1 Recommendations

1.1 Immediate solutions (years 1-3)

1.1.1 Chemical management

The reduction of efficacy of fly chemicals poses a significant risk to sheep farming going forward. There is evidence that all chemical groups are failing to some degree as a result of a building resistance in the fly population to all chemical groups. This poses a different risk to the problems associated with the development of insecticide resistance within internal parasites. Within this scenario, apart from buying in new sheep, the worms are basically linked to the farm, as well as administering a quarantine drench to reduce the risk of importing resistant worms with purchased sheep. Within fly populations on the other hand, resistance built up on one farm can rapidly spread across the district as the resistant flies start to dominate populations and can travel significant distances under the right conditions. Furthermore, resistance to multiple drugs in succession can emerge as an industry wide problem.

1.1.1.1 Enhance the awareness and availability of chemical resistance tests for flies.

A thorough industry knowledge of the current levels of chemical resistance in fly populations is a key piece of work that requires immediate investment. NSW DPI, with funding from AWI, have been conducting free chemical efficacy testing on *Lucilia cuprina* maggots. The results from this project (once completed) need to be reviewed to determine the district coverage that has been achieved through this project and the scale of chemical resistance that has been identified. Gaps in district or regional cover need to be filled so that a complete national picture of chemical resistance is understood.

The full price of the testing service is $3500 because of the need to grow the flies out for two generations prior to testing the survival rates to chemical application. This will be cost prohibitive for the majority of producers. A project to continue offering this service at a reduced rate or free is recommended. This project has a dual purpose. Firstly, it maps the current levels of chemical resistance among fly populations and identifies any hotspots that are worse than others and secondly, the results will be a really important message to encourage farmers to consider their current and future chemical control options. In addition, the data can build a national profile of emerging resistance as input for more complex modelling Artificial Intelligence and data sources on chemical and management practices to prolong efficacy of existing chemicals.

1.1.1.2 Conduct a chemical application audit

The methods used to mix and apply chemicals have evolved over time. There are a range of applications available to hire or purchase on the market. There is also a range of ways that they end up getting used on farm. It is hard to find information on how well the chemicals end up being applied. In addition to the application of chemicals, the methods used to ensure the chemical being applied is the correct concentration are also not perfect. The questions remain around the amount of active chemical that actually ends up being deposited at sites that are useful for mitigating against fly strike. An audit of chemical application methods, and active chemical deposition (efficacy) should be conducted.

1.1.1.3 Training of correct mixing, application and methods to reduce parasite resistance

A training module should be developed once more is known on the current application of chemicals, the current levels of fly resistance to chemicals to encourage best practice in chemical application. This training module should include the latest messages on rotating chemicals to reduce the rate of build of fly chemical resistance. Importantly this should consider the need to rotate active chemicals in lice treatments as fly populations can be inadvertently exposed to active chemicals as a result of lice treatments. This further increases the rate of build-up of insecticide resistance.

1.1.2 Fly-free farming industry campaign

A recommendation of this review is to focus the industries attention to a zero-flystrike target. Achieving widespread adoption of current and future technological interventions is going to be a very important component of reducing the incidence of flystrike. In addition to the technological and breeding advances recommended in this review, a multi-faceted adoption approach is required. Central to this recommendation is the development, piloting, refinement and roll out of a new flystrike workshop aimed to highlight all of the avenue's producers have got to reduce the incidence of flystrike and reduce the use of chemical preventive treatments. A component of this approach will be the identification and promotion of industry champions as is detailed below. A key to this campaign will be the renewal and continued updating of information used in the Flyboss website.

1.1.3 Improved identification of affected animals

While reducing flystrike to zero is the bold aim, the reality is that for the foreseeable future sheep managers will continue to need to be able to rapidly identify and treat affected animals. The behaviours of animals affected by flystrike are relatively unique and are often obvious to managers of sheep. However, surveillance of mobs for flystrike can be difficult particularly on large properties or when conflicting demands on the property are present e.g., seeding or harvesting time on a mixed farm. Sensor based early alerts are being investigated in both MLA and AWI funded research. There is an opportunity to build an understanding of the ability for video or image-based detection of affected animals. This would require a training set to be developed and the deployment of machine learning on this training set to understand the utility of image analysis in providing fly strike alerts. This can be incorporated with fly abundance data and high-risk climatic data when flystrike is likely to occur, to increase vigilance.

1.1.4 Improved management of affected animals

Despite our best efforts, there will be many sheep affected by flystrike in the future. Current farm management practices for dealing with sheep that are affected are widely varied and almost solely focussed on killing the parasite and preventing reinfection. The animal welfare outcome from these treatments hasn't been considered in any detail which does present as a potential gap in providing a duty of care to well managed sheep. A small project should be undertaken to gain veterinarian advice on the best treatment of affected animals to minimise mortality, pain and suffering and recovery times. This advice should be included in the fly management workshops developed as part of this strategy.

1.1.5 Industry champions

There are many producers in Australia that manage their sheep with very low incidences of flystrike. This is being achieved through a combination of genetics and management. There is an opportunity to develop a range of case-study material to be promoted by MLA through various forums to clearly demonstrate to producers that very viable operations have solved most of the flystrike issue. Importantly this is being achieved without the need for surgical treatments or excessive use of chemicals. The methods employed by these industry champions need to be much more widely known.

1.2 Medium term solutions (3-8 years)

1.2.1 Breeding better sheep

The development of genotypes and the exploitation of existing genotypes that are less susceptible to fly strike is one of the few solutions that has serious long-term positive impacts on the industry. It has many benefits including having a low barrier to entry (buying resistant rams is unlikely to be higher than buying non-resistant rams) and requires no change to a farming system. It does require greater uptake of breeding value technology in ram selection, identification of across flock sources of breeding replacements which is aligned with industry plans and the requirements of a thriving industry. It is noteworthy that the basic scientific principles of selecting resistant genotypes have been known for at least 30 years and in some industry knowledge-based cases close to 100 years. It is the push through for widespread adoption that has presented a significant barrier.

1.2.1.1 ASBVs for flystrike indicator traits

The indicator traits for flystrike have been well studied. While they don't account for all of the variation in flystrike, focussing the industry to make genetic improvement on these traits will have a positive impact on the incidence of flystrike. The traits meet all practical requirements for efficient indirect selection in that they are moderately to highly heritable, moderately to strongly correlated genetically with underlying resistance to flystrike, can be measured early in life and in both sexes, and are relatively cheap to measure.

There are four traits that are associated with breech strike that show considerable genetic variation and an opportunity for genetic improvement. These are dag (LDAG), breech wrinkle and tail (EBWR), urine stain (URINE) and breech cover (BCOV). The current level of recording of these traits is well below its potential. These traits are all very simple and very cheap to measure and assess yet the uptake has been extremely low. These traits are currently not considered in a single index to predict flystrike susceptibility or combined in the current industry indexes. Except for URINE, ASBVs are routinely reported for these four traits for Merinos within MERINOSELECT but none of them are reported for maternal or terminal sheep within LAMBPLAN. Even within Merinos the level of recording is very low. Only 14% of the 2018 drop Merinos that were entered into MERINOSELECT had a reportable breeding value for LDAG. A project to increase the amount of data collection across all of these traits, focussing on improving the linkage across properties is a priority going forward. In addition, these traits need to be included in at least a single flystrike susceptibility index and preferably also in some of the production indexes so that breeders that are concerned about flystrike can easily incorporate these breeding values into their selection decisions. A joint meta-analysis of all available data from diverse sources to produce a combined flystrike index is one cost-effective avenue to capture benefits from past investments and bring about a rapid consolidated position for immediate application to industry.

The genetic indicator traits for body strike are dermatitis, fleece rot, wool colour, fibre diameter variation and body wrinkle. Again, except for fibre diameter variability, these traits are poorly recorded in Merinos and not recorded at all in composite and maternal sheep. There needs to be a major project that rapidly and dramatically improves the availability of these flystrike indicator traits and combines them in a single body-strike index. It needs to be linked with an extension campaign that informs commercial ram buyers of the importance of selecting rams with favourable breeding values for these traits as well as incorporating these traits into ewe replacement selections.

1.2.1.2 Automating phenotype assessments

The indicator traits for predisposition to flystrike are largely a set of visual scores that can be assessed by anyone who cares to. All of the visual scores are based on a 1 to 5 scoring system because a relatively untrained operator is unable to score with more precision than these 5 options. The scores are therefore open to interpretation and there will be some differences between scorers in the actual score they record against an individual, as is the case with any subjective scoring system. The scoring systems also do not make allowances for high resolution differences in tail and breech wrinkle which are critical to breech-strike predisposition. In addition, these scores often need to be recorded at a time when there is a lot of activity on farms and they are often not collected.

Moving to automated or semi-automated allocation of visual scores of the indicator traits would provide a high resolution and standardised scoring system of the indicator traits and would reduce the time and commitment required from ram breeders to collect the relevant scores. The combination of relatively cheap cameras and machine learning capability provide an opportunity to automate the scoring of indicator traits.

A project should be initiated to build a training set that enables a machine learning enabled camera system to determine the expression of all of the indicator traits. This project would take several steps. In the initial phase a training set would be built that links an image of an animal (from an angle necessary to assess the indicator trait) to an expert derived visual score, preferably taken at a very early age since most indicator traits can be measured at birth, marking or weaning. The initial algorithms would be developed to train the machine to provide the expert score from a photo of any animal. The next step would be to train an object detector to estimate the actual level of the indicator trait. This could still sit within a scale of 1 to 5 so that the information could go into breeding values without require a re-format of these traits.

The potential outcome of this project is an image-based system that can allocate indicator scores for individual animals in an automated way. This will have three major advantages for industry. Firstly, it provides a lot of information that can be used to determine superior genotypes allowing genetic gain in the indicator traits. Secondly, it provides the basis of a system that can be used as an early detection or early warning system when sheep are at risk of flystrike. Thirdly it could identify animals within the current generation that would not require Mulesing as Mulesing is phased out.

The training data set would ideally be developed across all major breeds and an extensive range of bloodlines to maximize variation in the training phase which is indicative of the population at large.

Furthermore, initial animals may need to be scored and image recorded at various ages early in life to determine which time points are most robust or allow for variation in ages of recording by industry. Finally, it would be advantageous to have flystrike information available throughout at least the first year of the animal's life to build a platform for advanced AI based phenotyping as described below.

1.2.1.3 Beyond indicator traits for breeding-towards advanced AI based phenotypes

The current indicator traits for flystrike only explain a proportion of the variation in actual flystrike. The proportion of the variation that each of the indicators explain varies between years and sexes. There are clearly a range of things that are undetectable to human senses, ie. cryptic variation, that culminate in a case of flystrike. The collection of longitudinal data is likely to identify that there are machine-detectable factors that are predictive of susceptibility to flystrike in both the short-term and over the animal's lifetime. A project to collect images of sheep when they are young and gathering data of their lifetime incidence of flystrike provides an opportunity for a system to select animals that are less likely to get flystrike with greater precision than is possible with the current scoring of indicator traits. To unleash the full predictive power of artificial intelligence is perhaps the greatest opportunity of our generation to make a difference to flystrike in sheep. The data collection required for this project could be overlayed with other activities in the portfolio.

1.2.1.4 Progeny testing sires for flystrike susceptibility

Industry research programs and selection lines have clearly shown that there is a strong genetic aspect to flystrike, that the variation between individual sires in breech strike susceptibility is extremely large with ranges of 0-125% breech strike in progeny under a common environments, furthermore the progeny performance of such sire groups is highly repeatable across ages and environments. Similar expressions of resistance to body strike have been observed between industry sire lines, although flystrike is expressed at lower levels than breech strike. These factors indicate that industry has the potential to make significant gain in building resistance to flystrike. While demonstrating these concepts in research flocks is a useful proof of concept these programs do nothing to shift the industry toward making genetic gain. Our experience in getting industry uptake of breeders to actively breed for footrot resistance in New Zealand has shown the requirement to very purposefully build industry knowledge and genetic linkage. The identification of such sires allows immediate access by breeders to rapidly build up resistance in commercial flocks. It is a rapid and extremely efficient gateway to achieve this at a widespread scale.

A central progeny test site dedicated to gathering information on the indicator traits for flystrike as well as allowing the expression of flystrike itself would provide a very impactful resource for industry. This site could incorporate testing for resistance to worms as well. The site should be open to all woolled breeds of sheep. The base ewes could be a combination of a representative Merino type and a representative composite maternal type. The sires used in the progeny test should be a combination of Merino, maternal and terminal. The progeny should be run in common to allow for breed differences to be better understood. The progeny would be tailed but not mulesed and selectively crutched, short acting fly chemical would be used at tailing to stop tailing wounds getting affected, but no other chemical treatment would be used up until the challenge period. The sheep would need to be very closely monitored and any affected animals would be treated with short acting chemicals to kill maggots but not to provide additional cover. Sheep would be crutched and shorn in line with industry practice. The program would need to run for a number of years to cover the range of seasons required for expression as well as incorporating a range of sires. This work could form the basis for artificial intelligence training sets and consolidation of genetic parameters of traits linked to flystrike susceptibility in industry flocks. Consideration should be given to covering a range of environments that place different fly pressures on sheep and maximising the opportunity of getting a season more conducive to fly strike.

It is noteworthy that these sire reference flocks do not require the maintenance of industry selection flocks for flystrike, or the need for a genomics based resource flock as extreme resistant and susceptible genotypes could be rapidly identified from exiting sources and the use of genomic prediction will be secondary and genotyping should be limited to animals which have highly accurate breeding values for flystrike-ie. the sires. Over time the scope and opportunity for genotyping to augment indirect selection for flystrike can evaluated but should not be the major incentive for setting up such flocks (see below).

1.2.1.5 Development, testing and release of a fly strike breeding value

A key component of a new phase of work would be the development of a breeding value for flystrike that could be used across the industry. This would need to be developed with the MERINOSELECT and LAMBPLAN analyses. This work would be completed in conjunction with the progeny testing work and the building of advanced phenotypes. It would involve understanding the data structure required to generate a breeding value and adjusting protocols as necessary to ensure a reliable breeding value can be developed. The work would involve estimating genetic parameters, moving through a Research Breeding Value phase before eventually releasing an ASBV for breech strike and an ASBV for body strike. Once released as an RBV any breeder who follows the fly challenge protocol would be able to have flystrike breeding values generated. The work would include generating a more comprehensive database on the correlations between the indicator traits and actual flystrike. To date these correlations have largely been estimated in experimental flocks or in experimental selection lines. Predicting these correlations across unselected flocks from the whole range of genotypes and environments across industry will be informative and an important component of this work. This breeding value once developed should be incorporated into an industry index that incorporates the indicator traits, other health traits as well as the relevant performance traits. The flystrike breeding value would incorporate information from the correlated traits so that it could be predicted (with a lower accuracy) on sheep that had not been subjected to flystrike.

1.2.1.6 Supported industry flock fly challenges

In addition to a central progeny test, breeders entering rams should be encouraged to follow the same protocol on some of their sheep at home. This rapidly increases the number of sires represented in test populations and enables across flock breeding values to become reliable in a much shorter time frame than testing in industry flocks alone. In the initial stages of this work this should be industry supported and help should be provided to ensure protocols are followed, scoring systems are consistent across properties and to maintain a high standard of animal welfare. This would provide a range of scenarios to help the wider project clarify the data collection required for reliable production of breeding values for breech and body strike.

The industry flocks participating in this work should also be used to capture climate data at the same time. Automated weather stations should be deployed on each of the participating properties to help build a modern database linking short- and mid-term climate impacts on the incidence of flystrike and build models for predicting fly waves and other key observations relevant to fly populations and emerging resistance of flies to existing chemicals.

1.2.1.7 Genomic resource building

All sires that are progeny tested for indicator traits as well as the incidence of breech and body strike should be genotyped as part of the wider project. While genomics does not offer any stand-alone utility in the foreseeable future, having a genomic profile on each of the sires is beneficial for two reasons. Firstly, genomics captures realised genetic relatedness between individuals (provides a deep pedigree) and removes any physical pedigree errors in the sires being used. This improves the accuracy of the overall database. Secondly, it will be a useful resource that builds over time that can be utilised in the future to conduct additional genomic studies, or, after many years and many thousands of genotypes, investigate the opportunity of having sufficiently accurate breeding values generated from genomics alone. This would have many positive outcomes however it is important to clarify that this is a much longer-term goal than most of the work proposed. Other than ensuring a genomic database is built and maintained, we do not recommend instigating any work based on genomics alone until many years of industry data are collected.

1.2.2 Chemical rotation research

It seems new fly control chemical groups will be very scarce in the future and it is important that we accept the reality that the current chemicals we have available may be as good as it gets in terms of chemical control. It is therefore imperative that the current chemical groups are protected as best we can. Resistance has now been shown to the majority of fly chemicals in current use and this resistance is increasing all of the time. There are industry messages around rotating chemicals but understanding this and applying this in practice are loosely understood. A research project should be conducted to recommend chemical rotations strategies and then periodically (every 5 years) assess the fly populations for build-up of resistance.

1.2.3 Climate change modelling

The work carried out to help build reliable breeding values for flystrike traits will provide a modern resource of prevailing conditions and the resultant fly pressure. Within other aspects of this wider strategy these data sets will be refined into predictive equations. Once this is completed there will be an opportunity to overlay future climate scenarios from climate change modelling to predict the likely impact of breech and body strike into the future. This will be an important piece of work to help inform the importance flystrike mitigation should take in MLA strategic planning. Predictions of milder winters and increased summer storm activity is likely to see the fly season to extend for a longer part of the cooler months and to be more severe in the summer months. Thorough modelling is required to understand the likelihood of these changes happening and the scale of the impact on the industry if such changes did occur.

1.2.4 Enhancing predictive capacity

1.2.4.1 Automated fly wave monitoring

The current methods of understanding when flies are becoming active rely on farmers reporting flystrike or through manual checking of pheromone or baited traps. To automate this process would allow a much wider spectrum of monitoring and allow more precise prediction models to be built. A project should be initiated that delivers an automated fly trap. The device would act as a normal fly trap but would be automatically 'checked' using an in-built camera system that is machine learning enabled. To enable this a *Lucilia cuprina* identification algorithm would be defined by training a model to differentiate *Lucilia cuprina* from other fly species and allow for accurate counting. This could then be deployed on a camera that is powered by solar and is running the fly detector on the device. The system would use a wifi link to send fly counts back to a central system.

1.2.4.2 Region based predictive capacity

Enhancing the prediction of when fly waves are likely to occur is one way of minimising over use of chemicals and an opportunity to move into a region based integrated pest management program. All of the models that have been previously developed to predict fly wave dynamics based on formulas from historic data with relatively limited datasets. The opportunity to develop more accurate and more responsive predictive models is now available with the ability to deploy artificial intelligence to model development. A large model development project would provide Australia with the world's first early detection model for animal diseases.

Central to the project would be monitor farms that were initially used to inform the models these monitor farms would be equipped with a range of sensors to monitor the micro-climate in considerable detail. This would include monitoring the weather with some degree accuracy as well as monitoring soil conditions. The monitor farms would have a sentinel flock of animals that remained untreated and were checked daily for fly strike. These flocks would be kept as small as statistically possible. The farms would be fitted with the automated flytraps described above and animals monitored with remote sensors.

All of the information gathered on the monitor farms would be combined with weather predictions and regional weather observations to build a training set for the model. Sheep factors would also be included in the model to help refine it further. These would include breed, shearing time, lambing time, wool type etc.

Over a three-year period, the model would be trained based on farmer observations of monitor sheep and automated collection of all of the other data points. The project would then enter a validation phase where predictions were provided on flocks that have not been included in the training set and determine the reliability of predictions. The model would continue to be populated with new information and would continue to build over time as more data was generated. Once complete the model could use 'crowd-sourced' data from farms on flystrike and would continue to learn and improve.

