BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Understanding the behaviour and improving the welfare of chickens

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Introduction

This collection summarises the rich body of research on understanding the behaviour of chickens and using this knowledge to optimise welfare management of broilers and layers. Part 1 of this volume reviews advances in research on key aspects of poultry behaviour and welfare monitoring. Chapters include the genetics and epigenetics of poultry behaviour, sensory perception, pain and stress responses, learning and cognition as well as social behaviour. The section also includes coverage of wearable, video and acoustic technologies to monitor chicken behaviour and welfare as well as developments in welfare protocols. Part 2 discusses particular welfare issues affecting broilers and layers. Topics covered include welfare in hatcheries and during rearing, housing and management, the role of enrichment as well as optimising welfare during catching, transport and slaughter. The book also reviews advances in understanding specific welfare issues such as injurious pecking, bone and skin health.

Part 1 Behaviour

The first chapter of the book focuses on advances in understanding the genetics of poultry behaviour. Chapter 1 begins by examining the genetics of behaviour and goes on to analyse the different approaches for the mapping of genes for behaviour, focusing on top-down and bottom-up approaches. The chapter provides a clear explanation and exposition of the terminology used in genetics, gene mapping and selection. It then reviews the genetic basis of different behavioural traits in chickens, such as anxiety, brooding, feather pecking and aggressive male mating behaviour. A section on pleiotropy and the potential for selection in chicken is also provided, followed by an analysis of epigenetics and behaviour. It also highlights how genetic and genomic techniques are used by commercial companies, then closes with an overall conclusion on the importance of refining the genetic and genomic tools and provides resources for further information on the subject.

The subject of Chapter 2 is understanding the sensory perception of chickens. Chickens perceive environmental stimuli via their senses. The affinity and capacity of the different sensory modalities are therefore of paramount importance for the behaviour and welfare of broilers and laying hens, and sensory perception needs to be taken into account when we house and handle domestic poultry. Emphasis is put on the importance of vision, olfaction, taste, hearing and touch for the perception of the environment by the birds, and how different ages and different contexts influence how a chicken responds to its surroundings. Finally, the influence of different

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sensory inputs is summarised, together with important aspects of the senses for the welfare of chickens.

Chapter 3 considers subjective and affective states in chickens, and the importance of these for understanding states of suffering. The chapter begins by discussing the causes of three potential states of suffering experienced by poultry species, namely fear, frustration and pain, and the behavioural symptoms associated with these states. Birds can be frightened by stimuli that are sudden and intense, novel and which signal special evolutionary dangers. The lack of a nesting site and lack of a roosting site in battery cages are the main causes of intense frustration in laying hens. Pain can be caused by feather pecking and cannibalism, the artificial environment, surgical procedures, and breeding practices.

The next chapter concentrates on understanding chicken learning and cognition and implications for improved management. Chapter 4 begins by discussing early learning in domestic chickens, focusing on maternal and brood companion effects, then addresses habituation and associative learning. The chapter moves on to examine cognition, specifically focusing on social learning, visual and spatial cognition, time perception, transitive inference, numerical abilities, affective states, communication and memory. The chapter then discusses various methods for improving management through understanding the learning and cognitive abilities at various stages of a chicken's life. It also considers how positive or negative affective states might result in changes (biases) in cognitive processing and decision making. The chapter concludes by emphasising how knowledge of chicken learning and cognition can help to re-frame the treatment of chickens and provides sources for further information on the subject.

Chapter 5 reviews our understanding of poultry social behaviour and its impact on animal welfare. Sociality was a prerequisite for domestication that allowed animals to remain in groups under human custody. The social group provides opportunities to find food, protection from predation or weather conditions. However, very dense or large groups normally found in many production environments may increase competition and be a potential source of social stress. Social relationships within small groups of domestic fowl are based on the establishment of social hierarchies, but social dynamics of large groups are less rigid. . Social plasticity allows animals to better adapt to the diversity of environmental and social conditions that may be encountered though life. The chapter discusses how different management and environmental factors may affect the social dynamics of the domestic fowl and analyses the potential impact for their welfare. Special attention is dedicated to imprinting processes that may determine how domestic fowl respond to social models, and to the relationships developed in breeding flocks.