1.2.5 Building integrated pest management (IPM) systems

It is clear from our understanding of blowfly strike in sheep that many forms of control when used in isolation offer at best partial protection. It is also clear that sheep producers can integrate often on an ad hoc basis the various forms of flystrike control that may give them the best form of protection. Based on our current knowledge of blowfly strike control, we could enhance the efficacy of individual control strategies, by combining them in an integrated form of blowfly pest management control (IPM). An investment is recommended to build practical IPM strategies which incorporate and integrate current control methods in an optimal on farm application. The critical components should draw on strategic and reduced chemical control, breeding for resistance and exploitation of resistant genotypes, minimizing fly populations, management strategies which eliminate mulesing, and optimal use of predictive fly wave conditions. It is recommended that such IPM systems are built and validated across a range of sheep production systems and regions to cover the diversity in geographical, environmental and production systems. Adopted *in situ* IPM strategies should also incorporate bio-economic modelling of benefits of adopting such systems

1.3 Longer term (5-15 years)

1.3.1 Expert panel and strategic review teams

Flystrike research, development and extension has received a lot of attention over the years but most of the experts in the area are either nearing retirement or have already retired. This poses a significant risk for the industry with the potential of losing most of the expert knowledge. In addition, infrequent subject area reviews, sporadic project work and a significant reduction in state government funding across all areas means that there is limited recruitment of new scientists with an interest in this area. MLA should consider setting up a flystrike review panel (or could be widened to health traits generally) to report twice yearly to MLA management on developments. This panel should be charged with defining research areas that need to be completed, or existing objectives to be altered and re-directed where warranted, and these areas can then be tendered to research organisations. They could have a role in project development and completion by providing thoughts and advice to research teams. This would facilitate knowledge transfer as well as ensure integrated research outputs that are of high quality for MLA. This would also minimise the duplication of past or present activities.

We recommend that an initial undertaking for an expert panel would be a joint MLA and AWI desktop review of gene editing and gene drive technologies to control blowfly, lice and possibly internal parasites. This should be conducted to determine the likelihood of regulatory frameworks allowing the work to proceed as well as exploring how it fits with past research investments and capability.

1.3.2 Manipulation of the insect

The opportunity to modify *Lucilia cuprina* to reduce the population of the species in Australia is a real possibility with advent of gene editing technology and the associated gene drives. Due to regulatory limitations we have not investigated this option any further. This does not suggest that this is not an important avenue. Gene editing technology is improving all the time and the genome of *Lucilia cuprina* has been mapped, making this a serious option for the sheep industry. We have not investigated the necessary path or likelihood of success of this option. The impact of this technology and logistical hurdles to deploy this as a potential control option should be subjected to an expert review in the short term to identify technical, logistical and regulatory hurdles.

1.3.3 Vaccines

We cannot see any likely biological pathway that will enable vaccination against flystrike in the time frame necessary for this investment portfolio. Despite developments in vaccine technology generally, the world has not seen vaccines against multi-cellular ecto-parasites which have high and lifelong efficacy (Stutzer et al., 2018). Furthermore, the onset of immunological targets comes very late in the development of flystrike with first instar larvae infesting susceptible animals. The rapid spread of maggots that occurs and the presence of secondary fly species will make it very difficult to develop a product that can raise an impactful immune response in the sheep. It is far more strategic to reduce predisposition in the development of flystrike rather than control it after the animals have already become struck.

1.3.4 Mechanistic understanding of the biology

There have been decades of research aiming to understand the complex biology of the host-parasite relationship. This includes work that seeks to understand the odour profile that makes susceptible sheep attractive to fly oviposition. We see a strategic small-scale investment to explore and capture new opportunities through the deployment of PhD programmes rather than direct investment in strategic research projects which may not have immediate applications to advancing the desired outcome of ‘Zero flystrike’. Strategic PhD related areas of research could include sheep micro-biome research in the development of flystrike, in particular breech strike, development and regulation of dag formation, fly attractants and repellents, bio-marker profiles of extreme resistant and susceptible phenotypes and genotypes, as well as capture opportunities from other biological research in host-ectoparasite systems .

2 Introduction

Flystrike is well recognised as a continuing issue for sheep in every environment in which sheep are farmed. In most sheep farming regions one, or both, of two species are responsible – *Lucilia cuprina* and *Lucilia sericata*. The prevention of flystrike has received a lot of attention and investment in the modern era of sheep production, yet it still ranks as the fifth highest economic limitation to farming sheep in Australia. It is estimated to cost to the industry over $170M annually.

Industry investment has largely focussed on the development and testing of new prophylactic chemicals and the on-going use of old preventative measures. There has been very little in the way of new options to reduce or remove flystrike for some time. Largely, the options that have been developed by industry are not in line with current consumer expectations as they either require the use of insecticides or have negative welfare outcomes for the sheep. There have been very few introductions of novel options to reduce or remove flystrike as a result of research project outcomes. Largely, research projects have focussed on attempting to define solutions to flystrike that don't require significant changes to the normal management practices or to normal levels of productivity.

Despite a lack of change at an industry level there has been a sub-section of the industry that has tackled the flystrike problem through breeding animals that are much less prone to flystrike, often against the conventional wisdom of the industry. These breeders now report very low levels of flystrike with a very high potential that they could further reduce this to zero using additional breeding efforts and strategic management through tail docking, crutching and shearing. This outcome provides hope that a flystrike free future is a possibility if the industry is focussed on achieving this.

The economic impact of sheep myiasis is difficult to ascertain. Although the proportion of farms likely to be affected by flystrike is high (>80%), the prevalence in a national flock may appear relatively low at 1.5-2.0 % of all sheep farmed (Australia, UK & NZ). However, this does not reflect the substantial cost associated with widespread husbandry practices such as crutching, shearing, tail docking and mulesing to minimise the impact of flystrike. Furthermore, the sporadic occurrence of severe outbreaks with high prevalence (>10%) often attracts high mortality, and high labour costs, with continued surveillance of flocks at risk. The covert costs associated with decreased reproductive efficiency, and lifetime reduction in meat, wool and milk production because of severe flystrike, and decreased genetic gain in diseased flocks, are seldom accounted for.

McLeod (1995) showed the relative cost associated with blowfly strike control in Australia, which is predominantly a wool-producing country. Methods of control represented 80% of the annual cost attributable to flystrike, and labour represented the greatest single cost in this (88% of cost of control). Production losses contributed the remaining 20% to the annual cost (at that time) of $A161 million to flystrike, with mortality the single greatest cost component at 38%.

The predicted impact of myiasis on sheep production is even more difficult to estimate if relative risk scenarios need to be incorporated which allow for decreased reliance on current and highly effective control methods. Such scenarios are realistic considering increased resistance to current insecticides, decreased reliance on use of chemicals as dictated by consumer preferences, and decreased reliance on proven husbandry techniques such as mulesing and tail docking, on the grounds of animal welfare. In the long run, global changes in consumer acceptance driven largely by chemical free and high welfare demands may present market-resistance for Australian sheep products. It is inevitable that Australia will be faced with changes in fly-strike control in line with consumer expectations.

3 Flystrike and the community

3.1 Consumers and the community

For sheep farmers, it has long been a goal to limit the occurrence of flystrike and much research has been undertaken to pursue this. Nevertheless, there is a perception that some flystrike will still occur despite best efforts to limit its occurrence. Terms such as “lowering the risk” and “reducing the risk” are common. However, current public opinion is likely to vary from this view. Members of the public, who do not have an understanding of farming, will find images of flystruck sheep distressing and would query why it is tolerated to any extent and if it does occur why do sheep develop such severe lesions before treatment. The incidence and severity of flystrike is relatively unknown by the general public and therefore isn’t raised as an issue. However, with the large majority of the population having direct access to a smartphone, and widespread social media networks, it is safe to assume that public scrutiny will increase. The movement towards ethically farmed livestock is a trend that is here to stay, and its momentum will continue to grow. Furthermore, current environmental commentators would express concern that sheep are being treated with chemicals to prevent flystrike on a regular basis, not because they are flystruck, but because they may become flystruck. All of this to produce the “natural” products wool, lamb and mutton. We have effectively bred a type of sheep which is far from the natural type of the species and which has disease consequences not generally seen in the natural type. It is important that we reverse this and breed toward sheep that are resistant to developing flystrike.

The focus of research efforts should be to eliminate flystrike. To achieve this, some things will need to change. Lucas and Horton (2013) described results from their modelling exercise for three regions in Australia and the incidence of strike never reached zero, even when different shearing times were investigated. In this study unmulesed sheep had a considerably higher incidence than their mulesed equivalents. It isn’t clear what the impact of insecticide treatment had on the rate but presumably was effective for at least some of the period claimed. It illustrates the reliance on insecticides, especially when mulesing is not undertaken. In Table 5 in their publication they show the predicted number of sheep struck following optimum economic treatment of unmulesed sheep and it ranged from 11 per 1000 sheep to as high as 29 per 1000 (the denominator is somewhat vague). Nevertheless, although it is a small number of strikes, it never reaches zero. We think technologies are now available or within reach to industry to bring this down to zero and should be a realistic goal for the sheep industry.

3.2 The farming community

There is a major disparity between what practices farmers believe they should be able to undertake, and the attitude of the informed consumer, with many farmers openly disputing the existence and validity of their “social licence”. The belief that mulesing is a defendable practice that will remain as a viable fly control measure has seriously limited the potential to develop genotypes and management systems that are in line with current and future consumer needs and is extremely misguided. There seems to be a belief that there can be no compromises to current production and breeding methods to reduce and/or remove the risk of flystrike. The future is going to prove this assumption wrong. A necessary component of any MLA investment in flystrike will be heightening the awareness of the farming community to trends in consumer expectations and the increasing priority of avoiding pain and discomfort in farmed animals.

The use of chemicals in agricultural production systems is also coming under increasing scrutiny. There are major concerns around the associated impacts on human health as well as the non-target impacts of chemicals released into natural ecosystems.

4 Current knowledge

4.1 Myiasis of sheep

Myiasis is the infestation of organs or tissues of host animals by the larval stages (maggots or grubs) of dipterous flies. The fly larvae feed directly on the host's necrotic or living tissue. Toure (1994), Hall and Wall (1995) and Wall and Shearer (1997) describe myiasis of veterinary and economic significance in considerable detail. This section of the review builds on the reviews provided by Raadsma and Rogan (1987), Raadsma (1991a, 2000), Colwell and Wall (2018), James (2006), Sandeman et al. (2014a), Anstead et al. (2017). For more detailed information the reader is referred to these reviews.

Myiasis is often classified according to the anatomical location of infestation on the host, and is broadly speaking described as dermal, sub-dermal or cutaneous, nasopharyngeal, ocular, intestinal/enteric or urogenital. As outlined by Wall and Shearer (1997), it is often more appropriate to classify myiasis in terms of relationships between host and parasite, since this provides insight into the biology of the fly species, it's likely pathological effect, host responses and methods of control. Obligatory, facultative and accidental covers possible relationships between host and parasite. Obligatory ectoparasites must have a living host (often quite specific) to complete their development and are unable to survive in the absence of the host. Facultative species on the other hand can develop both in living and dead organic matter and can be further sub-divided into primary and secondary facultative ectoparasites. The major distinction within this classification is that primary species are capable of initiating myiasis but will also live as saprophages in carrion. Secondary species normally live as saprophages and are generally unable to initiate myiasis but invade pre-existing infestations. The detail is of significance, since the major species of blowflies in sheep are primary, facultative ectoparasites, as discussed below. Accidental blowfly species do not normally live on a specific host but will do so once any host is suitably predisposed, through other myiases or wounds.

Pathological effects of sheep affected by myiasis vary considerably, depending on the species of ectoparasites, number of larvae and site of infestation. Small infestations restricted to confined sites may have little or no discernible effects on the host. Large infestations with significant tissue damage result in rapid increase of body temperature, and respiratory rate, accompanied by anorexia and weight loss. In heavy and extensive infestations, animals are likely to suffer bacterial infections resulting in septicaemia, toxaemia, dehydration and, possibly, anaphylaxes. Severe infestations, if left untreated, are likely to result in the death of the animal.

4.2 Impact of breed on flystrike

There is a myriad of literature on flystrike in Merino sheep however the same is not true for other breeds. Scobie and O’Connell (2010) have reported flystrike in non-Merino sheep in New Zealand, as have Bisdorff and Wall (2008) in the United Kingdom, however there is a paucity of records from non-Merino sheep under Australian conditions. In an experiment designed to compare flystruck with non-flystruck sheep using molecular genetics the data shown in Table 1 were reported (Burrows 2018). Most of the breeds sampled came from different farms across five years, some breeds came from more than one farm, with consequent differences in environment and management. The breeds called “crossbred, “black-faced crossbred” and “composite” were perhaps commercial flocks while the named breeds were more likely stud flocks. Many farms had used at least one method of controlling flystrike so the proportion struck will be less than potential.

Table 1. The prevalence of flystrike in various breeds over a five-year study period (2013 – 2017) (Burrows 2018).

Breed	Number with flystrike	Total number	Proportion struck (%)
Merino	43	880	4.89
Corriedale	110	2240	4.91
Perendale	54	1150	4.69
Romney	31	1730	1.79
Dorset Down	7	357	1.96
Shropshire	14	365	3.83
Suffolk	17	682	2.49
Crossbred	72	3078	2.34
Black-faced crossbred	41	2120	1.93
Composite	9	209	4.31

Unfortunately, direct breed comparisons with adequate genetic sampling and representation (that is, several progeny from many sires) under common environments are rare and expensive to set up. Therefore, most studies can only draw on broad scale and anecdotal evidence derived from industry sources. Indeed, the Romney were, in this very simplistic Table, far less susceptible than any other breed which the current authors doubt while the Merino and Corriedale were quite believably more susceptible. A very small number of flocks could be identified from the same farm in the same year and in consecutive years, but with no guarantee that management of the breeds was identical. Considering the data in this way the Corriedale was more susceptible than the Shropshire in three consecutive years, with the Dorset Down less likely to be struck in two (and perhaps three if 0% was not reported) of those years. It would be of considerable interest to know how various meat breeds, maternal crossbreds and composites differ in their susceptibility to flystrike under Australian conditions.

A report from Horton et al. (2018) has used records from the Information Nucleus flocks. An average of 17.3% of Merino ewes were struck across all the data sources they utilised, whereas only 4.9% of non-Merino ewes were struck. In that report, the non-Merino ewes were first-cross Border Leicester X Merino. Although most were struck on the breech (84% across all animals) body strike was recorded in 25 non-Merino and 98 Merino ewes. The relative susceptibility of breeds to body strike versus breech strike is difficult to ascertain from low numbers of observations and warrants further investigation in non-mulesed flocks under common environmental and management conditions.

It is informative to interrogate the data more deeply because flystrike is so environmentally variable. Ewes on the same farm would have been subject to similar risks. The Trangie flock is very interesting in that 7% of the crossbred ewes died after being struck while only 4% of the Merinos died. This suggests mortality might be higher in the crossbreds, but Horton et al. (2018) were not willing to comment further because the difference was non-significant. The Trangie flock is possibly flock "IN02" though this was not clearly indicated in their report. Fleece production and value, lamb production and Merinos dominated the remainder of the report with no separation of the effects on crossbreds due to the small numbers affected. However, strike dramatically reduced the number of lambs born and weaned and the more severe the strike (subjectively scored), the worse the consequence on reproduction.

In the UK purebred non-Merino were less likely to be struck than crossbred non-Merino, but then those farming them may be more attentive and it would be interesting to test this experimentally. In Australia first cross ewes seem less susceptible and it is tempting to rank animals in terms of increasing susceptibility as purebred less susceptible than first cross, which in turn are less susceptible than Merino. As suggested above, it appears warranted to conduct further systematic observations on breed susceptibility to both body strike and breech strike in unmulesd sheep. Ideally this would be completed on Merino, first cross and non-Merino breeds as broad cohorts across diverse environmental and management systems.

4.3 Myiasis flies of importance in sheep

Myiasis flies of economic significance in sheep production belong to the superfamily Oestroidae, which is characterised by three major families of flies:

- *Oestridae* (bots and warbles);
- *Sarcophagidae* (flesh flies); and
- *Calliphoridae* (blowflies).

4.3.1 The Oestridae – bots and warbles

The Oestrid species of greatest economic significance in sheep production is the sheep nasal bot fly, *Oestrus ovis* (Horak 1977). They are obligate parasites to sheep and goats. Larvae of *O. ovis* develop in the head sinuses and nasal passages for all three major larval stages. At maturation, larvae are sneezed out. In general, infestations are relatively light (2-20 larvae) in the frontal sinus of infested animals. Mucoid nasal discharge, sneezing, nose rubbing, or head-shaking are clinical symptoms of infestation. Dead larvae in the sinuses can cause allergic reaction and inflammatory responses, followed by secondary bacterial infections. Death following infestation is rare. Production losses in the form of reduced weight gain, loss of body condition, and loss of wool and milk production have been attributed to infestation with *O. ovis.* On balance, such losses can be considered mild. Prevalence in individual flocks varies greatly ranging from 0-100%, and infestations have been reported from all sheep production countries worldwide. Treatment following a single oral dose of ivermectin or rafoxanide is systemically active and highly effective. No reports describing genetic variation in resistance between sheep have been found.

A review of *O. ovis* (Cepeda-Palacios et al. 2011) describes the ecobiology of the fly and some of the known factors as to how the fly finds the host on which to lay eggs. An earlier review (Dorchies et al. 1998) considered the pathophysiology of the infection and suggested lambs acquire immunity to *O. ovis*. There are also differences in natural infection rates between sheep and goats that are run together (Papadopoulous et al. 2006), the reasons for this are not resolved. However, in this myiasis, the larvae are present for a prolonged period and infection is seldom fatal so immunity may be a useful response compared to the fleece myiasis flies. Dorchies et al. (1998) were able to draw on *L. cuprina* literature but the reverse is not evident in the literature. This parasite has a global spread with Alcaide et al. (2003) citing literature across the Mediterranean. Scobie (unpublished) observed these in South Australia in a Mediterranean environment, with up to seven L3 larvae in the sinus of a single skull in a slaughter plant, and recovery of numerous pre-pupal larvae that had been sneezed out in an indoor research facility. Studies of the attraction of this parasite to sheep in Australia, may develop knowledge that could help understand the attraction cutaneous myiasis flies to sheep. In light of highly effective chemotherapy and relatively mild production losses due infestation, such investigations are of low priority.

4.3.2 The Sarcophagidae - screw-worm flies

The three species of obligate screw-worm flies which can cause potentially severe myiasis in sheep are *Cochliomyia hominivorax* (New World Screwworm Fly), *Chrysomya bezziana* (Old World Screwworm Fly), and *Wohlfarthia magnifica.* All three species will infect almost all warm-blooded animals and therefore do not have a host-specific relationship with sheep. Screw-worm myiasis occurs largely as a consequence of oviposition at sites of skin damage due to trauma, shearing, tail docking, or castration wounds. Oviposition also occurs near body orifices such as nostrils, eyes, mouth, ears, anus and vagina. Larvae from these three species hatch within 24 hrs, and are characterised by aggressive gregarious feeding behaviour, causing deep cavernous tissue wounds. Wounds rapidly become very extensive, attracting other female screw-worm flies and secondary myiasis agents. If left unattended, repeated infestation within the wounds rapidly leads to death of the host. Distribution is largely restricted to the southern areas of USA, Central America and northern South America for *C. hominivorax*. *C. bezziana*, is largely restricted to much of Africa, India, the Arabian peninsula, South-East Asia and New Guinea. *W. magnifica* is primarily located around the Mediterranean basin, in eastern and central Europe, and in Asia minor. Australia, as one of the major sheep producing countries in the world, is free from all screw-worm flies. However, introduction from neighbouring countries, where Australia maintains chemical lure baited trap surveillance, could pose a $500 million per annum threat to the pastoral industries of Australia. This should be considered a very conservative estimate since the Merino sheep industry would be highly exposed because of routine management practices which leave widespread surgical and shearing wounds in almost all sheep. There have been no documented reports on genetic variation between sheep in their predisposition to these flesh-eating flies.

4.3.3 The Calliphoridae - blowflies

The blowflies are the major cause of myiasis in sheep of economic importance in sheep in Australia, and the majority of this review and strategy is focussed on these flies. Lesser Chrysomya spp (*C. megaphala, C. rufifaces and C. albiceps)* occur throughout Australasia and oriental regions. Although these species are mainly sarcophagous and carrion breeders, they occasionally act as secondary agents in myiasis, infecting pre-existing myiasis wounds. On balance, the economic impact of myiasis attributed to these species is considered less important than the *Lucilia* species currently or the potential impact of the screw-worm flies.

An extensive review of the literature available on *Chrysomya rufifacies* was conducted by Baumgartner (1993). This included the taxonomy, biology, ecological role and the human medical importance of the fly. Particularly nasty was the attack on fetal membranes of new-born calves in Hawaii (Hardy 1980) where it could lead to the abandonment of the young by the mother. An interesting habit of the fly is that the maggots consume those of other species. The maggot of this fly can eat into the skin of sheep and rapidly lead to toxaemia and death. Recent literature on this fly is related to forensic entomology and human medicine. Since it has been found in flystrike cases on wool in the absence of other species it may initiate flystrike, or it may simply have eaten all other species first and become dominant.

Sheep myiasis attributed to *Lucilia sericata* and *Lucilia cuprina* is considered of greatest economic significance worldwide: these species are the primary agents of cutaneous myiasis. In most sheep farming regions one, or both, of these two species are responsible. In Australia and New Zealand *Calliphora stygia* is also implicated but generally accepted to only play a minor role. *Calliphora augur* was regarded as an Australian sheep blowfly in Victoria (Callinan 1980). Although both *L. cuprina* and *L. sericata* can cause myiasis in a range of domestic animals, they are of particular importance in sheep, and are known as "sheep blowflies". *L. cuprina* and *L. sericata* are facultative ectoparasites. Larvae develop following hatching of the egg clusters deposited on sites that are suitably predisposed. Their larvae infest and feed superficially on the living tissues (epidermis), lymphatic exudate, or necrotic tissue of the host. The mouth hooks are used to macerate tissues, and digestion occurs extra-orally by means of amylase in the saliva, and proteolytic enzymes in larval excreta.

A summary of the myiasis of current or potential economic significance to the Australian sheep industry is provided in Table 2.

Table 2. A summary of myiasis flies that are of potential significance in sheep.

Species	Classification	Host specificity	Site of infection	Occurrence	Impact on sheep production
OESTRIDAE					
Oestrus ovis	Obligate	High	Nasopharyngeal	All sheep producing areas	Mild / medium
CALLIPHORIDAE					
Lesser Chrysomya species					
C. megacephala, rufifacies, albiceps	Facultative saprophagous	Low	Secondary myiasis	Australasian / oriental	Low
Lucilia spp.					
L. cuprina, sericata	Facultative	High	Primary cutaneous myiasis agent at all predisposed sites	Worldwide	High-very high
Lesser Calliphora species					
C. augur, vicina, vomitora, albifrontalis, nociva, stygia	Saprophytic	Low	Primary / secondary myiasis	Australasian	Low-moderate
SARCOPHAGIDAE					
Cochliomyia hominivorax	Obligate screw worm	Low	Wounds, body orifices	Neartic & neotropical	Potentially very high
Chrysomya bezziana	Obligate screw worm	Low	Wounds, body orifices	Afrotropical / oriental	Potentially very high
Wohlfartia magnifica	Obligate screw worm	Low	Wounds, body orifices	Eastern palaeartic	Potentially high

4.3.4 Flies that globally cause flystrike

Flystrike is not unique to Australian sheep farms. Flystrike is a global issue for sheep and goat farms and has been reported in many countries including New Zealand, South Africa, Europe and the UK and Saudi Arabia.

Lucilia cuprina arrived in New Zealand in the mid-1970s and its subsequent spread down the country was well documented (Heath and Bishop 1995). However, flystrike was observed prior to the entry of *L. cuprina.* In the 1930s flystrike was reportedly caused *by Lucilia sericata* and *Calliphora laemica* (Fuller 1934) with *Calliphora laemica* causing more cases in the North Island and *L. sericata* in the South Island. The major species involved in myiasis of sheep were reported as *Calliphora stygia in* 1841, *L. sericata* in 1872 and *Chrysomya rufifacies* in 1911 (Heath 1994).

An extensive study reported by Heath and Bishop (2006) was carried out for 16 years following the introduction of *L. cuprina* to New Zealand. Of the 6047 samples where they could identify the species of fly, half the cases contained only one species. *L. cuprina* dominated those strikes (48.3%) followed by *C. stygia* (23.6%), *L. sericata* (21.5%) and *C. rufifacies* (6.6%). In 3219 cases, a mixture of *L. cuprina*, *L. sericata* and *Calliphora stygia* were common, while smaller numbers contained *C. rufifacies*. All four species of flies sometimes occurred together. In paired combinations *L. cuprina/L. sericata* mixtures were most frequently reared out of the samples. Notably, 26 samples contained other species including *Calliphora vicina*, *Calliphora hilli*, *Calliphora quadrimaculata*, *Xenocalliphora hortona*, *Musca domestica* and *Hydrotaea rostrata*. Some of these were found in isolation. We should note that these samples were collected by farmers and posted to the laboratory and smaller proportions may have occurred due to non-representative sampling, although protocols were provided. A small number of samples were also obtained from goats which contained *L. cuprina*, *L. sericata*, *C. stygia*, and *C. rufifacies* in mixtures and on their own. A greater proportion of samples were obtained from Merino sheep than would be expected from the proportion of the national flock that was Merino at the time. Romney and Coopworth were frequent, however Corriedale were poorly represented, possibly because they were predominantly farmed in dry and coastal areas, or perhaps the Merino farmers were more motivated. The breed mix in New Zealand has changed dramatically since the time of this study.

The work of Scobie et al. (2008) on two commercial farms of non-Merino sheep in New Zealand found very low levels of flystrike on one farm and none on another in the lower South Island. However, one of these was an organic farm and very small numbers were apparent, a number of which came from one sire group. This was reinforced in subsequent work on a research farm in the central South Island and a stud farm in the North Island where the progeny of certain sires were more likely to be flystruck (Scobie and O’Connell 2010). Breech bareness and the presence and amount of dags were both associated with the occurrence of of flystrike on these farms. (Scobie and O’Connell 2010).

Studies of Merino sheep in the warm and dry region of Marlborough (Scobie et al. 2011), and cold and dry central Otago (Scobie et al. 2012) examined breech traits but observed no flystrike. Protective measures such as chemical intervention and crutching were used on these farms but the dry years during which these investigations were undertaken lowered the risk. The environment is the principal reason that Merino farming has historically been restricted to certain areas of New Zealand.

In South Africa, Scholtz et al. (2012) found that Merino sheep selected for their ability to rear multiple lambs were lower in breech wrinkle and dag score during autumn and spring compared with those selected for lower weaning. The less fecund sheep were found to be slower to crutch as a consequence of the wrinkles and dags (Scholtz et al. 2012) and were more likely to be flystruck (Scholtz et al. 2010). Breech strike was most common (92%) and those that were struck were more likely to be struck in a subsequent year. The results of Horton et al. (2018) in Australia concurred with this in that Merino (17%) and crossbred ewes (5%) that had not been mulesed were flystruck. Furthermore, those that were struck had higher mortality, were more likely to be struck again, were lower in liveweight and condition score and the more severe the case of strike the less likely the ewes were to successfully reproduce. This bodes well for the Australian sheep flock, which can improve resistance to flystrike and increase reproductive performance.

The myiasis of sheep and goats throughout Europe has been reviewed by Sotiraki and Hall (2012). They reported flystrike caused by *L. sericata* and *Chrysomya albiceps* and the obligate sarcophagid fly *Wolfhartia magnifica* mainly in central and southern Europe. *L. sericata* on the other hand is more common in northern and central Europe. Myiasis by *L. sericata* follows the common theme in the Southern hemisphere and is attracted to urine or dag-soiled fleece, but of interest particularly with respect to South Australia and Western Australia is that in the Mediterranean environment of Europe *W. magnifica* was a greater problem than *L. sericata*. Other species that can be involved in myiasis of the fleece in Europe include *Lucilia caesar*, *Lucilia illustris*, *Calliphora vomitoria*, *C. vicina*, *Protophormia terraenovae* and *Chrysomya albiceps*.

Snoep et al. (2002) reported flystrike on Dutch farms where 2.9% of sheep and lambs were affected. Female lambs and adults were more susceptible than males, breech strike was most prevalent (69%) and incidence peaked during hot and humid weather conditions. There appeared to be no relationship with tail docking, breed, time of shearing, soil type, the environment or the method of application or type of insecticide. The total population was only 12,200 sheep run on 138 farms in very small flocks, however half of those farms were affected which illustrates the widespread nature of the problem that is not unique to Australia.

Alahmed (2004) reported myiasis of sheep in Saudi Arabia. In most cases (87%) the sheep were infested by *Chrysomya bezziana*, while *Chrysomya albiceps* and *Wolfahrtia nuba* were present in 9% and 4% of cases respectively. Although *C. bezziana*, also known as the screw worm fly, is very invasive, *C. albiceps* is very similar to/or conspecific with *C. rufifacies*. Infections occurred when temperature and humidity were optimal and were rare in the hot dry summer and during winter.

In Scotland, Morris and Titchener (1997) found *L. sericata* was the predominant agent of myiasis in sheep. In the south east of England 0.4% of adult ewes and 1.4% of lambs were flystruck, and since this was a survey, it is likely that this level of incidence occurred in spite of protective measures that might have been utilised (French et al. 1995). Bisdorff and Wall (2008) found that 91% of UK farmers treated with prophylactic chemical, 39% required repeat treatments and 11% treated three or more times, so clearly flystrike is a concern. Interestingly they reported that purebred (non-Merino) flocks were less likely to report flystrike than crossbred (non-Merino) flocks, and perhaps breeders with purebred livestock are more focused on the animal than those with crossbreds who would more than likely be commercial farmers.

Clearly *L. cuprina* is not the only fly causing flystrike throughout the world, and historically other species have been reported. Should the war on *L. cuprina* prove successful, particularly sterile-fly techniques, highly specific fly traps, pathogens and similar, it should be assumed that another fly species could fill this niche and none of the actions taken directly against *L. cuprina* should be expected to continue working. The current authors support strategies which reduce the susceptibility of the sheep to flystrike to combat the threat from all species.

4.3.5 The impacts of climate change

The distribution and activity of the various sheep myiasis agents are linked closely to the prevailing weather conditions. Historically, this has resulted in predictable seasons when increased flystrike is expected (if susceptible hosts are present). As the climate continues to change, so too will the seasons when flystrike should be expected. Modelling completed by Rose and Wall (2011) suggests that in the United Kingdom, the season where flystrike is expected could increase by as much as 2 months each year. This is based on knowledge of the temperature profile when *L. sericata* is active. Perhaps of greater concern is the change in prevalence of different agents of myiasis. Under some climate change scenarios, the much more pathogenic *Wolfhartia magnifica* could replace *L. sericata* in the United Kingdom (Rose and Wall 2011; Wall et al. 2011). It is important for the Australian sheep industry to understand the impact various climate scenarios will have on future pressure from myiatic flies. Working on the assumption that the overall impact will place even greater pressure from flies (and potentially from screw worm flies), climate change scenarios will be an important motivator for sheep farmers to reduce the susceptibility of their sheep.

4.4 Lucilia cuprina and *Lucilia sericata*

Blowfly strike by both *L. cuprina* and *L. sericata* occurs most commonly in the peri-anal area of sheep and is strongly associated with faecal and urine soling of the breech/tail region. In addition, bacterial dermatoses as consequence of prolonged wetting of the skin, with or without additional involvement of *Dermatophilosis congolensis*, or infections attributable to footrot, are major predisposing factors in blowfly strike involving *L. cuprina*. There is little recorded involvement of dermatitis in the pre-disposition of sheep to body strike by *L. sericata*. Microbial agents producing attractants for gravid females encourage oviposition, with females laying eggs in batches of 200-250. Under suitable conditions eggs hatch within 24 hrs, allowing first instar larvae to feed on soluble extraneous protein in the immediate environment. On development of mouth hooks in latter stages, second and third instar larvae will feed more aggressively. Oviposition sites, and pre-existing strikes, are attractive to gravid females, and it is common for extensive development of strikes over the body if left untreated. Sheep which are not suitably predisposed will not allow attraction, initiation and the development of blowfly strike.

L. cuprina has been described as stenothermal (Ash and Greenberg 1975), indicating it can tolerate only a small range of temperatures. Ash and Greenberg (1975) argued this was the reason that *L. cuprina* had a restricted range in the USA. However, the arrival of *L. cuprina* into New Zealand has broadened the area which has a flystrike problem and has also extended the season (Heath and Bishop 2006) in comparison to that seen when only *L. sericata* was present.

An interesting comment from Wardhaugh and Morton (1990) referred to reducing fly numbers but this "demands a greater understanding of sheep-fly-weather interactions than currently exist". As 1990 is now a long time ago, the question arises whether that has changed in the following years. This is of particular interest in the face of climate change when seasons and areas at risk may increase.

There has been considerable research on fly biology over time. The question then arises as to which important biological factors remain poorly understood if we are to effectively model these flies. Wardhaugh (2001) reviewed the biology and ecology of the fly up until that date. In this review he noted several deficiencies. These were:

- Defining what adult *L. cuprina* feed on which determines oviposition timing and success
- Defining the relative success of sheep and carrion as oviposition sites
- Factors affecting survival of eggs and larvae on sheep
- Factors that control the induction of inhibited development ("pre-pupal overwintering")

Most of these questions remain, however this lack of knowledge should be kept in perspective in its importance in an integrated strategy aimed at reducing flystrike to zero. Indirect information on fly abundance and activity could be obtained from large scale field observations and modelled into fly strike models as discussed further on.

4.4.1 Diapause

Ash and Greenberg (1975) indicated that *L. cuprina* does not undergo a true diapause, rather a form of quiescence. However, McLeod (1997) dismissed this terminology as being inappropriate and described *L. cuprina* as undergoing a facultative diapause. This terminology has subsequently been used by many authors. Fraser and Smith (1963) claimed they had shown that diapause is directly induced by factors in the environment of the larvae during the critical early post-feeding phase. De Cat et al. (2012) also showed that larvae, for which the adults were on a continuous 24-hour light cycle, could be induced to inhibit development under different soil temperature conditions. Earlier work had implicated a maternal influence (Dallwitz and Wardhaugh 1984) being the day/night length. None of these early studies were clearly able to define the factors involved. McLeod (1997) observed some larvae completing pupation through winter, which again questions the diapause description, although the adults in this case were not subject to low daylight conditions.

The end of diapause is similarly poorly defined. Wardhaugh (2001) stated that larvae may enter diapause over a period but emerged synchronously as conditions became warmer – presumably above a minimum threshold. Such a threshold is not yet clearly defined. In the study reported by De Cat et al. (2012) larvae were placed in chambers in the field and were subject to normal diurnal and weekly variations. Nevertheless, they concluded that a sustained period of low temperatures is required to induce inhibition. Interestingly, they noted that similar studies in Canberra were consistently 1-5°C cooler to achieve the same result they achieved in Western Victoria. De Cat et al. (2012) concluded that "further study to define thresholds and duration of low temperatures" is required. McLeod (2001) observed that a soil temperature (5cm depth) of about 13-18°C was required to stimulate recommencement of pupal development. De Cat et al. (2012) observed that an increase in soil temperature of 1.5°C over a 4-day period and soil temperatures remaining above 11°C for at least 7 consecutive days induced larvae to resume development. For modelling purposes these temperature descriptions are quite different.

The majority of these pupal development studies have been conducted in the field with the consequent problems of confounding changes in multiple variables. More carefully controlled experiments using incubators should allow a better understanding of this phenomenon. Where studies have been conducted in a laboratory then the range of temperatures utilised has invariably been limited. Access to better more flexible modern incubators would allow more precise measurements to be made. The onset of the fly season is a critical time point yet remains poorly defined.

Larvae pupate in the top layers of the soil. During warmer months this is likely to be deeper than for overwintering where larvae are only 2-3cm deep. This will affect predictions as soil temperatures are commonly measured at 10cm. Wardaugh (2001) observed "information pertinent to understanding pupal survival in the field are not available". As indicated above, since 2001 several studies have been published but most from field plots where several variables can confound each other.

For *L. sericata,* conditions to induce diapause appear to be somewhat different from *L. cuprina* although the biology is not completely understood. The development times during the season follow a reasonably well described pathway albeit with a limited spread of temperatures investigated (Ash and Greenberg 1975). Interestingly, at lower temperatures *L. cuprina* develops faster than *L. sericata* even though the former is considered a more tropically adapted species. The term facultative diapause is still used to describe the situation for *L. sericata*. Tachibana and Numata published two papers (2004a, b) showing that various combinations of day length and temperatures, for both the parent generation and the larvae going into diapause, influenced the proportion of larvae entering diapause. There is also a suggestion of a requirement for a period of chilling during diapause before reactivation. Thus, as for *L. cuprina* there is not a complete understanding of the factors that induce or break diapause. Information is critical in modelling and predicting the build-up of flywaves and activating alternative control methods to reduce fly numbers.

4.4.2 Adult Flies

The information on this stage is reasonably comprehensive, with the possible exception of understanding the feeding habits of adult flies and being able to model that in the overall life cycle. The following was summarised by Wardaugh (2001) from various publications. Adult females are known to utilise faeces of sheep and other animals as a source of protein for ovarian development. To develop the first batch of eggs requires 57 degree days above 8°C although this can be influenced by sub-optimal nutrition such as low protein diets for sheep resulting in low protein faeces. A female will develop a batch of eggs every 4-8 days but rarely survive long enough to produce a third batch. Overall, this level of understanding is good, although there are still variables that would be hard to include in a model. At this time Wardaugh (2001) also commented that the data he referred to were obtained in the Southern Highlands and considered further study in more arid areas "worthy of further study". Some of this has occurred but again such publications refer to being an incomplete study.

The spatial distribution of flies is an important consideration to any modelling exercise. As above Wardhaugh (2001) observed in his review that "factors regulating the movement and spatial distribution of *L. cuprina* are not well understood". Different catch, release, and recapture studies have shown varying results, with most concluding *L. cuprina* is a reasonably sedentary species but can move several kilometres on occasions.

4.4.3 Distribution of *Lucilia cuprina* and *Lucilia sericata*

In combination, the effects of *L. cuprina* and *L. sericata* have been reported from all major sheep producing countries worldwide. In general, it is believed that *L. sericata* is the most important agent of sheep myiasis throughout the cool-temperate habitats of northern Europe, and New Zealand. *L. cuprina*, on the other hand is widespread in warm-temperate and sub-tropical regions, including Australia, New Zealand, southern Spain, and northern and southern Africa. In Australia *L. cuprina* is present in over 90% of flystrike cases. A notable exception of the importance of *L. cuprina* in sheep myiasis appears in USA, where it is known to be present but considered unimportant.

Given the widespread importance of *L. cuprina* and to a lesser extent *L. sericata* in sheep myiasis, this review will restrict itself to these species. Other Calliphorid species of interest in sheep myiasis include *C. augur*, *C. vicina*, *C. vomitoria*, *C. albifrontalis*, *C. nociva*, and *C. stygia*. Although these are primarily saprophytic and carrion breeders, their role as agents as occasional primary and mostly secondary myiasis warrant their mention in this review. These species are widely distributed throughout the Australasian region, but on balance their economic significance is low when accounting for the economic impact of the essential primary myiasis caused by other species, in particular *L. cuprina*. Specifically, in the development of flystrike by *Lucilia cuprina* and *Lucilia sericata* it is appropriate to classify strikes on the basis of the location since each is determined by a specific subset of predisposing factors.

4.4.4 Classification of flystrike by *Lucilia cuprina* and *Lucilia sericata*

4.4.4.1 Breech Strike

This is the collective term for all strikes occurring in the tail and crutch region of sheep. In the absence of preventative strategies this would be by far the most common form of strike in sheep (Tillyard and Seddon 1933, Belschner 1937; Watts et al. 1979). Sheep are predisposed by soiling of the breech with urine and faeces and the subsequent development of a dermatitis (Bull 1931, Seddon 1927). Breech strike is significantly higher in ewes than males, and strongly influenced by wool length, skin fold development in the breech and tail region, tail length, bare area in the crutch region and occurrence of scouring. Greeff et al. (2018) examined an extensive range of factors in association with the prevalence of breech strike in unmulesed and uncrutched ewes and wethers and found that these factors only accounted for up to 50% of the variation in breech strike (see 4.4.5.1 below), whereas Smith et al. (2009) reported that breech wrinkle, tail fold and breech bare area accounted for most of the variation in breech strike. It is possible that other fine-scale attributes which lead to moisture retention in the tail or crutch region and subsequent dermatitis and olfaction leading to fly attraction, oviposition and strike establishment are not adequately accounted for by adopted classification systems.

4.4.4.2 Poll or head strike

Poll or head strike predominantly occurs in rams of all age classes. Although it is a widely held belief that it may develop following wounds sustained during fighting, the majority of strikes appear to develop at the base of the horns presumably when excessive skin debris is moist enough to allow for bacterial proliferation and fly attraction with subsequent strike development (Seddon 1967; Raadsma 1987). Poll strike is much less prevalent in wethers and poll rams. Shearing (wigging) and chemical control are most common forms of control for this type of strike.

4.4.4.3 *Pizzle strike*

This form of strike mainly occurs in young rams and wethers when long wool around the preputial opening becomes soiled with urine or exudate from balanitis (pizzle rot). The prevalence of overt strikes are usually low (<2% of all male sheep affected) (Belschner 1937; Watts et al. 1979, Raadsma 1987). Pizzle dropping is of limited efficacy in preventing this type of strike and removal of wool around the pizzle is the most common form of control, followed by chemical control. Both ewes and wethers can become affected by belly strike when grazing long wet pasture for prolonged periods in unusually wet seasons. Chemical control through automatic jetting races or shower dipping would be a common control strategy for targeting this region on the body but potentially of limited efficacy as these areas could remain wet for prolonged periods whilst grazing wet pasture.