The next chapter examines poultry welfare monitoring, specifically focusing on wearable technologies which provide the best opportunity for

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obtaining data on individual birds within large flocks. Chapter 6 begins by discussing the use of radio-frequency identification technology (RFID) systems in chickens and other housing systems. The chapter then goes on to address wearable sensors and accelerometers, focusing on the effects of these sensors on chicken behaviour and how different behavioural activities can be classified. It also highlights how these sensors can be used for monitoring disease and euthanasia in chickens, as well as monitoring perching, jumping, falls and collisions. A section on the importance of using wearable technologies for measuring physical activity levels is also included, followed by a case study that analyses outdoor stocking density in free-range laying hens. The chapter concludes by providing potential areas for future research, particularly those that might support the transition from research tool to commercial application. Examples of resources for further information on the subject are provided.

Expanding on topics previously covered in Chapter 6, Chapter 7 focuses on group level technologies used for poultry behaviour and welfare monitoring. Commercial poultry are frequently kept in groups of thousands of individuals where tagging or identifying every bird is logistically impossible. Group, rather than individual, level approaches to assessing their health and welfare are therefore currently the most feasible. This chapter covers developments in ways of automating welfare assessment for poultry with particular emphasis on broiler chickens and the use of visual images from CCTV and video, sound and temperature sensing. A specific example of camera technology to detect flocks with high levels of hockburn and other health issues is described. Despite considerable potential for using technology to assess poultry welfare it is not currently widely used in practice. Reasons for this and the potential costs and benefits of applying Precision Livestock Farming to poultry are discussed in relation to the importance of making sure that technology is used to improve rather than diminish animal welfare.

The final chapter of Part 1 concentrates on improving welfare assessment indicators and protocols for poultry. There have been considerable advances in welfare assessment in the past few decades. Chapter 8 explains some of the terminology related to welfare assessment and why the emphasis is moving towards including animal-based indicators of poultry welfare rather resource-based indicators. The chapter also reviews some of the more commonly used laying hen and broiler welfare assessment indicators, focusing on those that reflect the behaviour of birds. Among the clinical indicators discussed are assessments of pecking damage and bird cleanliness. Behaviour indicators include those that are recorded from undisturbed birds, such as vocalisation, and those that use a test situation. A welfare assessment protocol is a description of the procedures to collect the indicators. In the final sections of the chapter, methods to prioritise between different indicators are discussed. This remains an important question for animal welfare science in general, and

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understanding how different indicators relate to bird preferences and cognitive biases is an emerging area of research. Future trends to improve poultry welfare assessment are discussed.

Part 2 Welfare issues in breeding, management and housing

Part 2 begins with a discussion of welfare issues affecting broiler breeders. The demand for broiler meat has been growing for decades, and broiler meat represents the major animal protein source in many countries around the world. To meet this demand, a consistent selection for fast growth is employed in the broiler industry. Chapter 9 first focuses on housing conditions of broiler breeders then reviews growth potential and feed restriction. Broiler breeders are often severely feed restricted and this chapter reviews the consequences in terms of physiological stress, hunger and repetitive pecking or drinking behaviours. The chapter moves on to address the current welfare issues in broiler breeders such as unfulfilled behavioural and physiological needs, aggression, mutilation and the associated welfare problems. It concludes by providing an analysis of the significant challenges that need to be addressed in the future and offers examples of resources that could be used for further information on the subject.

Chapter 10 provides an extensive review of an area where research effort is greatly needed. It considers the factors that affect the health, behaviour and welfare of young chicks and growing birds. It starts by assessing how the welfare of parental stock can influence offspring via direct or epigenetic effects. The chapter then reviews research on incubation and hatching practices to optimize chick welfare within commercial hatcheries. The potential of on-farm hatching to alleviate some of these problems is discussed. Finally, the chapter assesses rearing practices to optimize pullet welfare, including the importance of enrichment in, for example, in reducing the risk of developing injurious pecking behaviours, reducing risk of injury by improving spatial and navigation skills, and in producing birds that are more resilient and less fearful.

The next chapter focuses on welfare issues in poultry housing and management of broilers. Chapter 11 begins by providing an international perspective on broiler production systems and the differing legislative frameworks operating around the world. The chapter highlights how genetic selection influences growth potential and broiler welfare. The chapter moves on to discuss broiler behaviour and space use, then examines how differing production systems, breeds and stocking densities affect the prevalence of mortality, leg health, skin infections, heat stress, antibiotic usage and ability to perform behaviour. It also addresses the relationship between growth rate and broiler welfare, followed by a discussion on the effects of management practices

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and environmental conditions, including litter and air quality on broiler welfare. The chapter concludes by emphasising the importance of improving broiler welfare in different production systems and provides examples of resources for further information.