4.4.4.4 *Body strike*

Strike involving any part of the body other than breech, head and pizzle are termed “body strikes”. Most affected sites are shoulder, nape of the neck and back over the loins (Belschner 1937; Raadsma and Rogan 1987). Body strike outbreaks develop rapidly after periods of prolonged and heavy rainfall during warmer months of the year. Young sheep, regardless of sex, with 3-6 months wool growth are particularly susceptible. Body strike outbreaks can develop in successive waves where fly populations build up from over-winter hibernations, coinciding with increasing numbers of sheep becoming affected with the pre-disposing dermatoses of fleece rot and or dermatophilosis (see below). Outbreaks of body strike may vary on a farm by farm basis, but usually are determined by regional rainfall, both the total amount of rainfall and the number of wet days. The economic impact of body strike, both in terms of production losses and seasonality, will thus vary by year and season. A wide range of control options are available for controlling body strike (see below), however shearing, chemical control and genetic control are the most common forms.

4.4.4.5 *Secondary strike*

Sheep may become struck because of other diseases such as acute conjunctivitis or footrot. Clean surgical wounds are rarely struck by primary blowflies but both surgical scabs or post-partum staining of the udder in lambing ewes may predispose sheep to crutch strike by black bush flies (spp. were not checked, Raadsma, H.W., unpublished). Secondary strike by other fly species (as reviewed above) infesting primary strike sites is also a common form of flystrike if such strikes are left untreated. Chemical control is a common form of control for secondary strike.

4.4.4.6 *Covert strike*

Strikes which are not overtly detected and targeted for treatment are commonly known as covert strikes. Wardhaugh et al. (1989) defined and classified such strikes and prevalence may be sufficient to allow fly populations to continue at low levels and act as reservoirs for opportunistic outbreaks under suitable environmental conditions.

4.4.5 Predisposing factors for strike development by *Lucilia cuprina* and *Lucilia sericata*

In order to better understand the role and opportunity for indirect selection for flystrike or indirect control, the role of predisposing factors is crucial in each form of flystrike. This is particularly relevant in potential breech and body strike control. As defined under the aetiology above, normal dry fleece and skin is an unsuitable environment for flystrike to develop. Any factors which expose fleece and skin to prolonged wetting and bacterial proliferation render sheep susceptible to predisposing dermatoses, subsequent attractiveness and suitability for flystrike to develop. In the case of breech strike and body strike unique predisposing fleece and skin characteristics allow development of flystrike to occur and as such have been reviewed separately here.

4.4.5.1 Breech strike

The development of breech strike and its predisposing factors and scope for genetic control has most recently been reviewed James (2006). Breech wrinkle has long been associated with predisposition to breech strike, with investigations as early as 1915 (Froggart 1915) and was intensively investigated by Seddon and colleagues in the 1930's (Seddon et al. 1931) and eventually resulted in the development of the Mules operation. More recent studies by Greeff et al. (2010, 2013, 2014, 2018), Smith et al. (2009) and Scholtz et al. (2010, 2013) confirmed the importance of breech wrinkle in the development of breech strike. However, this factor alone does not account for all the observed variation in breech strike (Greeff et al. 2018). Additional factors deemed to be critical in the pre-disposition to breech strike were tail wrinkle (Seddon and Belschner 1937; Joint Blowfly Committee 1933; Greeff et al. 2014), tail length following tail docking (Gill and Graham 1939; Riches 1941; Watts and Luff 1978), dag formation, dag moisture and scouring (Morley et al. 1976; Watts and Luff 1978; Greeff et al. 2013, 2014; Pickering et al. 2015), and the amount of breech and tail wool cover (Morley 1949; Scobie et al. 2002; Greeff et al. 2014; Pickering et al. 2015). The critical underpinning factors of these predisposing factors relates primarily to the retention of moisture in the breech area, with the sequalae of dermatitis, fly attraction, oviposition stimulation, hatching of eggs and growth of first instar larvae.

It was first recognised by Bull (1931) that the development of breech strike was strongly associated with the development of a predisposing dermatitis of resident bacteria and moisture held in the breech area. Subsequent studies by Burrell et al. (1982a) investigated the micro-flora in breech strike and a possible role for control through vaccination. A high-resolution analysis of the micro-biome in the development of breech strike is warranted since this area is likely to be contaminated by faecal and urine contamination, and as such distinct from the dermatoses leading to the development of body strike (see below).

4.4.5.2 Body Strike

The aetiology for development of body strike is similar to that of breech strike, with the exception that natural rainfall is the primary initiator in the predisposing dermatoses of fleece rot and dermatophilosis with subsequent fly attraction, oviposition and hatching of eggs and growth of first instar larvae under favourable conditions. The importance of bacterial dermatitis as an essential factor was recognised very early in the history of blowfly research (Seddon 1927; Seddon and McGrath 1929; Bull 1931; Belschner 1937) and were subsequently defined as fleece rot and dermatophilosis. Norris et al. (2008) provided the most recent review on fleece rot and dermatophilosis in sheep.

Fleece rot. Fleece rot is defined as a mild superficial dermatitis following prolonged wetting and proliferation of skin microflora. Exudation resulting in matted bands of serous exudate with extensive yellow grey and or green discoloration are clinical signs of fleece rot (Hayman 1953). The role of a wide range of fleece skin microflora but in particular *Pseudomonas aeruginosa* and *Pseudomonas maltophilia* are thought to be the major pathogens in the development of fleece rot (Merritt and Watts 1978; Burrell et al. 1982a, b; Burrell 1990). The role of other Pseudomonad species*, P. alicaligenes, P. mendocina*, and other genera including *Proteus, Staphylococcus, Bacillus, Enterobacter* and *Flavobacterium* species as causal agents have not been fully discounted (Burrell and MacDiarmid 1984; London and Griffith 1984; MacDiarmid and Burrell 1992). The role of vaccines in control of fleece rot and therefore indirect control of body strike was explored previously (Burrell et al. 1982a, b; Burrell 1990) with moderate success, but abandoned in late 1990, when multivalent serotypes of *P. aeruginosa* offered no cross protection, and not all fleece rot lesions were associated with *P. aeruginosa* (Kingsford and Raadsma 1997; Dixon et al. 2007), thus further complicating the development of multi-valent multi-species vaccines. With the advent of new environmental pathogen screening though S16 RNA and e-DNA genomics, combined with new vaccine technologies, this avenue for future control could be considered.

Dermatophilosis. A serious dermatitis following extensive skin wetting and invasion by *Dermatophilus congolensis* first identified in early 1930s. This dermatitis results in a strong exudative response on sites affected. Recurrent activation of previously affected lesions result in continued exudative crusts leading to so called “lumpy wool”. Affected animals create a highly attractive environment for flystrike to develop. Although infection can spread from sheep to sheep through close physical contact (yarding wet sheep, shearing or though wetting from common sources such as shower dips). Although *D. congolensis* is always implicated by definition in dermatophilosis, variation in strain grouping and virulence has been reported. Little is known about the genetic predisposition of sheep to this disease or its genetic correlation with body strike susceptibility. Control through vaccination with both live and killed vaccines were explored but offered limited efficacy. Of note is that most studies on micro-flora and causative agents have been conducted in Merino sheep, to what extent the same factors contribute to these predisposing conditions in non-Merino is largely unknown.

5 Current knowledge of flystrike control methods

5.1 Management methods to reduce the incidence and prevalence of flystrike

Physical management processes that render the sheep less susceptible to fly attack are commonly practiced across all sheep growing areas of Australia. Most of these interventions are focussed on reducing the susceptibility to breech strike by keeping the area around the anus free from any accumulation of moisture. There is no doubt that corrective surgical procedures such as tail docking and removal of skin folds in the breech area (mulesing) are amongst the most effective methods to reduce the predisposition of sheep to flystrike. Such measures, although questioned on the basis of animal welfare (French et al. 1994), offer life-long protection against flystrike in sheep. For this reason, the use of the surgical control methods is widespread in Australia, where the numbers of sheep managed by individual farmers is very high. The use of mulesing and tail docking is less widespread in developing countries, or countries where sheep production is less extensive, allowing for a much lower ratio of sheep per labour unit, and hence greater scope for individual animal attention. Strategic removal of wool from the main areas inherently susceptible to flystrike also greatly reduces pre-disposition to flystrike, but protection is generally not long lasting.

The Australian wool industry has now become reliant on a combination of effective management practices, opportunistic use of insecticides, and the use of suitable genotypes for the management of flystrike. It is the view by the authors in this report that the emphasis or need for additional/replacement blowfly control options will certainly increase in the future. Use of insecticides will decrease as consumer demands favour lower chemical residue contamination in wool, and blowflies are likely to develop genetic resistance to current insecticides. The use of surgical modifications as we know them today, will eventually cease on the grounds of animal welfare, driven by consumers. As such there will be a directional change in flystrike control methods as we currently see being used by industry.

5.1.1 Tail docking

Tails are routinely removed in young lambs to reduce dag accumulation in later life which predisposes the animal to flystrike. A New Zealand review by Fisher et al. (2004) attempted to understand the appropriate length of the tail. They concluded in Merino sheep that had the shortest tails were worse for flystrike. In non-Merino sheep in New Zealand, too few lambs were flystruck to support any conclusion (Pomroy et al. 1997; Scobie et al. 1999), because dag accumulation was very low in both of these experiments. Graham et al. (1947) found dag accumulation increased with increasing tail length in Merino sheep, and urine staining was worst in sheep whose tail had been docked very short. Furthermore, Riches (1941, 1942) observed during a three-year period, flystrike of sheep was clearly worse for those with very short tails compared with short or medium length tails.

Table. 3. Effects of tail length of sheep on the presence of dags, flystrike, health issues, and production and management practices from several studies undertaken in New Zealand, Australia and the USA (from Fisher et al. 2004).

Tail length	No Tail	Short	Med	Long	Reference; Country
Dags, staining & flystrike					
Dags (0=none, 5=most)					
- Experiment 1	0-0.5		0-0.6	0-0.7	Scobie et al. (1999); NZ
- Experiment 2	0.3-1.1		0.8-1.3	0.7-1.6	
Dags (%)	8	15	35	52	Graham et al. (1947); Australia
Urine staining (%)	98	92	83	91	Graham et al. (1947); Australia
Flystrike (%) - 1938-39	19-61	17-56	5-32		Riches (1941, 1942); Australia
- 1939-40	0-8	0-7	0-2		
- 1941	51	33	14		
Health & Welfare					
Tail infection (%)	96	64	13		Johnstone (1944); Australia
Perineal carcinoma (%)	17	1-6	0		Swan et al. (1984); Australia
Rectal prolapse (%)	8	2-4			Thomas et al. (2003); USA
Management					
Shearing - number of blows	41		41	41-48	Scobie et al. (1999); NZ
- time (sec)	60		62	63-72	
Crutching (min/12 lambs)					Scobie et al. (1999); NZ
- no dags	5.2		6.2	7.4-8.4	
- dags	8.2		10	12-12.8	

5.1.2 Mulesing

The process of mulesing was introduced in the early 1930s and was substantially modified from early procedures to be known as the “modified-Mules operation” in the 1940s and subsequently was further modified in the 1950s and early 1970s to be known as the “Radical-Mules operation” (reviewed by Morley and Johnstone 1984). The operation has found widespread adoption ever since. It had a significant impact on the incidence and prevalence of flystrike, particularly in Merinos. Lee and Fisher (2007) reviewed the prevalence of flystrike in mulesed and unmulesed sheep. The proportion of sheep being flystruck was uniformly low in mulesed sheep, but in unmulesed sheep the proportion varied from negligible levels to almost the entire flock, depending on the weather. The susceptibility to flystrike is enormously impacted on by genotype.

With widespread global consumer changes in beliefs around animal welfare, mulesing has already been banned/phased out in some major sheep production countries (NZ, South Africa) or never adopted (UK, Europe). Australia remains one of the last and largest sheep production countries where mulesing is still widely practiced. Despite a national commitment to phase out this practice, a large cross section of the industry has remained reliant on this practice for flystrike control.

5.1.3 Pizzle dropping

Pizzle dropping has been practised previously and is probably still practised in some parts of the industry. For a range of reasons this will not be considered further in this review:

1. Pizzle strike is rarely featured as a major cause of flystrike
2. The process of pizzle dropping is not in line with future industry values
3. Pizzle dropping does not alter the predisposing cause of “pizzle rot” (balanoposthitis)
4. The number of adult wethers is much lower than it has been historically and this is likely to continue

5.1.4 Crutching

Flystrike prevention is the major reason for crutching but is not the only one. Crutching also removes dark fibre contamination in the wool clip, reduces the additional staining of other sheep when penned for shearing and reduces faecal contamination on carcasses of slaughtered animals. Crutching is the removal of wool which has accumulated faeces and or urine which both provides a moisture source for maggots as well as an attractant for gravid female flies. Crutching is very effective at reducing breech strike risk. It is very time consuming and a considerable cost on a business, so it is only carried out either once or twice per year. There is limited information about the most appropriate area to crutch. The focus of most operators is to remove all signs of faeces and urine from all areas. It is possible that this is not necessary and only areas that are otherwise predisposed need to be focused on. The timing of this practice is critical in terms of having the maximum impact on reducing the incidence of flystrike. Largely crutching is undertaken based on historic timing of fly-waves as well as the amount of dag or urine accumulation that has occurred in a given season. The use of sheep with reduced breech cover and increased naturally large peri-anal bare areas is discussed further on. Systems that allowed a more accurate assessment of the most important time to crutch would be very useful.

5.1.5 Shearing time

The removal of all wool from sheep can have a major impact on the reduction of flystrike risk. The routine practice of shearing sheep prior to the summer months (peak fly activity) brings about a useful reduction in fly risk.

5.2 Chemical control of flystrike

The use of insecticides has been a core component in the control of blowflies since the early 1900s. Insecticides are generally applied to key areas on the body in the prevention of strike or used in dressings of existing strikes to prevent re-strikes. The use of preventative chemicals is one of the greatest tools that Australian sheep farmers have in the fight against flystrike. The development of new chemical compounds has been highly effective in flystrike prevention, with some formulations offering up to 16 weeks protection, which is enough to protect sheep through a high-risk period. One of the striking features of the history of insecticide use for flystrike control, has been the enormous capacity of the primary blowfly to develop genetic resistance to almost all chemical compounds. Insecticide resistance to multiple compounds is generally widespread and greatly reduces the efficacy of this control option. Resistance to available insecticides has also forced the chemical industries to develop new compounds often, at great expense, with potentially little return on investment if the compound shows efficacy against blowflies only. For a comprehensive review of the use of insecticides for flystrike control, the reader is referred to Levot (1993, 1995) who provides both an historical account and outline of management strategies to deal with insecticide resistance. Although the repertoire of chemicals has changed considerably over the 100-year history, the application technology has changed relatively little. The relatively crude methods of insecticide application in wool often leads to unpredictable amounts of chemical being deposited on the animal. Significant residual levels of chemical at the time of wool harvest can lead to consumer resistance for wool and can limit the time periods during which chemicals may be used. Despite the potentially negative aspects of chemicals in blowfly-strike control, where effective compounds are available, the cost of controlling blowfly strike by chemical means may well be lower than adopting long-term control strategies through selective breeding. However, this scenario assumes that chemical compounds will remain unaltered in their efficacy over time, hardly a realistic expectation.

The ongoing use of these chemicals has potential problems across three major areas: consumer acceptance; non-target impacts; and the development of insecticide resistance. Looming large is the development of insecticide resistance by *L. cuprina* to available insecticides. A continuing series of reviews are available (e.g Sandeman et al. 2014a; Anstead et al. 2017). So far it has been possible to develop new chemicals as old ones fail but this will become progressively harder. (Table 4).

There is a tendency to assume that general recommendations can be developed that are effective for all insecticides. To some extent this is true but different insecticides have very different modes of action and the changes in physiology will be very different. Some genetic changes are easy for the insects to make and others clearly more difficult. The rapid development of resistance to benzolphenyl urea insecticides versus the continued success of cyromazine with only limited resistance apparent after many years is a nice example. The biological fitness of the resistant insects will vary. Consequently, for some insecticides it may prove there is rapid reversion to susceptibility but to others very little (where there is little effect on fitness). This will influence policies such as rotation of insecticides and potentially the use of combinations. There appears to be little information on reversion to susceptibility.

The lesson from anthelmintics is the usefulness of combinations to delay the development of resistance in nematodes. Many of these ideas in helminthology originally came from insect control yet there is seemingly little study on this for flystrike control.

A key factor that has been promoted with success for nematode control is to maintain a small population of unselected nematodes “in refugia” which can then act to dilute out the influence of resistant survivors in an animal and limit the number of survivor breeding with survivor situations resulting in in homozygote. It is difficult to see how this could be incorporated into flystrike control. The aim continues to be “no flies”. As *L. cuprina* struggles to develop on carrion it may need tolerance of flystrike on live sheep to achieve a usable refugia and as such is against welfare considerations. We do not yet have sufficient understanding of the numbers either way, although it would seem that numbers developing from carrion and other sources are unlikely to be adequate (Lang et al. 2001). Continuing effort is required to develop new approaches to limit development of insecticide resistance. Anecdotally farmers are reporting that the period of cover being offered by fly chemicals is reducing year on year. This is strongly supported by recent results from AWI funded research investigating fly chemical resistance. Of 50 fly sent in from farmers from NSW all of the samples displayed resistance to either cyromazine or dicyclanil or both. Resistance to these two chemicals is now evident in all states except Tasmania (no samples from Queensland were included) (Narelle Sales, NSW DPI Webinar). Continual monitoring of fly resistance to chemicals is an important future activity.

Table 4. Chemical groups used in recent times for the control of flystrike including any fly resistance that has been detected and the resultant implications. Modified from Sandeman et al. (2014a)

Insecticide group	Period used	Resistance detected	Practical implications
Organophosphates	1957-2016	1965	Flystrike protection reduced from >16 weeks to 2-4 weeks. Larvicidal effectiveness significantly reduced
Triazine (cyromazine)	1979-present	2011 2020	Low level, no implications if applied as per label Significant resistance now evident*
Pyrethroids (cypermethrin)	1988-present	None	None
Benzoylphenyl urea (diflubenzuron)	1991-2008	1998	High level of resistance by 2002 rendering it ineffective. Fly claims removed in 1998
Spinosyns (Spinosad)	1992-present	None	None
Avermectins (ivermectin)	1993	None	None
Pyrimidine carbonitrile (dicyclanil)	1998-present	2011 2020	Low level only, none if applied as per label Significant resistance now evident*

* Additional information from Narelle Sales, NSW DPI, project results from AWI research.

5.3 Controlling dag formation

Dags are without question the major cause of flystrike. Were it not for body strike, and a small proportion of strikes initiated in urine stain it would be possible to stop flystrike by preventing dags.

In New Zealand 81% of flystrike occurs on the breech and is almost universally associated with the amount of dags (Heath and Bishop 1995). In the United Kingdom 67% (French et al. 1995) of flystrike occurred on the breech, while in Australia 65% were breech strikes (Greeff and Karlsson 2009). Increasing the amount of dags has frequently been associated with flystrike in non-Merino sheep. Leathwick and Atkinson (1995) reported a linear association between the dry weight of dags and the proportion of lambs that were flystruck under New Zealand conditions. Pickering et al. (2015) found breech strike was strongly positively correlated with dag score (0.71). The association with dags has also been shown in Australia in Merino sheep (Greeff et al. 2014). Little scientific evidence is reported for non-Merino sheep in Australia, though we anticipate breech strike to be related to dag score. The process of mulesing sheep in Australia has been shown to reduce overall dag score by between 8 and 10% in Merino sheep (Horton et al. 2020).

Inducing scouring exacerbated dag formation and consequently increased the proportion of flystrike in experimental flocks (Watts and Marchant 1977), and quite the opposite is evident following dag removal by crutching. However, despite frequent crutching of Romney lambs fed ryegrass with toxic endophyte, the breech was still the most common region struck (Young et al. 2004). Sewell et al. (2009) found body strike was more prevalent on Merino sheep grazing pastures with toxic endophtyes. On the other hand, grazing *Lotus corniculatus* compared with *Lolium perenne* has been shown to reduce the amount of dags and flystrike in sheep in New Zealand (Leathwick and Atkinson 1995). Leathwick and Heath (2001) reported that grazing sulla (*Hedysarum coronarium*) and *L. corniculatus* both reduce dag build up and flystrike. Little of this knowledge has been adopted or exploited in Australia or New Zealand. Further studies of the effect of forages on flystrike are warranted under Australian conditions in meat producing sheep.

In crossbred sheep in New Zealand the heritability of dag score has been reported numerous times but Pickering et al. (2015) for example estimated that in Romney-based flocks it was 23 %. Since 23 % is due to genetic effects, the remaining 77% of variation in dag score is due to either measurement error or environmental effects. The environmental factors include endoparasitism, lush pasture with a lack of fibre, an imbalance of nutrients in that pasture, toxins in pasture from either the plants, pasture microbes or an interaction between more than one factor (reviewed Waghorn et al. 1999). Grain feeding, acidosis or infectious intestinal microbes can also cause scouring and dags and can therefore affect lot fed meat sheep. Lactation causes a dramatic increase in voluntary feed intake with a resultant increase in throughput. Parturition is often timed to coincide with high quality pasture. The known peri-partrient relaxation of resistance (PPRR) may exacerbate this, e.g. through increased parasitism. With such a long list of potential causes of dag formation, it is not surprising that dag score has a relatively low heritability. It is unlikely that all these factors would be acting on a given flock at one time, for example grain feeding will probably not occur when lush pasture is available. Farmers could probably determine the causative agent if they knew these factors and thought about what was going on with their pasture or feeding at the time, but very often they blame parasites and reach for the drench gun. Drenching has been shown to reduce dag build up and breech strike in Australia (Morley et al. 1976; Watts et al. 1978) but will only work in sheep where endoparasites are the cause. Wider education of farmers around the factors that cause dags might reduce the incidence of flystrike and potentially reduce the use of anthelminthic compounds and resistance to them.

Dag score has been shown to be repeatable under pasture feeding conditions in Merino sheep in Australia (Larsen et al. 1995) and Romney sheep in New Zealand (Bisset et al. 1992). Unfortunately, selection of sheep for resistance to internal parasites has tended to exacerbate dag build up (reviewed Bisset et al. 2001) largely under New Zealand conditions in crossbred sheep. This has been supported by work in Merinos by Williams et al. (2010). This correlation is thought to be as a result of an inflammatory immune response to larvae that have been ingested. This results in the larvae being rapidly expelled which is helpful in reducing worm burdens however it can result in greater dag formation (Williams 2010).

Scouring of sheep in Australia is a distinct regional and seasonal problem, particularly in Merino hoggets (reviewed Larsen et al. 1999). It occurs at a time when large amounts of lush feed are available, and while actively growing grass and clover are high quality forages, it is postulated that the hypersensitive reaction to a large influx of internal parasites causes liquid faeces, dags and potentially flystrike. Feeding a fibrous supplement such as pasture hay or even cereal straw in this season has been investigated in Victoria. Davidson et al. (2006) examined the potential with Merino sheep at Dookie on a mixed clover, ryegrass and phalaris pasture. Lower dag scores were achieved in the group fed fibre, but although there was less flystrike in the group fed fibre, too few sheep were flystruck to establish statistical significance. Of merit to the current section of this review, only sheep with high dag scores were affected by flystrike. Some success in reducing dags in Merino hoggets has been achieved under similar conditions in New Zealand (T.J. Fraser pers comm), but likewise too few sheep were used to establish differences in flystrike rates. The extent of this problem in non-Merino breeds in Australia has not been reported, crossbred lambs under similar conditions can potentially cope with greater parasite loads and lush feed and less fibre.

5.4 State of farmer knowledge

Of interest to this team of reviewers who have worked on flystrike on and off for many years is the lack of adoption of the methods that have been developed to control flystrike. There is a dearth of research information on the incidence and impact of flystrike in non-Merino sheep in Australian conditions, and there is very little published literature about the state of farmer knowledge around flystrike prevention and control. A very small study conducted in Tasmania over two decades ago suggested that this sub-group of farmers had a good understanding of the predisposing risks for flystrike but lacked a succinct plan on how to minimise the impacts at the whole farm level (Horton and Champion 2001). Generally, this study showed that farmers understand the areas on their farms where sheep are most prone to flystrike and times of year and conditions that are likely to result in increased incidence of flystrike. Anecdotally, this can be expanded to current farmer knowledge across the nation. Farmers understand their properties and sheep well and often apply preventative treatments in response to these risks. However, these treatments tend to be more based on the calendar than short-term environmental cues.

It is important to know the current level of understanding of flystrike prevention and to evaluate the impact of Flyboss™ at the same time. Focus groups are useful at determining the broad areas to target and to understand the issues faced by farmers (Wilkinson 2005; Turner et al. 2014,2017). It would be important to involve focus groups to help develop new extension materials and activities to make sure the right areas are focussed on. The focus groups could initially cover Merino producers, non-Merino producers and industry service providers as three distinct groups. The knowledge gained from the focus groups could then be used to inform the development of an extension campaign which can then be piloted with other groups of farmers and further refined.

5.4.1 Flyboss™

Flyboss (http://www.flyboss.com.au/sheep-goats/) is a web-based information portal with associated interactive decision support tools. Flyboss is assumed to be the industry supported portal for flystrike information, but state departments and other organisations also have flystrike information on their websites. There have been associated workshops in the past however the current calendar on the associated Paraboss site shows only one up and coming event for 2020 being a industry professional workshop to be held in March. The workshop seems to cover all Paraboss aspects and therefore will only provide limited information on fly control strategies. We are unable to find any consistent farmer education being rolled out across the industry that is directly relevant to flystrike.

Flyboss has functioned as very useful resource for the industry and is particularly useful for teaching an IPM approach to flystrike. It would be interesting to know the degree to which the site has resulted in practice change over time but we have been unable to find any material that has evaluated the level of use of the Flyboss site or its impact on practice change on farm. This information is perhaps known but is not in the public arena. It would be interesting to develop a monitoring and evaluation system to enable the quantification of the impacts of Flyboss on knowledge, awareness, skills and attitude of individual farmers that are using the site. It would also be of great interest to understand how they are using the site and the aspects that they believe are working and well, and those that could be improved. Such a study would be very informative for an enhancement of the Flyboss site. The Flyboss site was established 10 years ago and the presentation and information are starting to reflect this. It would be useful to update the format of the website and refresh the presentation of information on the site.

The interactive Flyboss tool provides the opportunity for a producer to optimise fly control methods in an average year which has considerable utility in strategic planning around flystrike and understanding the impacts of an IPM approach. There is scope to refresh the graphical presentation of information to a more modern design. A very useful addition to the site would be an additional tool that enables to you to test tactical management opportunities. For example, if you were able to enter actual weather data based on the farm or district data and then model the impacts of potential tactical strategies based on the actual scenario. This would encourage more regular traffic to the site and help farmers make rapid decisions about their available options.

The information on the Flyboss site requires a review and revamp to bring it up to date with the latest known information. It would be useful to also re-develop the website to provide a more user-friendly structure and material. It is very important that there is a central portal for flystrike where trust information is housed and decision support tools can be found. It is therefore imperative that the Flyboss site is maintained and regularly updated.

5.4.2 Breeding for performance not welfare

The industry is heavily focussed on breeding for performance with very little consideration given to what this means for flystrike susceptibility of the animals. This is particularly true in the Merino industry but also holds true for most of the prime lamb industry. There is only a small proportion of ram breeders (and by definition ram buyers) that are focussed on breeding sheep that are less prone to flystrike. The majority of breeders are focussed on improving productivity and assuming that chemicals, surgery and management will be able to minimise the risk of flystrike. This stance is supported by all of the industry indexes which do not penalise sheep with increased risk of flystrike. There is a general belief in the industry that breeding for the traits that reduce the susceptibility to flystrike results in lower wool cut. However, there is a lot of good evidence that this is no longer the case. The lack of uptake of breeding technologies necessary to breed for a less susceptible sheep is a serious impediment to the industry moving away from chemical and surgical interventions. The industry needs to rapidly change the way it breeds sheep. Despite parts of the industry knowing this for decades this has yet to be achieved. Perhaps the current failing of reliable chemicals will finally create the inertia of change. A serious extension effort is necessary to bring this issue to the fore. As previously stated, the ability to perform surgery or to apply chemicals has a limited lifespan and the industry is no closer than it was 10 years ago to farm without these options.

5.4.3 Heavy reliance on mulesing and tail-stripping

The entire industry is heavily reliant on mulesing and/or tail-stripping as an insurance policy against breech strike. This is to the point that non-mulesed animals sell at a discount to mulesed alternatives. As previously discussed, this option is likely to be removed through market forces in the short to medium term. A significant shift in industry perception is required but it remains unclear how this can be achieved. Research, development and adoption efforts should continue to help to understand and demonstrate farming systems that do not require surgical interventions so that when farmer attitude or legislation does change, that reliable and proven alternatives exist.

5.4.4 Sub-sections of industry leading the way

Some producers have adopted a sheep genotype that is much less susceptible to flystrike. In the case of Merinos these animals have no breech wrinkle and reduced occurrence of dags. It is hard to know exactly what proportion of the industry has moved this way. Approximately 6% of the wool sold is Merino wool that is declared as non-mulesed (www.mecardo.com.au) which is likely to be from sheep these genotypes. Anecdotally, there is a larger proportion of this that have moved to a less fly-prone genotype but they are still mulesing because of a market premium for mulesed ewes. These breeders have tended to breed for a fleece structure that is much less prone to holding moisture and therefore less likely to develop dermatitis or fleece rot. A feature of these sheep is that they are long stapled and are shorn twice annually reducing the time available for dag and urine stain build up. These producers, whilst few in number, report exceptionally low levels of flystrike on both breech and body.

In the prime lamb industry a very small number (<10) of breeders are actively selecting against dag and have made good progress. This will be made a lot easier by the availability of a dag breeding value within the Lambplan analysis. It will also be made a lot easier by the development of flystrike breeding values as suggested later in this review.

6 The role of genetics in the prevention of flystrike

6.1 Incentive for genetic improvement in susceptibility to flystrike

High labour costs, reduced reliance on insecticides, and animal welfare concerns related to current control methods in particular Mulesing, form the main incentives for breeding for lower susceptibility to flystrike as a long term and permanent control option.

It is projected that in combination with other forms of blowfly control, resistant sheep will require less frequent preventive and therapeutic treatments, reduced labour input in flock management, and will incur lower production penalties associated with flystrike in affected flocks. However, genetic change in resistance is not without cost in the sense that it will need to be combined with other breeding objectives and is likely to reduce the rate of genetic gain in these traits. It will also make breeding programmes more expensive and complicated.

Most of the research evaluating breeding for resistance has assumed that proven and highly effective management practices, such as mulesing and tail docking, will continue to be available to industry. However, animal welfare concerns are bound to limit the use of these tools in the control of fly strike and will change current thinking on the control of blowfly strike as detailed below.

6.2 Feasibility of breeding for less susceptibility to flystrike

Breeding sheep which are less susceptible to flystrike is considered a major form of control. Although this option has been considered for over 150 years, it has fallen in and out of favour as other control options were available to producers. Genetic control of the host should be considered a long-term proposition where benefits are permanent, cumulative and welfare friendly. Although we often consider the term “genetic resistance to flystrike”, the more correct term is to genetically reduce susceptibility and pre-disposition to flystrike as the main mechanisms to reduce the occurrence of flystrike. Technically we differentiate pre-disposition from resistance as a mechanism to control flystrike when maggots are actively challenging the host. Under this definition resistance implies rejection of larvae by the host after strike has been initiated. Under normal development of flystrike such rejection has not been documented, nor is it seen under repeated challenge as an acquired response, and only partial resistance has been reported following experimental vaccination.

Raadsma (1991a) detailed the feasibility of breeding for resistance to blowfly strike. Under conditions of continued mulesing and tail docking, only body strike was the main form of flystrike which warranted consideration in a genetic improvement programme at the time. The state of knowledge as it was available then showed that:

- Considerable genetic variation existed within and between flocks in resistance to body strike, and in its main predisposing factor, the bacterial dermatitis - fleece rot;
- Major genetic differences between strains and bloodlines (stud-lines) in resistance to fleece rot/body strike were a major avenue for rapid genetic change in susceptibility;
- Heritability of susceptibility to body strike was sufficiently high (>0.25) that direct selection through culling of affected sheep under high disease expression should be effective.

Additional estimates were reported for non-breech strike in Merino and Merino crossbred types by Bird-Gardiner et al. (2013) for 0.16 (0.06)-0.32(0.16) for flocks within the range of 0.0-6.9% struck;

- Indirect selection for reduced susceptibility to body strike would be more effective through reducing susceptibility to fleece rot, based on the heritability (0.3-0.4), its high genetic correlation with body strike resistance (>0.9) and the greater level of expression of this trait (Raadsma, 1991c);
- Indirect selection against susceptibility to fleece rot/body strike on the basis of fleece and skin traits was calculated to have strong potential. However, feasibility based on a limited range of known fleece traits showed indirect selection to be less effective than direct selection using fleece rot. Skin traits still required evaluation;
- The genetic basis of susceptibility to both fleece rot and body strike were not fully understood;
- The genetic relationship between susceptibility to fleece rot/body strike and other diseases of economic importance such as internal parasites and foot rot, was unknown;
- The genetic relationships between suscepitibility to fleece rot/body strike and other economically important production traits such as fleece weight, fibre diameter, body weight and reproductive performance were poorly understood; and
- Projected advantages of genetically less susceptible sheep could be demonstrated in single-trait selection flocks selected for and against resistance to fleece rot.

Raadsma and Rogan (1985) reviewed potential alternative flystrike control strategies. Breeding was considered the most promising means to control breech strike in the period preceding the development of the Mules operation (Seddon 1931; Mackerras 1936; Belschner 1937). Indeed original preliminary findings by Seddon (1931) demonstrated that Merino sheep could be classified based on a simple subjective score of breech conformation in three classes of relatively resistant, average and highly susceptible groupings and that matings according to classification score would result in progeny with expected susceptibility classes and corresponding expression of breech strike. This suggested that first indirect selection for breech strike susceptibility was feasible and that benefits were heritable.

6.3 Heritability of flystrike

Genetic variation in susceptibility to flystrike underpins the notion that selective breeding will be successful. In the case of body strike and the predisposing dermatoses of fleece rot and dermatophilosis, estimates of within Merino breed genetic variation are documented and reviewed by Raadsma (1991a, 2000) and remain relatively unchanged with no additional studies. The genetic variation described by Colditz et al. (2005) following implanting of first instar larvae was not considered relevant for industry purposes as it was largely an experimental observation to provide better understanding of the genetic basis of resistance. Under such challenge systems, natural defence barriers of the fleece are experimentally bypassed, and heritability of larval survival was 0, i.e. no genetic variation was observed (Colditz et al. 2005), whereas heritability for larval size was low (0.20), and unlikely to be of industry value as animals would still be struck. Furthermore, Colditz et al. (1996) showed no differential survival of larvae following implantation in long-term selection lines selected for differential resistance to fleece rot and body strike. These results suggest that the genetic variation expressed in resistance to body strike is largely governed through the fleece barrier and skin response to wetting and bacterial dermatitis.

The most relevant recent studies on genetic variation in susceptibility to breech strike have been summarised in Table 5 below. In Merino there have been three large studies, in Australia by Greeff et al. (2016) and Smith et al. (2016) and in South Africa by Scholtz et al. (2010, 2013). These authors report substantial genetic variation in natural susceptibility to breech strike in unmulesed but tail docked sheep. Estimates suggest a moderate to high heritability (0.20 -0.51) on the underlying scale for this trait in both ewes and wethers (Table 5). Potential discrepancies in heritability estimates reported from the same study involve sampling of industry sires, expression of breech strike (prevalence on the observed scale), management strategy, whether the animals were crutched or uncrutched and time since shearing at time of strike. This provides first-hand evidence that selective breeding for reduced susceptibility to breech strike in unmulesed Merino sheep is feasible.

In non-Merino sheep, limited reports in genetic variation to breech strike in un-mulesed sheep come from Pickering et al. (2015) (commercial Romney), Brandsma and Blair (1997) (commercial Perendale), and Bird-Gardiner et al. (2013) (commercial Merino crossbreds) where heritability of breech strike incidence was in the range of 0.18-0.32. Note that these estimates were on the observed scale of flystrike incidence, rather than the underlying scale of liability to flystrike and as such are likely to be underestimates of the true heritability of susceptibility to breech strike in sheep.

Table 5 Heritability breech strike incidence in research and commercial resource flocks.

Source	Resource flock	age	N (sires/dams)	Prevalence/cohort	h^2 observed	h^2 underlying
Greeff and Karlsson 2009	Merino selection flock	Birth-hogget	1667 (46/1061)	24%	Na	0.57 (0.28)
Greeff et al. 2013	Merino selection flock	Birth-Hogget	2776 (70/1567)	20%	0.29 (0.08)	0.37 (0.07)
Greeff et al. 2014	Merino selection flock	Birth-hogget	2833 (49/1535)	31% ewes 21%rams	na	0.51 (0.10)
Greeff et al. 2019	Merino selection flock	Birth-hogget	10,358 (227/3713)	18% uncrutched 6% crutched 12% mulesed	0.11 (0.02) 0.09 (0.02) 0.08 (0.05)	
Smith et al. 2009	Merino selection flock	weaner	1656 (34/ ?)		0.32 (0.11)	NA
Scholz et al. 2010	Merino resource flock		2918 (247/1250)	6% mulesed 10% unmulesed	0.074 0.157	0.34 (0.11) 0.51 (0.22)
Scholtz et al. 2013	Merino resource flock	hogget	2198 (247/?)	11%	Na	0.20 (0.06)
Bird-Gardiner et al. 2013	Merino and F1 Merino CRC Info. Nucleus	hogget	1352 580	8.6% all breeds 14% Merino	0.32 (0.10) 0.43(0.13)	
Pickering et al. 2015	Commercial Romney				0.32 (0.10)	
Brandsma and Blair 1997	Commercial Perendale				0.18 (0.04)	

Most of the observations have been done in young sheep since prevalence of breech strike is highest in these cohorts and, expression in older age groups may be confounded by management practices such as lambing, crutching and shearing.

Based on these findings, there is sufficient evidence to assume a moderate heritability of breech strike incidence in genetic evaluation programmes, and should observed expression of flystrike be recorded in unmulesed and uncrutched sheep, it should be feasible to generate EBV from direct observations for this trait. Genetic progress using EBV for breech strike susceptibility has been modelled in a recent study by Brien and Walkom (2019) and is discussed further below. Of interest is that a residual heritability greater than 0 (0.07-0.34) was observed in multiple studies where sheep were mulesed and subsequently struck. This suggests that there are additional genetic factors leading to breech strike that are in addition to skin folds, bare area or tail presence. Possible factors accounting for this have been detailed below.

In line with genetic investigations, Greeff and Karlsson (2009), Greeff et al. (2014, 2016, 2018), Smith et al. (2016) report enormous differences in natural expression of breech strike in progeny groups of commercial industry sires. The range of expressions of breech strike varied from 2.5% to 102.9% (animals being struck repeatedly). This opens the possibility to conduct sire reference comparisons for industry sires to fast track identification of superior germplasm for industry to move to flocks which would not require mulesing, since prevalence of 1-2% of breech strike is comparable to what is seen in mulesed flocks.

Relatively little is known about strain/bloodline/flock variation in expression of breech strike. Although the studies reported by Greeff et al. (2014), Smith et al. (2009) and Scholtz et al. (2010) were conducted on diverse genetic resource flocks representing medium and fine wool Merino's expression was confounded with challenge environment.

6.4 Recent developments in our genetic understanding of susceptibility

6.4.1 Mechanisms of susceptibility

Recent investigations on the mechanisms of resistance to fleece rot and flystrike have shifted from the factors associated with fleece characteristics as reviewed by Raadsma (1991a, 1993), to skin-based and immunological factors. Despite the strong range of immunological and inflammatory responses of the host upon larval attack, repeated infections generate no substantial acquired resistance. Multiple repeated infections by larvae showed a weak and poorly sustained protective immune response (Sandeman et al. 1986; Eisseman et al. 1990). The weak acquired resistance responses result in slightly fewer larvae surviving, and reductions in larval growth rate. During larval challenge, sheep generate strong antibody (humoral-primarily IgG1) responses to a wide range of larval products, in particular excretory enzymes, gut and salivary gland proteins (Bowles et al. 1987; Seaton et al. 1992; Tellam et al. 1994). In addition, there are major cellular responses evoked during flystrike, particularly in the skin. These are characterised by the rapid influx of neutrophils, eosinophils, macrophages, and lymphocytes (CD4-helper cells and gamma delta cells) (Bowles et al. 1992). In conjunction with the cellular responses, a wide repertoire of T-cell cytokine and inflammatory agents have been demonstrated, including IL-1a, Il-1b, IL-6, and Il-8. The inflammatory cytokine TNF alpha remained unchanged during infection. The T-cell dependent cytokines Il-2 and IFN-gamma also increase, but not Il-4. The acute inflammatory response is characteristic of strikes and does not differ markedly between repeated infestations. The capacity of *L. cuprina* larvae to degrade and digest antibody (Sandeman et al. 1995) may actually enhance larval growth by strong inflammatory and antibody responses. It is unlikely that these immune responses are natural mechanisms of resistance.