Chapter 12 examines welfare issues in poultry housing and management of laying hens. Laying hens produce a large number of eggs on an annual basis. In recent years, permitted housing methods in the EU have changed to enriched cages and cage-free systems (i.e. barn, free-range and organic production methods), but worldwide hens are still also housed in conventional cages. The chapter provides a clear description of the characteristics of each of these systems. Conventionally caged hens have weaker bones and are their behaviour is severely restricted by lack of resources and small space allowances. Hens from enriched cages benefit from some improvements such as nest boxes, perches, greater space, and litter for pecking and scratching. Cage-free hens have the most behavioural freedom and better bone strength, but they are also at risk of greater keel bone damage (particularly with multi-tier structures), exposure to pathogens (particularly with free-range and organic), and greater mortality. This chapter considers how current research is being directed to mitigate some of the welfare risks associated with cage-free systems. This is an important goal given the drivers favouring a move towards cage-free systems in many countries.

Chapter 13 focuses on the role of perches in chicken welfare. The chapter carefully distinguishes different aspects of perching that are often conflated. Night-time roosting and day-time perching are both adaptive strategies to avoid predators, but both may serve other functions. Perching motivation and perching ability are both influenced by genetics and age-related changes and there has been more research on layer strains than in broilers. Both are considered in this chapter. The chapter discusses the ontogeny of perching, the anatomic prerequisites for perching and the properties of perches from the view of chickens by focusing on perception and motivation. The primary motivation for chickens appears to be to gain access to an elevated position, with a lesser motivation to grasp a structure with the foot. The chapter concludes by emphasising the structural properties and arrangements of perches that can best meet the needs of laying hens (whilst reducing the risk of keel bone damage) and of broiler chickens.

The subject of Chapter 14 is improving welfare in catching and transport of chickens. It opens with a discussion of the broiler chicken pre-slaughter phase and the associated welfare concerns, focusing specifically on age of depopulation, thinning versus whole flock removal, feed and water withdrawal, catching and loading, transportation, lairage and the economic impact of the pre-slaughter phase. This is followed by an analysis of the various steps that can be taken to improve broiler welfare such as fitness assessments, the use of

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mechanical catching as opposed to manual, control of the thermal environment broilers are transported in and more efficient training of staff involved in the process. The chapter also briefly discusses the pre-slaughter phase for laying hens as a comparison, before concluding with a section on future research trends for broiler chicken welfare in terms of pre-slaughter and transportation.

Chapter 15 focuses on improving welfare in poultry slaughter. Poultry production involves the killing of very large numbers of birds so there is a compelling need to protect welfare at slaughter. In most countries, slaughter must be preceded by stunning to induce unconsciousness. The major stunning approaches used in chicken slaughter are electrical stunning and methods that modify the atmosphere (via introduction of gas or reduction in air pressure). The chapter opens with a discussion on welfare issues related to lairage and pre-slaughter handling, when directly relevant to the experience of birds. It briefly outlines some relevant regulatory frameworks, with a focus on the European Union which is widely recognised to have the most stringent legal protection for animals at the time of killing. It then discusses current and emerging methods, concluding with prospects for improvement of welfare based on available systems and identification of knowledge gaps for research.

The next chapter examines causes and prevention of injurious pecking in laying hens. The high prevalence of injurious pecking (IP) in laying birds is a major concern from animal welfare, societal, and economic points of view. IP is defined as bird-to-bird pecking that results in or has a high likelihood of causing integument injury and psychological harm to the victim. Chapter 16 describes three forms of IP – tissue pecking (TP), aggressive pecking (AP), and different forms of feather pecking (FP). Furthermore, it explores the two major views explaining the origin of severe FP, the most prevalent form of IP. The first, the traditional ethological view, emphasizes the role of the environment in creating motivational frustration, for example that inadequate foraging substrates will result in an increased tendency of birds to peck at feathers as a substitute. In contrast, the dysfunctional view identifies underlying neurobiological (and potentially gastrointestinal) dysfunctions induced by intense or sustained stress as the cause of severe FP. Finally, the chapter concludes by highlighting risk factors and management strategies that are used to reduce IP.

Chapter 17 explores bone health and associated problems in layer hens. This chapter provides a summary of the basic skeletal system and its development, specific problems of bone health, and efforts to reduce the problem. Adult hens must support normal biological functioning while producing a large number of eggs which require mobilization of resources including minerals and energy. Laying hens and associated commercial egg production is one of the most universal agricultural products across the globe. Likely as a consequence of this mobilization and related factors, laying hens have weakened skeletal systems leading to specific problems including fractured keels during the laying period,

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and a susceptibility to other bone injuries during removal from cages or barns at the end of lay. To combat these problems, multiple strategies are being investigated to try to resolve these problems. These strategies include revised breeding goals, and adaptations to nutrition, housing, and management. The importance of early rearing is also reviewed as some housing and management systems provide better opportunities for appropriate skeletal and spatial cognitive development than others.