Sheep selected for increased and decreased resistance to fleece rot and body strike, as described by Raadsma (1991a, 1992), provide powerful experimental resources to understand the genetic basis of resistance. Investigations by O'Meara et al. (1992, 1995) showed that sheep from the resistant line showed substantially greater inflammatory skin responses after intradermal injection with excretory-secretory larval products compared with sheep from the susceptible line. Investigations by Colditz et al. (1992, 1994), on the other hand showed that resistant sheep exhibited lower plasma leakage and skin inflammatory responses when challenged with specific and characterised endogenous inflammatory agents. Despite these differences between the selection lines in inflammatory responses, no difference was observed in antibody titres and specificity directed against *L. cuprina* larval antigens (O'Meara et al. 1995, 1997), or larval survival and growth rate between sheep from the resistant and susceptible lines following experimental implantation (Colditz et al. 1996). Although these results appear in conflict at face value with the large and consistent difference in prevalence of body strike under natural and induced conditions between these lines (Raadsma 1992), they can be ratified when considering that the lines were primarily selected for and against fleece rot, and the latter condition provides the major opportunity for flystrike to develop. The differences in resistance are thought to be partly due to wool and skin differences in response to moisture and bacterial agents as detailed by Raadsma (1991a, b), and no specific mechanisms directly targeted against larvae operate in these flocks. This hypothesis is further supported by the higher antibody responses to bacterial antigens and compliment activation in resistant sheep, compared with responses from susceptible sheep (Chin and Watts 1991).

Norris et al. (2008) describe the skin responses during *D congolensis* infection, which is accompanied by intense neutrophil infestation following inoculation. Few differences in lymphocyte sub-types (CD4+, CD8+, gamma-delta T cells) haven been observed between chronically infected sheep and newly infected sheep, whilst elevated CD1+ cells were seen in sheep recovered post infection (Ellis et al. 1987; Sasiak et al. 1996). No clear mechanism of innate or acquired immunity has been elucidated to date in this disease.

Relatively little research has been conducted since the pioneering studies on factors predisposing sheep to breech strike. The most recent studies were conducted by Greeff et al. (2016) in an attempt to identify additional indirect selection criteria. The authors recorded and scored over 230 trait/time combinations in relation to breech strike incidence. Although many were production and breech conformation or wool related, the studies were not necessarily designed to elucidate mechanisms of strike development or resistance. The most promising traits thought to have potential utility as indirect selection criteria are detailed below.

6.4.2 Use of indicator traits for indirect selection

6.4.2.1 Body strike

For genetic reduction in the susceptibility to body strike, there is little doubt that direct selection against the main predisposing dermatitis, fleece rot, is highly effective. From known genetic parameters, we can calculate the co-heritability as described by Raadsma (1991a) from rg.h1.h2, where rg is the genetic correlation between resistance to body strike and the indicator trait, and h1 and h2 are the square root of the heritability estimates of the two traits. The use of fleece rot as an indirect selection trait has further advantages in that the prevalence is usually higher than body strike, hence more effective selection differentials can be achieved. Fleece rot is also easy and cheap to score and it does not incur the costly production penalties associated with direct selection against body strike. A detailed and effective scoring system to assess susceptibility to fleece rot and hence body strike should be used in commercial practice. A fleece rot scoring system and associated breeding value has already been developed and is routinely scored at sire evaluation studies but is rarely used outside these sites.

Under some circumstances, direct selection against fleece rot suffers from the same problems as direct selection against body strike, in that the prevalence is too low to allow effective selection in years of low rainfall. In this case considerable effort has focussed on the identification of skin and fleece traits which could be used as indirect selection traits. Raadsma (1991a, 1991b, 1993) and O'Meara and Raadsma (1995) reviewed the range of indirect selection traits that may be appropriate for selection to increase resistance to fleece rot. Recent developments have shown an on-farm skin-test based on weal development following intra-dermal injection with blowfly larval excretory enzymes to have a high genetic and practical potential to be used as an indirect selection trait. The co-heritability with resistance to fleece rot was estimated at 0.25, and the test would allow many animals to be screened at relatively low cost (Raadsma et al. 1992). The test requires further development and evaluation under field conditions, and appropriate genetic parameters with production traits need to be obtained.

6.4.2.2 Breech strike

Indirect selection traits against fleece rot and body strike as discussed here are unlikely to be effective against breech strike, although further clarification between common traits predisposing sheep to both forms of strike is warranted.

Recent activities have seen an extensive range of body conformation and wool quality traits being examined in their phenotypic and genetic relationship with breech strike. In Merino these have been primarily been conducted by three groups: Greeff et al. (2016), Smith et al. (2016) and Scholtz et al. (2010). In non-Merino breeds information from Pickering et al. (2015) is relevant since mulesing in these breeds is not warranted and other factors are key determinants of genetic susceptibility to breech strike.

In Merino the range of skin and fleece examined is extensive, in particular the studies by Greeff et al. (2014) have examined over 62 traits for their potential suitability as indirect selection traits. In order to have high potential for indirect selection it is suggested that such traits have:

- Strong genetic correlation with strike;
- High heritability;

- Early expression in life preferably on a continuous scale;
- Easy and cheap ways to be measured; and
- An ability to be measured in both sexes.

A collective summary identifies breech wrinkle, tail wrinkle (and indirectly neck and body wrinkle), breech/crutch wool coverage, anus/vulva bare area, urine stain, dag score and dag moisture content as being potential indirect selection criteria (Table 6). That is, these traits have a moderate genetic correlation with breech strike, are moderately heritable and meet the criteria set out above. Of note is that no single factor alone is likely to be sufficient to allow indirect selection for breech strike susceptibility, and development of an index of all the indirect selection traits should be a very high research priority to maximise indirect selection for breech strike. In addition, significant effects on accuracy determined by time of measurement (birth, marking, weaning, hogget) and environment under which some traits are expressed, may limit full utilisation of development of an optimal index for indirect selection suitable for all environments. Nevertheless, the information knowledge base is sufficiently strong to begin implementing a programme of indirect selection and further refinement of both phenotyping and genetic prediction is highly recommended.

Table 6 – Genetic potential of key indirect selection traits for reducing susceptibility to breech strike in Merino and non-Merino sheep.

Study	Trait	Age	heritability	rg	heritability	co-herit	efficiency	rp
Armidale NSW	**Weaner strike**							
Smith et al. (2016)	Neck wrinkle	Birth	0.42	0.42	0.18	0.12	64%	0.05
Smith et al. (2016)	Body wrinkle	Birth	0.36	0.41	0.18	0.10	58%	0.07
Smith et al. (2016)	Breech wrinkle	Birth	0.37	0.47	0.18	0.12	67%	0.08
Smith et al. (2016)	Breech cover	Birth	0.22	0.59	0.18	0.12	65%	0.03
Smith et al. (2016)	Breech wrinkle	Post-wean	0.30	0.62	0.18	0.14	80%	0.20
Smith et al. (2016)	Dag score	Post-wean	0.16	0.81	0.18	0.14	76%	0.24
Smith et al. (2016)	Neck wrinkle	Yearling	0.33	0.37	0.18	0.09	50%	0.11
	Lifetime strike							
Smith et al. (2016)	Breech wrinkle	Yearling	0.37	0.39	0.27	0.12	46%	0.23
Smith et al. (2016)	Breech cover	Yearling	0.30	0.36	0.27	0.10	38%	0.10
Smith et al. (2016)	Crutch cover	Yearling	0.45	0.08	0.27	0.03	10%	0.11
Smith et al. (2016)	Dag score	Post-wean	0.15	0.49	0.27	0.10	37%	0.05
Smith et al. (2016)	Urine stain	Post-wean	0.22	0.48	0.27	0.12	43%	0.27
	Key-production							
Smith et al. (2016)	Fibre diameter	Yearling	0.72	-0.25	0.18	0.09	50%	-0.08
Smith et al. (2016)	Fibre diam. CV	Yearling	0.58	0.31	0.18	0.10	56%	0.11
Western Australia	**Best traits**							
Greeff et al. (2016)	Dag score	Yearling	0.50	0.52	0.12	0.13	106%	
Greeff et al. (2016)	Tail wrinkle	Hogget	0.22	0.66	0.12	0.11	89%	
Greeff et al. (2016)	Dag moisture	Yearling	0.30	0.33	0.12	0.06	52%	
Greeff et al. (2016)	Urine stain moist	Post-wean	0.26	0.66	0.12	0.12	97%	
Greeff et al. (2016)	Neck wrinkle	Yearling	0.23	0.66	0.12	0.11	91%	
Greeff et al. (2016)	Body wrinkle	Birth	0.33	0.34	0.12	0.07	56%	
Greeff et al. (2016)	Face cover	Weaning	0.64	0.43	0.12	0.12	99%	
Greeff et al. (2016)	Breech wrinkle	Hogget	0.16	0.38	0.12	0.05	44%	

Greeff et al. (2016)	Breech cover	Hogget	0.15	0.28	0.12	0.04	31%	
South Africa	**Strike up to hoggets**							
Scholtz et al. (2010, 2013)	Dag score	Hogget	0.24	0.47	0.20	0.10	51%	
Scholtz et al. (2010, 2013)	Neck wrinkle	Hogget	0.31	0.78	0.20	0.19	97%	
Scholtz et al. (2010, 2013)	Body wrinkle	Hogget	0.34	0.74	0.20	0.19	96%	
Scholtz et al. (2010, 2013)	Breech wrinkle	Hogget	0.36	0.78	0.20	0.21	105%	
New Zealand	**Breech strike-Romney**							
Pickering et al. (2015)	Dag score	Lambs	0.23	0.71	0.32	0.19	60%	0.62
Pickering et al. (2015)	Breech bareness	Lambs	0.35	-0.33	0.32	0.11	35%	-0.06

These results strongly indicate that indirect selection based on a number of breech traits is potentially highly effective in selection against breech strike. Of the traits examined dag score and breech wrinkle appear most important, however trail wrinkle, tail width, breech cover and peri-anal bare area also worthy for inclusion as indirect selection traits. Of interest is that breech wrinkle is strongly genetically correlated with neck and body wrinkle, and these could potentially be used as proxy indicator traits for breech wrinkle.

Results presented in the major studies show that at face value the indicator traits appear to be less efficient than direct selection (Table 6) when expressed as a ratio of their respective genetic parameters. However, a major caveat is that under direct selection, adequate selection differentials are not realised when prevalence of strike is sub-optimal, i.e. for a 20% strike incidence, selection of the most resistant 60% of ewes and 5% of rams would be limited. Whereas, the subjective breech traits offer a scaled scoring, and indeed Greeff et al. (2016) suggest that all the top traits identified in their study allow 1x to 3.5x greater response of indirect selection over direct selection.

The indirect selection traits examined here, also show that traits can be measured very early in life, as early as birth in some cases, are cheap and easy to measure and allow for rapid genetic progress. It is hard to envisage any other strategy which would be more cost effective. There is room for improvement as suggested below and new technologies offer the potential for highly efficient cost-effective indirect selection strategies that are readily available for the Merino industry to use.

Of note is that the indicator traits apart from wrinkle scores, are not necessarily strongly correlated, thus the combination of traits in an indirect selection index may be significantly better than any trait alone. It is surprising that this has not been developed despite the information being readily available from the different resource flocks and some traits already offered as ASBV for augmented selection against breech strike. A joint meta-analysis across all available data sets with relevance to Australian Merino sources is highly recommended to obtain the highest accuracy in genetic parameters and allow development of an index to maximise accuracy for indirect selection. Smith et al. (2016) also found dag score to have a moderate heritability and a strong genetic correlation with breech strike, but did not recommend the use of this trait given that in the Tablelands environment dags occur infrequently, however on a national scale recording for dags would be highly advantageous to include this in an indirect selection index.

A major omission in the Australian context is that most information has been derived in Merino breeds and there is a substantial knowledge gap in relative importance of various indirect selection traits for Maternal and terminal sire breeds.

6.4.3 Use of gene markers and genomic selection

The search for genetic markers expressed either as gene products (cell surface or immuno-regulatory proteins) or polymorphisms at the DNA level and resistance to flystrike or its predisposing dermatoses has been limited. Raadsma et al. (1992) and Engwerda et al. (1996) examined differences in frequency of polymorphic variants of IgE, TNF alpha, IL1 beta , IL4 and IFN-gamma gene polymorphisms between flocks selected for resistance and susceptibility to fleece rot and flystrike. No obvious difference was consistent with resistance or susceptibility. It should be noted that such association studies are at best indicative and may not have sufficient power to detect linkage between candidate genes and resistance. Primarily as a function of insufficient research activity, there is no conclusive evidence either way that gene markers can have a role in selective breeding for resistance to blowfly strike. Possible research to evaluate genetic markers for resistance is discussed below.

The most significant development in genomic and gene-marker technology has been access to large scale genotyping platforms with many thousands of markers being screened across the genome in a single assay at relatively low cost. This has recently been expanded to include whole genome resequencing with most, if not all, genomic variants on an individual being captured. Matching analytical developments have seen the application of these genomic platforms in both research and commercial data sets and applications for prediction of genetic merit or genomic breeding values (GBV), molecular breeding values (MBV), or genomic assisted breeding values (gEBV). One of the major genomic strategies has been to map genes or QTL of large effect at ultra-high resolution, and in some cases to causative mutations through so called Genome Wide Association Studies (GWAS). The second major genomic strategy is to calculate realised Genomic Relationships, and mapping gene marker effects in strong linkage disequilibrium (LD) with underlying causative gene variants. These methods are not mutually exclusive, but by far the greatest impact has been to integrate genomic relationships with phenotypes in existing genetic evaluation programmes.

In the case of flystrike relatively few genomic studies have been conducted, possibly largely through lack of well characterised phenotypes (ie strike data in unprotected sheep) matched with suitable pedigreed and genotyped resource flocks. Dominik et al. (2019) reports on the first GWAS to our knowledge for breech strike in a Merino selection flock of industry sourced animals selected on the basis of likelihood to get struck, or rather not based on indicator traits (as described by Smith et al. 2016). Preliminary results showed no single gene effects or genes of very large effect. In other words, genetic predisposition is likely to be polygenic with many genes of small effect. No reports have been found which predict accuracy of genomic selection directly for genetic merit EBV of breech strike or body strike.

Pickering (2013) undertook both GWAS and genomic selection analyses on data collected from Romney-based breeds in New Zealand. Samples were collected from flystrike affected and unaffected animals in a case-control study across 9 farms in the North Island and 2 in the South. The GWAS was performed on a dataset of 8705 genotyped animals and phenotypes from around 3 million pedigree-recorded animals. They reported a number of immune, diarrhoea and wool growth genes were associated with flystrike and dag score. The genomic selection analysis was dedicated to dagginess at 3 and 8 months of age, and quantitative analysis found no genetic correlations with live weight, fleece weight, reproduction, faecal egg count, wool traits or breech bareness. Unfortunately, the range in the traits was very limited due to their restriction with the Romney.

Burrows (2018) also conducted a small case-control study of flystrike, in this example predominantly based in the South Island of New Zealand. Their candidate gene approach found that sheep with certain variants of the Fatty Acid Binding Protein 4, Fibulin and Ras guanyl releasing protein 1 gene were potential candidates for flystrike marker genes. However, the use of candidate genes should be seen as limited in indirect selection, since the gene effects are too small to make realistic differences.

Bolormaa et al. (2017) reported on the accuracy of genomic selection for indicator traits related to both breech strike (breech wool cover, crutch cover, dag score, and breech wrinkle) and body strike (fleece rot, fibre diameter variability, and wool colour) in a resource flock of 5726 Merino and Merino crossbred sheep. Although confirmation was provided that all indicator traits were heritable, no genetic correlation with breech strike or body strike susceptibility was available. Bolormaa et al. (2017) also report that accuracies of genomic prediction of these traits were relatively low for yearling (0.13-0.28) and for adult traits (0.07-0.30). It should be noted that the predictions were based on adjusted phenotypes assuming underlying true breeding values. A number of possible reasons may account for the low accuracies observed, which could include that the reference population was not substantive enough, the marker density was too low, or validation against adjusted phenotypes was not a suitable representation of underlying true breeding values. Other studies in the same resource flock using between 10,000 and 26,000 animals with full genome sequence data, show marginal improvement in accuracy of genomic prediction with a 0.07-0.09 increase above base estimates for disease and fleece traits (Al Kalaldeh, et al. 2019; Moghaddar et al. 2019). Moghaddar et al. (2015) on the other hand show that with a medium density SNP genotyping panel, genomic predictions were quite high (0.57-0.76) when the test population was closely related to the reference population and animals with highly accurate EBV were used in the test set (accuracy >0.92). Using animals with poor genetic relationship to the reference population resulted in substantively lower accuracy (0.19-0.67) for the same traits. The impact of increasing marker density from 50K to 600K had marginal impact on accuracy of genomic prediction. In the case of flystrike, a resource population would have to be highly representative of the entire Merino population and animals with highly accurate breeding values for flystrike need to be available. This would require substantial investment. Nevertheless, based on these results genomic prediction offers little benefit over directly measuring these indicator traits since they meet all the criteria for suitable indirect selection against both breech and body strike. Namely the traits are highly heritable, have a strong genetic correlation with flystrike susceptibility, can be measured early in life, are expressed in both sexes and foremost are cheap and easy to measure. Unless more robust estimates of genomic prediction direct against breech and body strike can be found which surpass the accuracy and utility of indirect selection traits, genomic prediction should not be a priority for further investments, unless this information can be obtained from opportunistic data sets collected for other purposes.

6.4.4 Resistance and other breeding objectives

As discussed in the previous text (Raadsma 1991a), resistance to blowfly strike is not likely to be the sole breeding objective, and breeders are required to combine resistance with other economically important breeding objectives. From preliminary data we have some understanding of the genetic and phenotypic relationships between important production traits and resistance (Raadsma 1991a). For wool sheep it is likely that selection for increased resistance will lead to a slight reduction in fleece weight (unfavourable), decrease in fibre diameter (favourable) and no effect on body weight. Preliminary correlated responses in selection flocks for resistance and susceptibility to fleece rot and blowfly strike as presented by Mortimer et al. (1998) and confirm these initial observations. However, more robust and reliable information on appropriate genetic parameters and relative economic weightings are warranted to develop comprehensive breeding programmes that incorporate resistance to blowfly strike.

A recent study by Brien and Walkom (2019) examined the scope to include breech strike resistance in a multi-trait selection strategy for Merino sheep. These results were modelled in MERINOSELECT based on available knowledge and a range of input assumptions. Predicted responses to selection were strongly dependant on assumed heritability of breech strike and the economic benefits of selection for reduced susceptibility. Gains were within the range of 2% to 21% reduction in strikes/ewe/year following a 10-year selection strategy. When assuming average prevalence of breech strike in winter and summer rainfall flocks of 10% and 18% respectively, breech strike was predicted to approach <2% in unmulesed sheep, which is similar to efficacy of mulesing. Brien and Walkom (2019) suggested that driving the prevalence of breech strike to 0% under all years was thought to be impossible given the residual environmental factors remaining in high risk environments. The study is useful in setting a foundation for expected responses in breech strike and production traits in multi-trait selection strategy. However, the scope of these studies could be expanded by judicious use of sires with extreme EBV of breech strike susceptibility, cost and accuracy of indirect selection, including genomic selection and potential to improve resistance to both body strike and breech strike and strike combined with other health traits.