The final chapter of the book addresses poultry health monitoring and management, specifically focusing on bone and skin health in broilers. Chapter 18 builds on the information provided in Chapter 11 and opens with a discussion on leg disorders and lameness. It differentiates developmental and infectious causes of lameness and shows how these are related to impaired walking ability. Traditional and novel, automated techniques for qualitative and quantitative assessment of leg health are reviewed. It also examines the prevalence of lameness and specific leg pathologies, followed by an analysis of key risk factors associated with lameness such as age, sex and body mass, genotype, stocking density and environmental conditions. The challenges of assessing the welfare impact of lameness in terms of bird movement, pain and behavioural restriction are considered and recent experimental results reviewed. This is followed by a section on the various strategies that can be used to prevent and control lameness. Contact dermatitis is also discussed in terms of the risk factors, welfare impact and methods of prevention and control. The chapter concludes by emphasising the importance of developing ways to monitor and manage these issues in broilers.

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Part 1

Behaviour

Chapter 1

Advances in understanding the genetics of poultry behaviour

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1 Introduction
2 The genetics of behaviour
3 Mapping genes for behaviour
4 Behavioural types and their genetic basis
5 Pleiotropy and the potential for selection
6 Epigenetics and behaviour
7 Commercial aspects and research
8 Conclusions
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1 Introduction

The ultimate aim when analysing the underlying genetics of behaviour, or indeed the genetics of any quantitative trait, is often to find the causal polymorphisms or mutations, and the genes that they modify, that give rise to the observed changes in the phenotypic response. However, it is often both highly complex and also very rare to identify these precise mutations (Flint, 2003). Indeed, it is hard enough to identify the causal genes with a high degree of certainty, even without identifying the precise mutations that affect them. More generally, we wish to identify the genetic architecture of a given trait (Falconer and Mackay, 1996, Lynch and Walsh, 1998). In this case, the genetic architecture refers to the number of genes (or rather the number of polymorphisms that affect the trait – the quantitative trait loci (QTL), where they are located, and what their effect size is (Falconer and Mackay, 1996, Lynch and Walsh, 1998). A QTL refers to a discrete genomic region that affects the trait. Note that the QTL can be a region containing a few or, often, many genes. A distinction is made between such loci, and the identification of the actual causal nucleotide or mutation (coined a Quantitative Trait Nucleotide (QTN) (Mackay et al., 2009)), or indeed the gene that the QTN controls – the Quantitative Trait Gene (QTG)

http://dx.doi.org/10.19103/AS.2020.0078.01
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Table 1 Glossary of terms used

Term	Definition
Epistasis	An interaction by two (or more) separate genes that affect a phenotype. In the case of QTL mapping, this refers to a situation where the two QTLs interact with one another to affect the phenotype in a manner that differs from the standard effects of each QTL on its own.
Pleiotropy	Where one gene may have multiple different phenotypic effects. In the case of QTL mapping, this refers to a situation where a single QTL locus has effects on multiple different phenotypes.
Additive effects	Additive effects in QTL mapping refer to the cumulative effect of each allele that is present at a QTL. For example, if an individual is homozygous for a particular QTL genotype, the total effect on the phenotype is twice the additive effect of that particular locus.
Dominance effects	Similar to additive effects, dominance effects in QTL mapping refer to the interaction between two alleles at a particular QTL. If one allele is dominant over the other, the dominance effect describes the degree of dominance (partial or full) and the direction of effect (which allele is dominant).
Microsatellites	These are one of a number of different molecular markers that are used for gene mapping experiments. Microsatellites refer to small copy number variants (with a motif that is generally 2 or 3 base pairs long, but with this motif repeated many times over). They are generally present in non-conserved regions of the genome and are usually selectively neutral, allowing them to often be very variable in length between individuals, making them particularly amenable to genetic mapping experiments.
Resequencing	This refers to when a particular individual or group of individuals have their genome sequenced for the exact base pair composition that makes up their DNA molecules. Initially, sequencing used to be performed using methods such as Sanger sequencing, whereby 1 kilobase region would be sequenced. More recently massively parallel sequencing means small regions (generally 100–150 base pairs) are sequenced, with millions of reads being produced per individual and then aligned with the known genome of the species being sequenced. In this way, exact genomic differences (most commonly single nucleotide polymorphisms or SNPs) can be identified between individuals.
Haplotype blocks	This refers to a region of an individual's genome where there has been no or little recombination. Haplotypes are groups of alleles that are close to one another and inherited together as a block. When recombination occurs this will break up this haplotype.
Recombination Rate	Recombination rate refers to the probability of a recombination event occurring during meiosis in gamete formation. When a crossover or recombination event occurs, the genetic information on one chromosome is mixed with the genetic information from the other chromosome in the pair. Recombination rate is typically referred to as the probability of a recombination occurring in a given region of the genome. So for example the recombination rate in chickens is around 1 recombination every 350 kilobases, while in humans and mice the recombination rate is around 1 recombination every 1 megabase.