6.4.5 Resistance to other diseases

There is now a considerable body of evidence on genetic aspects of disease resistance in Merino sheep as reviewed by Gray et al. (1995) and Raadsma et al. (1997a, 1997b, 1998). The primary focus of such studies has been on resistance to internal parasites, footrot, blowfly strike (and its major predisposing dermatoses - fleece rot and dermatophilosis), showing that it is feasible to change resistance to each disease through selective breeding. However, there is a paucity of information on predicting the likely consequences of selecting for resistance to one disease on correlated responses in resistance to other diseases. This is significant, given that the important diseases identified above, have common environmental (climatic) risk factors and are likely to occur in the same flock. Furthermore, strong favourable or unfavourable genetic correlations between resistance to multiple diseases may provide insight into the nature of disease resistance genes. Raadsma et al. (1997b) report on an investigation in which resistance to all major diseases was investigated in a single experiment, and predictions could be made on likely changes in disease resistance following selection for any of the major diseases. In the case of predisposition to flystrike, resistance to fleece rot had no genetic relationship with resistance to dermatophilosis, showing that genes controlling these two important risk factors act independently. Predisposition to blowfly strike, was also unlikely to lead to favourable or unfavourable changes in resistance to internal parasites or footrot. Selection for resistance to multiple diseases simultaneously will thus be considerably slower than selection for resistance to any one disease alone, since there seem to be no genetic synergies between resistance to the most important diseases in sheep (Raadsma et al. 1997a, b).

7 Novel control opportunities and technologies

Significant research effort has been devoted to developing alternative and/or complementary forms of blowfly strike control. Those which have received the most attention and those that should be focussed on are described below.

7.1 Breeding novel sheep genotypes

7.1.1 Short tail breeding

Breeding sheep with short tails has a range of benefits including reduced flystrike risk. This approach has had a considerable amount of interest in recent years. Breeders should avoid genes that affect skeletal development and are homozygous lethal (James 2006), which would be self-limiting. James (2006) reviewed heritability estimates for tail length from all over the world, excluding Australia (Table 7). For non-Merino sheep heritability was high, ranging from 0.5 to 0.84, while for Merinos in America (Shelton 1977) the estimate was 0.39. One recent report from Australia found tail length was highly heritable (0.80 ± 0.13), and it was correlated with breech strike (-0.15 ± 0.11) despite tail docking (Greeff et al. 2016). There is therefore potential to select for short tails even in Merino sheep, but the use of very short tailed breeds such as the Finnish Landrace would hasten progress for the likes of the Border Leicester for example which is a core component of first and second cross meat sheep in Australia. Indeed, some Border Leicester breeders in Australia have used Finnish Landrace given the similar breeding goals such as lustrous wool and high fecundity. Additionally, the Texel and Dorper breeds both have genes for short tails and given work in New Zealand (Scobie et al. 2007), it would be equally easy to incorporate these into terminal sire lines. This would put genes for short tails in the maternal and terminal sire lines from separate gene pools to maximise heterosis in the second cross lamb.

Table 7. Estimates for the heritability of tail length in sheep

Breed	Estimate	Reference
Finn	0.77 (0.42) (sires) -0.12 (0.45) (dams)	Branford Oltenacu & Boylan (1974)
Combined standard breeds	0.50 (0.24) (sires) 0.84 (0.41) (dams)	Branford Oltenacu & Boylan (1974)
Rambouillet	0.39	Shelton (1977)
Part Mouflon	0.71	Shelton (1977)
Finn x Cheviot	0.82 (0.10)	Scobie and O’Connell (2002)
Fat tail (Menz & Horro breeds)	0.37 (0.15)	Ermias and Rege (2003)

7.1.2 Shedding Tails

Whatever the length of the tail, and whether physically docked or genetically docked, wool on the tail can become soiled and flystruck. Scobie et al. (2016) reported what is most likely a few genes that cause moulting of the wool from the tail of the sheep. This was recorded during the spring in hoggets, but the very best lambs exhibited it at weaning (Scobie, D.R., unpublished). The major results are repeated here (Table 8). Sheep that moulted the wool from the tail exhibited less dags at weaning and again at hogget shearing and greater breech bareness. Although a small number of weaned lambs (n = 50) were flystruck during the trial (n = 1263), most occurred on one occasion reported elsewhere

(Scobie and O'Connell 2010). There were insufficient results to conclude whether flystrike was influenced by moulting but given the consequential absence of wool and dags we assume that it would. We know these genes are found in East Friesian, Finnish Landrace and Texel breeds (Scobie, D.R., unpublished) and have successfully been introduced into fine-wool composite sheep (Ferguson, M.B., unpublished)

Table 8. Number of animals (n) and least squares means for tail length at 5 weeks of age, breech bareness score, and dag score at 4 months of age (Dag wean), live weight at 12 months (Live wt), and dag score (Dag shear), clean fleece weight (CFW) and fibre diameter (FD) at 14 months of age, for animals that had; not moulted (Not), partially moulted (Partial) or completely moulted their tail wool (Complete) by shearing at 14 months of age. Mean standard error of difference (SED) and significance (Sig; * <0.001, ** <0.01 and ns = not significant) are shown. (From** Scobie et al. (2016))

	Tail Moulting				
Trait	**Not**	**Partial**	**Complete**	**SED**	**Sig**
n	401	278	584		
Tail (mm)	221	213	210	2	***
Breech Score	2.70	2.97	3.36	0.06	***
Dag wean	0.65	0.63	0.50	0.06	**
Live wt (kg)	43.8	43.4	43.3	0.4	ns
Dag shear	2.11	1.91	1.22	0.10	***
CFW (kg)	1.65	1.56	1.47	0.03	***
FD (μm)	30.2	30.0	29.7	0.2	**

7.1.3 Shedding sheep

Sheep that shed their wool or do not grow wool at all have become an increasing portion of the Australian lamb industry. Wiltshire sheep have been in Australia for a very long time (Thatcher and Pascoe 1973), however they almost disappeared and had little impact when wool prices were high. In New Zealand, O'Connell et al. (2012) conducted an experimental breeding program selecting Wiltshires for increased or decreased hogget fleece weight. After a short period, the line selected for low fleece weight produced negligible quantities of wool, although they did have woolly birth coats which are a potential benefit in a cold wet New Zealand spring. However, O'Connell et al. (2012) warned that selecting lambs which shed very well could lead to selecting singletons and a reduction in fertility, because better fed lambs shed earlier and more extensively. The work of Litherland et al. (1992) is widely cited with respect to flystrike, though it is important to note only 30 ewe lambs of each breed were used. Scobie et al. (2002) used both sexes of lambs of three non-Merino breeds along with Wiltshire and not one of the 51 Wiltshire lambs was struck, compared with 12 of 205 Finnish Landrace X Dorset Down, 61 of 289 Finnish Landrace X Romney and 6 of 48 Feral sheep X Merino. It was speculated that lustrous wool drapes over the anus in docked lambs which led to the high proportion of Finnish Landrace X Romney becoming struck (21%) compared with the other two crosses. In unpublished data, only one lamb of either selection line of Wiltshires exhibited flystrike, of all the lambs, hoggets (n = 1049) and adults of the self-replacing flocks reported by O'Connell et al. (2012). These were run on Winchmore station between 2000 and 2010, when other flocks on the same farm (Scobie et al. 2002; Scobie and O'Connell 2010) were devastated by fly waves. Clearly the

Wiltshire is worthy of greater consideration in the lamb production industry in Australia. It does have a very long tail, but the wool moults from this area as well, resulting in some Wiltshire breeders leaving the tails intact. A caveat is that in Wiltshire crossbreds that partially shed their fleece, body strike can occur and can become serious (S. Jolly, personal communication, 2018), but this is possibly because farmers take their eyes off the sheep because they are so resistant to breech strike, and when a body strike challenge occurred they were not prepared.

7.1.4 Woolless sheep

Without doubt woolless sheep are a solution to flystrike, perhaps more so than those which shed their fleece. Of course they are bred solely for meat production (of interest to Meat and Livestock Australia), and given the coloured and or medullated fibres and very poor fleece, these breeds were of great concern and considered somewhat of a scourge to wool production (Fleet et al. 2001; Fleet and Bennie 2002). Fleet et al. (2002) compared the production, reproduction and carcass characteristics of Damara X Merino lambs with Merino lambs. However, there were no data for flystrike; these sheep were run at Minnipa Research Station in South Australia therefore it is possible the Merino control flock did not experience a flystrike challenge. Further, there was no mention of farming such sheep.

Numerous woolless breeds are now found throughout Australia. Breeders continue to tail dock some of these breeds, for no good reason, but could easily abandon the practice when tail docking is brought into question. The Cleanskin Sheep Association form an umbrella organisation that covers Dorpers, Damaras, Wiltshires, Van Rooys, Wiltidams, Australian Meat Masters, Dampers, Australian White, Coolalee, and BreedersBest. The Cleanskin sheep website simply states "… few problems with flystrike and lice".

7.2 Advanced use of quantitative and molecular genetics

There are a few areas that warrant further consideration in breeding for resistance to flystrike. These are briefly outlined below.

7.2.1 Across flock predictions

Although the Merino is relatively susceptible to flystrike, extensive variation has been observed between stud lines in their relative susceptibility. Sheep from some stud-lines require minimal intervention for flystrike control and would provide a rapid means for sheep breeders to access superior genetic seedstock. The difficulty lies in reliable and convenient means to predict the relative susceptibility of the many stud lines available to breeders. Comparative benchmarking with appropriate reference links across environments is one avenue to overcome this difficulty. Identification of resistant studs based on indicator traits or genetic markers for resistance genes may provide additional avenues (Raadsma 1991b). The use of genomic flock profiles could aid in the use of across flock predictions for suitable bloodlines to source breeding replacements in augmentation with EBVs. At present, relatively little data is available for Merino and non-Merino breeds in their susceptibility breech strike. This could be overcome with increased recording and comparative bench marking under common management and environments but would require substantive industry participation.

7.2.2 Molecular characterisation of resistance

With the development of a high-resolution genetic linkage map of highly polymorphic micro-satellite DNA markers (Montgomery and Crawford 1997) it is now feasible to identify chromosomal locations for genes contributing to resistance of sheep to disease. Should genes with sufficiently large effect be identified, indirect selection for resistance with the aid of markers (marker assisted selection-MAS) can provide a means for increasing resistance without the need for direct challenge. Although many experiments are currently in progress to identify such markers for production traits and disease resistance, relatively few experiments have been designed for resistance to blowfly strike. Dominik (2019) reports on a preliminary GWAS analysis in relation to breech strike selection lines and could not detect any chromosomal locations harbouring genes of large effect. Norris et al. (2005) conducted gene expression analyses following skin challenge in genetic selection lines selected for and against fleece rot susceptibility and report no obvious differential pathways that accounted for the substantial differences in susceptibility between lines. Although resistance to both breech and body strike is believed to be multi-factorial and polygenic, more integrated comprehensive studies during the development of flystrike may be warranted.

7.3 Control of blowfly populations

The manipulation of pest populations through biological or genetic means has worked remarkably well for some arthropod pests (i.e. screw worm control).

7.3.1 Genetic control

In the case of blowfly populations, genetic control through irradiated or genetically modified release stocks has been shown to be technically possible, but economically unattractive. For a full review of this topic, the reader is referred to reviews by Foster (1998) and Foster et al. (1992).

Genomes of eukaryotic organisms are composed of billions of DNA bases. The ability to change these DNA bases at precisely predetermined locations holds tremendous value not only for molecular biology, but also for medicine and biotechnology. Therefore, introducing desired changes into genomes, i.e., “genome editing”, has been a long sought-after goal in molecular biology. To this end, the discovery of restriction enzymes that normally protect bacteria against phages in the late 1970s, was a turning point that fuelled the era of recombinant DNA technology. Early studies demonstrated that mammalian cells can incorporate an exogenous copy of DNA into their own genome through a process called homologous recombination and allows targeted gene integration into the genome. This provided unprecedented power to characterize the functional roles of various genes in model organisms by targeted gene editing as powerful reprogrammable gene-targeting tools. CRISPR-Cas9 is becoming an indispensable tool in gene editing platforms. CRISPR stands for clustered regularly interspaced short palindromic repeat DNA sequences. Once known as the bacterial immune system against invading viruses, in combination with the programmable capacity of the Cas9 enzyme, this tool is now revolutionizing diverse fields of medical research, biotechnology and agriculture. The exponential growth in scientific reports using CRISPR-Cas9 technologies in biological applications is evident over the last 5 years with more than 40,000 references to CRISPR and Cas9 in the public domain. There are numerous reviews of applications, see for instance Aldi (2018) for a historical review and potential applications of this technology.

Of particular interest is the application of gene editing technologies in combination with biased or preferential inheritance. The mechanism known as 'gene drives' where edited allelic variants are preferentially inherited in future generations, thus super-charging the distribution of allele frequencies throughout populations. The potential application of gene drives to preferentially increase the frequency of desired alleles is not so much of interest in sheep to increase resistance alleles (since this requires genetic modification and no single alleles are known to convey a high degree of resistance), but rather in modification of pest species and in particular blowfly populations. The gene drive technology fits with a logical extension of genetic control of blowfly populations and the large amount of research conducted by CSIRO in the late 1970-1980s. In conjunction with blowfly genome data, new potential targets for both sterile male/female or non-viable progeny become amenable for targeted gene drives. The logistical, regulatory and safety mechanisms and the potential evolutionary resistance mechanisms to gene drives, are hurdles which should be carefully considered as part of future pest eradication programmes.

The elucidation of the nuclear DNA of *L. cuprina* (i5k Consortium 2013) provided many interesting insights into *L. cuprina* but none that are sufficiently well developed to utilise for any control options at this stage. Dearden et al. (2017) addresses potential applications of gene drives in pest control including blowfly control. With the advent of CRISPR techniques there is potential that genetically modified flies with a deleterious gene associated with a gene drive could markedly reduce blowfly populations. For the future this scientific technology will continue to develop and although no easy solutions are yet apparent, this type of research should continue. Indeed, rather than being a follower species, *L. cuprina* is sufficiently important to be a pioneer species showing the way for others.

7.3.2 Potential biological control agents

Biological control of *L. cuprina* populations through predation by microsporidium *Octosporea muscaedomesticae* (Smallridge et al. 1995), or entomopathic agents delivered through engineered fleece microflora (*Bacillus thuringiensis* toxins, Pinnock 1994; Lyness et al. 1994) have been demonstrated to be efficacious on a limited scale. However, these control strategies have to overcome significant practical limitations before use on a large scale.

Potential biological control agents were recently reviewed by Leathwick et al. (2019). This review covered fungal and bacterial agents. The list of potential bacterial controls was short, including *Bacillus thuringiensis*, *Brevibacillus laterosporus*, *Serratia marcescens* and *Serratia liquefaciens*. Fungal pathogens on the other hand were diverse including *Metarhizium anisopliae*, *Tolypocladium cylindrosporum*, *Octosporea muscaedomesticae*, *Entomophthora muscae*, *Entomophthora schizophorae*, *Conidiobolus coronatus* and *Beauveria bassiana*.

The *Serratia* bacterium were dismissed by Leathwick et al. (2019) because they do not form spores and are therefore unlikely to survive in harsh environments. The toxin from *Bacillus thuringiensis* was found to control flystrike in Australia (Lyness et al. 1994) and New Zealand (Heath et al. 2004). Research into this promising control method has ceased. Again Leathwick et al. (2019) dismissed *B. thuringiensis* because the fly larvae need to ingest the toxic protein produced by the bacteria, and larvae could survive in parts of the fleece, or at levels within the fleece, for example close to the skin that are not protected by the toxin. The final species in the list of bacteria, *B. laterosporus*, was lethal to *L. cuprina* and other fly species including *Chrysomya putoria* and *Musca domestica*. The research was conducted in Brazil (Pessanha et al. 2015,) with some gaps in knowledge of how this would act if it could be introduced to Australia.

Leathwick et al. (2019) were much more supportive of fungal pathogens to control flystrike flies. A principle reason for this is that the fungi simply need to come into contact with the fly rather than be ingested by the larvae or adults. Leathwick et al. (2019) also concluded that products to be sprayed on the sheep to control flystrike are likely to be more expensive than chemical agents and while the efficacy of many chemical products is reducing due to resistance, good control is still possible. They lent support to biological agents that could be used in baits or lures for adults or perhaps in soil where the pupae may reside. *M. anisopliae* is effective against *L. cuprina* and *L. sericata* by contact with the tarsae of the fly and caused mortality of 30 to 70% of flies. *T. cylindrosporum* was effective against *L. cuprina*, *L. sericata*, *C. rufifacies*, *C. stygia* and *M. domestica* in laboratory assays which makes this fungus particularly attractive for controlling a broad spectrum of flies that have been involved in myasis of sheep (Heath and Bishop 2006). Investigation of *O. muscaedomesticae* was undertaken some time ago (Cooper and Pinnock 1984) and is perhaps worth revisiting. The *Entomophthora* are common in Australia and could be transmitted from lab-reared adults, but the *Conidia* might struggle to survive in extreme conditions. One fungus (*Conidiobolus*) was wisely ruled out because it causes disease in humans and other animals. *Beauveria bassiana* shows some promise to control both *L. cuprina* and *L. sericata* and is available in a commercial product (Mycotrol®) for use in horticultural settings. *M. anisopliae* is also available in a commercial product (Nutri-Life Myco-Force ™).

Australian Wool Innovation (AWI) has invested in a research project on *Wolbachia* which is a symbiotic bacterium in the gut of blowflies. It affects reproduction in the flies and there is hope that it will supress fly populations.

7.3.3 Immunological control of blowflies

Vaccination against the larval stages of blowflies, or the main pre-disposing dermatoses of blowfly strike (namely fleece rot and dermatophilosis) are potentially highly attractive control strategies. Where vaccination has been shown to be an effective means of disease control in livestock (primarily microbial infectious agents), there is little doubt that such means are cost effective and amenable to widespread and sustained use as a single control option. In the case of parasitic diseases, vaccination is less effective and often requires additional methods of disease control. The development of immunological means of blowfly strike control has been a long and arduous route (Sandeman 1990). Initial stimulation for the work was derived from the observation that sheep with repeated infection developed a weak and non-sustained immunological response to blowfly strike. In addition, the control of the cattle tick *Boophilus microplus* though vaccination against antigens not normally seen by the host (concealed antigens) has been shown to be effective. Despite 15 years of intensive research, there is currently no vaccine against blowfly products which offers sufficient protection. At best, blowfly vaccines show a marginal reduction in larval growth rates under highly artificial conditions of flystrike. The key to this may be that repeated strikes develop a weak and unsustained immunity, at least in Merino sheep which remain the host of fascination for investigators. For a comprehensive review of the development and current status of such vaccines, the reader is referred to Tellam and Bowles (1997). Similarly, vaccines with partial efficacy against the microbial agents which cause fleece rot and dermatophilosis, have been developed (Burrell and MacDiarmid 1983; Burrell 1985; Sutherland et al. 1991), but provide insufficient protection against blowfly strike. It is not until we have a clear and comprehensive understanding of the aetiology of blowfly strike, associated immune responses, and identity of the key immunogens, that we can develop effective vaccines, although the likelihood of such vaccines is extremely low (Sandeman et al. 2014b). There may be slightly better prospects for vaccines against the predisposing dermatoses on the basis of preliminary evidence presented by Burrell and co-workers in the late 1980s and reviewed by Norris et al. (2008), however the multitude of bacterial species and sero-vars with unlikely cross protection, brings out all the problems associated with multi-valent commercial vaccines.

7.3.4 Other forms of blowfly control

Other forms of blowfly control have focussed on physical trapping of blowflies to reduce fly density (Anderson et al. 1990; Morris et al. 1998; Wall and Smith 1997; Smith and Wall 1998). In a similar vein to large scale biological control programmes, this form of control has not been shown to be feasible or effective on a large scale. The development of transgenesis in sheep has presented researchers with the theoretical option to develop production in host sweat or wax glands of novel parasite control genes such as chitinase or Bt toxin (Ward et al. 1993). At present such research is largely conceptual, is not likely to be ever legally possible and is far removed from practical application.

7.4 Integrated Pest Management Strategies

It is clear from our understanding of flystrike in sheep that most forms of control when used in isolation offer partial protection at best. It is also clear that sheep producers are able to integrate, often on an ad hoc basis, the various forms of flystrike control that may give the best form of protection. Based on our current knowledge of blowfly strike control, we could enhance the efficacy of individual control strategies, by combining them in an integrated form of blowfly pest management control (IPM). This section will deal briefly with IPM to describe its advantages and prerequisite characteristics for success. Most of the material comes from Bram (1994) who describes integrated control of ectoparasites.

7.4.1 Definition and general components of Integrated Pest Management

In the livestock context, integrated pest management consists of the systematic application of two or more technologies in an environmentally compatible and cost-effective manner, to control arthropod pest populations that adversely affect livestock production. In addition, it is now recognised that such integrated control programmes need to be sustainable in their efficacy. In designed IPM programmes, technologies are applied deliberately and systematically (rather than at random) to optimise efficacy of the combined control strategy.

Chemo-prophylactic control is likely to remain the backbone of any pest management system. Not only should novel compounds be considered but also novel modes of delivery to allow judicious use of insecticides at any stage of production. For some forms of pests, biological and mechanical control can provide strong complimentary components of an IPM programme. In addition, genetic manipulation of the pest and the host through conventional selection may provide useful tools. With the addition of immunological control, a combined arsenal of technologies can be applied to pest control. The key features of IPM programmes is the strategic use of such combinations.

7.4.2 Feasibility of control of blowfly strike through IPM

From population studies involving field data and modelling on both *L .cuprina* and *L .sericata*, it is evident that the two critical determinants affecting prevalence of blowfly strike are population density of blowflies at low densities, and sheep susceptibility once a threshold of blowfly population density has been exceeded (Wardhaugh et al. 1989; Wardhaugh and Morton 1990; Wall et al. 1993b, 1995; Vogt and Woodburn 1994; French and Morgan 1996; Gleeson and Heath 1997; Fenton et al. 1998, 1999). The climatic variables of temperature and rainfall are of overriding importance in the determination of blowfly population and sheep susceptibility. Integrated control strategies which can manipulate blowfly populations, sheep susceptibility, and predict optimum interactive use of the various control strategies should lead to effective IPM for blowfly control for a wide range of environments under which sheep are farmed.

From details presented above, it is obvious that many of our current control strategies for blowfly strike can be readily applied to an IPM programme. It is unlikely that the core components in blowfly strike control will change from those currently employed by industry, rather the manner in which they should be used in combination may change (Karlsson et al. 2001). There is a paucity of information on the critical interaction of the variables, which control blowfly populations. IPM requires a clear understanding of the degree of control which is possible through chemo-prophylaxis, the rate of development of resistance, the extent of protection offered by resistant hosts (through management or genetic), and environmental factors which influence blowfly populations. We have knowledge of the individual components but no formal evaluation or prediction of an integrated approach. From an on-farm perspective, Flyboss does allow producers to combine management and chemical options in an integrated way to minimise the exposure of sheep to flystrike.

7.4.3 Modelling benefits of inclusion of breeding in IPM programmes

There are now a number of models which can simulate or predict blowfly abundance and activity. Predictions of flystrike prevalence can be made through incorporation of environmental, seasonal, and known risk factors leading to flystrike (Wardhaugh et al. 1989; Wall et al. 1993a; Fenton and Wall 1997; Fenton et al. 1999). Although such models are extremely useful in predicting blowfly activity and potential impact, they do not extend far enough to model the optimum use of IPM. Incorporation of pesticide management strategies, and inclusion of genetic selection for increased host resistance are two additional components which warrant serious consideration. The modelling should include the likely impacts of climate change (Wall et al. 2011). There is now reliable and consistent evidence that selective breeding of sheep for resistance to body strike, poll strike in rams and possibly breech strike (Raadsma 1987, 1991a, 1991b; Raadsma and Rogan 1985, 1987; Raadsma et al. 1998; Smith 2016; Greeff et al. 2016), can become a major tool in IPM (Karlsson et al. 2001). In addition, selection decisions for increased resistance need to be compatible with the overall breeding objective for sheep production under high risk of flystrike.

7.5 Improving the prediction of fly waves

7.5.1 Models to Predict Occurrence

These rely on a detailed understanding of the life cycle of the fly. Development of the fly when the weather is relatively warm is generally well understood. However, key parameters for a model are triggers that signify the start and end of the fly season. There appear to be differences between *L. cuprina* and *L. sericata*. Typically for each species there is a range of temperatures in which development occurs readily that has been well described – certainly sufficient for use in computer models. However, determining if there is variation from provenance to provenance has not been established to any large extent.

There is a growing history of attempts to model *L. cuprina*. McLeod (1997) compared several proposed models and Wardaugh (2001) produced a model that would seem to be basis for existing *L. cuprina* life cycle models. In the model described by Wardaugh (2001) the requirement for growing-degree-days is defined for each stage. The accuracy/precision of this model appears to have been fully tested.

Wardhaugh et al. (2007) produced a model to estimate the incidence of flystrike and found that pasture growth index was the most important explanatory variable. They utilised questionnaires to farmers in three distinct regions and their model developed different constants for each of these regions. Hence broadening the model to other regions is not straight forward. Fly density had a lag of several weeks behind the curve for Pasture Growth Index and these relationships were not that close but the predicted curves (separately) for body and breech strike were remarkably close. Thus, adjusting this type of model for each region would be a challenge. Having a model when the proxy for flystrike is an indirect measurement of pasture growth illustrates the deficiencies in our understanding of the biology of the flies and earlier models.

7.5.2 Use of new technologies to assess the occurrence of flystrike on a sheep

In recent years there has been an explosion in the use of various monitoring devices for a range of purposes. For humans, they are commonly used for monitoring common variables of interest to sports people. For animals, pedometers and triaxial accelerometer studies have been used on dairy cattle to assist oestrus detection, lameness, ill health etc. The uptake has been slow but has recently been increasing. Accelerometers are now available commercially in eartags and the supporting algorithms can assess grazing, idling etc.

For sheep, studies are less advanced, although eartag devices have been shown to be successful in recent trials where they have been used to detect lameness (Barwick et al. 2018). More recent studies have been published using GPS to measure movement as an indicator of gastrointestinal parasitism (Falzon et al. 2013). Other current studies are investigating algorithms for triaxial accelerometers +/- GPS to compare activity with the level of internal parasitism. Algorithms have been developed for accelerometers worn on neck collars (S Ikurior, personal communication, 2019) to assess grazing, walking and resting for this purpose. Flystruck sheep tend to have typical behaviours associated with the pruritis of new strikes and then become lethargic. The advent of 5G communications will facilitate the transfer of such data to a central processing facility and flag sheep that have just become flystruck. Individual sheep can then be compared to others in the same mob and back to their own data prior to the strike.

It will take something like the uptake of this technology to seize on the early stages of flystrike and the answers it can give. It will require better batteries, a reduction in the cost of devices, and their size to become compatible with sheep.

7.6 The skin microbiome and the role of moisture

The most workable definition of a micro-biome is the collective association of all microbial lifeforms with an organism and includes bacteria, fungi, protozoa, and viruses. Global research efforts have recently recognised the importance of such micro-biomes in both maintaining homeostasis of host systems but also potential for major causative disruption when unbalanced through external forces- such as antibiotic use, or immune disruption. The increased interest has also been driven by the development of tools –particularly in genomic and bio-informatic platforms which allows for broad scale screening of micro-biomes at relatively little cost.

From earlier studies in pathogenesis on breech and body strike, investigations in sheep micro-biomes have largely been through targeted investigations of specific mostly bacterial populations as described above. Although key bacterial species have been identified, there remains a significant knowledge gap in the role of undefined microbial species in the development of myasis. For example, Kingsford and Raadsma (1997) only detected *P aeruginosa* in 14% of clinical cases of fleece rot based on 16S rRNA typing, leaving room for other causative microbial factors to be important as observed by Dixon et al. (2007). A good deal of prior research has showed that both *Dermatophilus congolensis* (Gherardi et al. 1981), and *Pseudomonas aeruginosa* (Kingsford and Raadsma 1997) have been associated with flystrike. These cause dermatitis and fleece rot respectively, which both devalue the fleece and are therefore worthy of investigation. The presence of *Proteus mirabilis* was also an attractant to flies (Emmens and Murray 1982; Burrell et al. 1982, 1984; Burrell and MacDiarmid 1984; MacDiarmid and Burrell 1992). However, modern techniques enable us to understand the microbiome of various ecosystems like the soil, the gut and most importantly the skin. Indeed, there is evidence of relationships between skin and gut microbiomes Gilbert et al. (2018) and evidence that show differences in the skin microbiome affect human attractiveness to mosquitoes (Verhulst et al. 2010). In a similar vein, the rapidly changing micro-biomes during wetting of skin and fleece of sheep and its specific role in development of dermatitis, fly attraction, oviposition, egg hatching, larval growth, larval survival, and indeed pathogenesis and morbidity of sheep following flystrike have not been examined at the scale now possible through meta-genomics. There is a role for such studies provided they are carefully designed to examine all relevant stages during flystrike development.

The fleece/skin microbiome in relation to breech strike development has received relatively little attention. The most recent and comprehensive survey was conducted by Greeff et al. (2016) who examined bacterial profiles in animals from the resistant and susceptible end of the spectrum using 16S RNA profiling from dry fleeces without the presence of flystrike. Although an extensive range of bacterial species were recovered from the skin samples, no clear relationships were found between any bacterial species and breech strike susceptibility. A number of factors related to divergence in resistant and susceptible genotypes, animal sampling and timing of sampling may be possible contributing factors, however no single outstanding discriminatory factor in the micro-biome and breech strike under non-wetted skins could be implicated at this stage. Extended studies are potentially of interest during the development of breech strike as such micro-flora profiles could change rapidly under such conditions.

Changes in the moisture of the fleece have been associated with flystrike (Lipson et al. 1982; Hall et al. 1980) which will be no surprise to anyone involved with sheep farming. Young et al. (2004) and Sewell et al. (2009) suggested that a change in skin temperature may be associated with flystrike in sheep affected by endophyte toxins. Particularly of note in these examples was the potential for body strike to be affected. Differences between breeds in the incidence and severity of *D. congolensis* was reported between Clun and Kerry lambs in the United Kingdom (Hart 1967). How meat breeds are affected in Australia should be investigated.

Perhaps the most dramatic of all changes which is not researched, but commonly practiced, is the dramatic change in flystrike susceptibility when sheep are shorn. Shearing is a good therapy for fly struck sheep. A simple wash with clean water or drying with sand has been observed to quickly reduce attractiveness of the struck sheep to flies when chemical treatments were unavailable following removal of the affected fleece (Scobie, D.R., unpublished). As always, exceptions do occur and New Zealand farmers will tell of sheep that get flystruck within weeks of shearing or “straight off shears”. Some claim that the flies are attracted to faeces that are rubbed on the sheep while yarded after shearing. Scobie (unpublished) has witnessed a large number of Merino weaners in South Australia with less than 15 mm of wool affected by body strike on considerable areas. This was possibly associated with dermatophilosis which was present but not rampant at shearing. However, the strikes (or re-infection) were not sustained during hot dry weather. Universally, observations of strike on short wools are under temperature and humidity conditions that are ideal for flystrike. However sheep with 4-10 months wool growth are by far the most susceptible stages for development of flystrike and the predisposing dermatoses of fleece rot and dermatophilosis (Raadsma 1991a), fleeces from such sheep are easily wetted and dry out slowly, compared to either sheep with shorter wools (which dry out easily), or full fleeces (which are relatively more difficult to wet to skin level).

The importance of moisture in the development of breech strike is well understood. However, the use of inherent fleece factors related to skin/fleece humidity have received less attention. Greeff et al. (2016) also examined the role of fleece moisture, wax, suint, and dust derived from mid-side samples as a predictor of susceptibility, but could find no significant differences between the breech strike resistant selection line vs the susceptible line. The limited separation of the resistant and susceptible line in breech strike incidence and the site of sampling (mid-side) may be possible contributing factors.

Of more interest was the study by Greeff et al. (2016) in the study of micro-climate in the breech area through use of *in situ* data loggers. This was a novel and potentially interesting approach, not only for mechanistic determination, but potentially as longer-term monitors of conditions leading to the development of breech strike. Although preliminary results on humidity and temperature and the relationship to genetic rank of breech strike susceptibility was inconclusive, further observations are warranted, potentially in more extreme sire progeny groups during prolonged observations. Moisture status at skin level in relation to micro-anatomical structures around tail and breech folds also warrants further examination in the role of skin fleece microbiome and initiation and development of flystrike.

7.7 The use of Artificial Intelligence and data analytics

Extraction of information from large scale digitized data sets through artificial intelligence (AI) is unprecedented both in scale and the rate of change. Novel sources of data capture include digital imaging, GPS location and movement, high resolution bio-markers and bio-sensors, and complex systems. In parallel, developments in AI has given rise to ultra-sophisticated platforms to analyse such data sets and make predictive outcomes. In particular, Deep Learning, a new Machine Learning technique with state-of-the-art Neural Network architecture, give rise to efficient exploration of ultra large data sets and predict outcomes not readily seen by conventional human-driven analyses. In combination, this technology is projected to be the most disruptive technological advancement of the current century. This opens up many untapped possibilities to be exploited for novel applications and industries.

The Australian sheep industry is ideally placed to evaluate the impact of such technologies on profitability and advanced farming systems. In particular the prediction of flystrike susceptibility and occurrence stand to benefit from a significant investment in AI technologies. Specifically AI could be applied to:

a. Advanced prediction of current phenotypes for breech strike susceptibility using digital information capture. Information on tail wrinkle, breech wrinkle, breech crutch cover, urine stain and dag score are all amenable as inputs for AI based prediction. The advantage is that it allows for high accuracy and consistency and low-cost measurement early in life.

b. Advanced prediction of breech and body strike susceptibility using digital image capture of cryptic variation accounting for unexplained variation in susceptibility. Known indicator traits do not capture all the variation in flystrike susceptibility. Additional phenotypes could potentially be captured more accurately when sheep phenotypes are trained against flystrike outcomes direct without preconceived subjectivity and bias. Such advanced phenotypes allow better informed selection decisions and could augment existing phenotypes or replace them with simple analytical measures in real time. Additional information could also augment management decisions on which sheep to mules during transition phases or which sheep pose high risk groups for flystrike.

c. Use of artificial intelligence could also be used to monitor fly abundance through trap data, or model abundance and high-density refuge based on topographical /vegetation data on farm.

d. The building of regional predictive models of fly waves will almost certainly require artificial intelligence applications to integrate complex multi-source data on weather, farm characteristics, sheep susceptibility and fly populations as they all interact and change rapidly as seasonal conditions change. To maximize benefits from such models they need to be able to be updated in real time and adjust to new parameters becoming available. Ie AI to be continually updating the models through ongoing learning.

e. Use of AI in combination of chemical treatment options and minimising emerging resistance in the field. The complex interactions between various chemical usage, application technologies, fly populations and sheep susceptibility and management all aid to the longevity of chemical control options. The use of AI to model outcomes from such complex interactions is a sensible use of this technology to prolong life of existing chemicals and optimize efficacy.

f. AI is potentially the gateway to monitor behavioural profiles of sheep through sensor based early alerts which could potentially distinguish fly struck and non-struck animals and therefore be used as an additional detect tool for fly struck sheep. There is an opportunity to build an understanding of the ability for video or image-based detection using flock monitor systems or drone technology.

Although these examples are only indicative of the many applications that could be subjected to AI, the main investment requirement by industry is to generate suitable and accurate input data sets for AI to be trained on. Typically, such data sets are quite extensive and need to be sampled across a wide range of conditions to maximize predictive capacity and utility. A recommended investment strategy is detailed below.

8 Strategy and Investment

8.1 Human Capital

Technology is improving all the time and there is no doubt that technologies that are developed for another purpose may present new opportunities within flystrike control as highlighted above. However, unless there are dedicated teams or individuals that are looking to continue to improve flystrike control it is unlikely that these opportunities will be realised. The industry needs to continue to invest in human capital via mechanisms that encourage career scientists into the area. Scholarships for PhD or Masters research into the area is a mechanism that needs to be explored.

8.1.1 Past investments

It is clear from the extensive survey of global research efforts, that past knowledge is often lost or forgotten, and new investments substantially duplicate past work without building on existing knowledge. It is important that past research reports and projects, especially where non-published, are made freely available, and new proposals are benchmarked against past work and investment.

In a similar vein both wool and meat industries in Australia have heavily invested in very large resource flocks, often at enormous expense to generate genetic parameters on core traits. Yet in most instances the measurement of difficult and expensive to measure traits such as flystrike-both body and breech, are overlooked. This not only represents a missed opportunity which could have been obtained at marginal extra cost, it also represents a loss on relationships both phenotypic and genetic between flystrike and other core production and other disease traits. Finally, resource and reference flocks are often heavily focussed either wool or meat breeds, and when confounded with environment, little comparative performance in diseases such as flystrike susceptibility can be made. Better and more comprehensive planning in establishing resource flocks in the future is warranted to generate information in line with future expectations of the sheep industry.

8.2 Enhancing farmer knowledge

While there remain some significant knowledge gaps to reduce the incidence and prevalence of flystrike within the Australian sheep population a lot of information is known but not implemented. There are a lot of producers who have bred a type of sheep and enhanced their management that now rarely have issues with flystrike. A component of an investment strategy has to be around implementing information that is known. This opportunity extends beyond producers into all aspects of investment in the sheep industry. For example, current Sheep Genetics indexes places no emphasis on flystrike traits.

9 Conclusions

Myiasis of sheep remains a serious health problem posing significant constraints on production efficiency. In sheep the nasal bot fly is possibly the most prevalent form of myiasis but can be easily controlled and poses limited impact on production. Infestation with screw worm flies on the other hand pose enormous constraints on sheep production. Fortunately, most of the important sheep production countries in the world are free from this parasite. In combination the greatest impact of myiasis in sheep is caused by *Lucilia* species (*L. cuprina* and to a lesser extent *L. sericata*) worldwide.

An extensive range of control methods are being used to either reduce blowfly populations or increase resistance of the host. Within the current range, use of management practices such as tail docking, mulesing, shearing, and internal parasite control are highly effective. In addition, the strategic use of insecticides still forms the backbone of flystrike control programmes despite the widespread development of resistance by blowflies to a wide range of chemicals, and reduced consumer acceptance of chemical residues in wool. In the case of the relatively susceptible Merino, selection of resistant genotypes has proven to be effective to reduce susceptibility to body strike and breech strike. Genetic improvement of host resistance to flystrike in non-Merino sheep has not yet been demonstrated but is thought to be feasible. Additional strategies to reduce the population of blowflies through trapping, biological or genetic control has limited scope on a large scale or proven not to be cost effective. Vaccination against blowfly larvae or the main predisposing agents of blowfly strike are not sufficiently reliable to offer widespread protection in the field.

In isolation, each of the current control strategies have limitations for high level sustainable control of blowflies. The integration of our current knowledge of blowfly control-strategies to deliver sustainable integrated pest management programmes can now be achieved. Although interactive control is currently in place, it occurs on an ad-hoc basis rather than part of a designed integrated programme. The management of insecticide resistance, strategic use of chemicals and manipulation of host resistance, in combination with suppressing blow fly populations should all be important components as well as breeding for increased resistance.

Through the deployment of artificial intelligence and a pragmatic approach to the use of quantitative genetics significant gains can be made in the fight against flystrike.

10 Investment strategy

A short to medium term investment portfolio is proposed that will future proof the Australian sheep industry against flystrike into the future.

The strategy has three pillars:

1. Less susceptible sheep
2. Resilient management systems
3. Reliable insect control options

10.1.1 Pillar 1 – Less susceptible sheep

This pillar is about making a serious effort to breed genotypes that become less prone to flystrike over time. It also assumes that modifications to animals, surgical or otherwise will not be possible in the future. Put simply it is about breeding better sheep.

Project	Estimated time frame	Estimated investment
ASBVs for indicator traits	4 years	$450K
Automating phenotype assessments	2 years	$350K
Beyond indicator traits for breeding	5 years	$1,200K
Progeny testing sires for flystrike susceptibility	5 years	$1,500K
Development, testing & release of a flystrike breeding value	5 years	$400K
Supported industry flock fly challenges	3-5 years	$300K
Genomic resource building	3-5 years	$100K
Resistant sheep	**Total**	**$4.3M**

10.1.2 Pillar 2 – Resilient management systems

This pillar is about the people. Providing farmers with the necessary information and knowledge to reduce flystrike to zero on their properties.

Project	Estimated time frame	Estimated investment
Expert panel and review teams	5 years	$300K
Industry champions	3 years	$200K
Climate change modelling	3 years	$200K
Improved detection of affected animals	3 years	$400K
Improved management of affected animals	1 year	$100K
Fly free farming workshop development and prototyping	1 year	$300K
Fly free farming roll out	3 years	$500K
Flyboss revamp	1 year	$200K
Automated fly wave monitoring	2 years	$400K
Region based predictive capacity	4 years	$1,200K
Resilient management systems	**Total**	**$3.8M**

10.1.3 Pillar 3 – Reliable insect control methods

This pillar is about gathering a complete understanding of the usefulness of current chemicals and ensuring that preventative chemicals remain effective over time.

Project	Estimated time frame	Estimated investment
Chemical rotation research	10 years	$500K
Chemical application audit	1 year	$200K
Enhance awareness and availability of chemical resistance tests	3 years	$700K
Development of IPM systems	3 years	$500K
Reliable chemicals	**Total**	**$1.9M**

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