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(Mackay et al., 2009). The effect size refers to whether a few genes of large effect are controlling the trait, or many genes of small effect. For example, the most extreme possibility is the infinitesimal animal model (Fisher, 1958) that assumes that many thousands of loci each with a tiny effect size make up the trait. Similarly, are the loci that control the trait purely additive or dominant in their effect, or are epistatic effects apparent between loci (Lynch and Walsh, 1998)? See Table 1 for a glossary of these and other terms. In these instances, the exact location of the QTN is not known, but rather a region of the genome is identified. In the case of domestic birds such as the chicken, comparisons are often made between divergent populations, classically wild and domestic birds (Jensen and Wright, 2014, Wright, 2015), or commercial broiler and layer breeds (Nones et al., 2006). This is particularly important as when identifying the genetics of a trait, it is the variation present within that trait that is being mapped. Such comparisons maximise the degree of variation present and are a powerful tool for genetic mapping.

2 The genetics of behaviour

In general, the genes and mutations underlying behaviour are even harder to identify than more standard morphological characteristics, and as such very few QTN and QTG have been identified for behaviour. Successful examples of behavioural QTG identification are typically limited to *Drosophila* (Anholt and Mackay, 2004, Mackay, 2004, Fitzpatrick et al., 2005), mouse and rat models (Chiavegatto et al., 2008, Gyetvai et al., 2011, Kim et al., 2009, Tomida et al., 2009, Wang et al., 2012, Yalcin et al., 2004, Heyne et al., 2014), and the honeybee (Robinson et al., 2008, Robinson et al., 2005). The ramifications for the identification of such behavioural genes are many and varied. From a medical perspective, anxiety-based disorders are highly prevalent and damaging in modern society, being one of the top ten causes of disability world-wide (Murray and Lopez, 1996, Vos et al., 2015). However, the identification of susceptibility loci for such traits is highly limited (Kas et al., 2007), with usually only a handful of loci identified (though in some of the largest studies more loci are now being identified albeit with very low effect size (Ripke et al., 2014)). This is despite the often high heritability estimates for diseases such as schizophrenia (McGue and Bouchard Jr, 1998), bipolar disorder (Burmeister et al., 2008) and major depressive disorder (Burmeister et al., 2008). From a non-medical perspective, very little is known about what mutations or polymorphisms affect behaviour in a non-morbid fashion, that is, the alleles that are responsible for natural quantitative variation. These can be vital for understanding responses to stress and also natural resistance or susceptibility to particular conditions, which may be particularly relevant for domesticated chickens. With regard to evolutionary theory, behavioural personality studies have been performed on a wide range

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of species (Sih et al., 2004); however, the genes basis of such traits still remain largely unexplored.

3 Mapping genes for behaviour

The mapping of genes for behaviour is similar to mapping other quantitative traits, with the exception that the traits under examination are in general harder to define and measure reliably. The methods generally employ either a top-down or a bottom-up approach. Essentially this refers to whether one starts at the phenotype and attempts to work down to the gene level (top-down), or whether one starts at a gene level and attempts to work up to the phenotype (bottom-up) (Boake et al., 2002).

3.1 Top-down approaches

3.1.1 Pedigree analysis and heritability studies

Initially, the use of statistical analysis of pedigrees can demonstrate an actual heritable component to the trait of interest, through breeding designs, artificial selection or the like. At this point the aim is simply to show that a genetic component exists for the trait to be studied. The requirements for this are only the behavioural phenotypes for all individuals and knowledge of their relatedness (the pedigree). Heritability studies can be used to further dissect traits down to distinguish between broad sense and narrow sense heritability, with the genetic component further divided into additive and dominance components (additive in this case refers to the effect from those loci that give a cumulative effect, whereas dominance represents the interactions between alleles at the same locus) (Lynch and Walsh, 1998, Falconer and Mackay, 1996).

3.1.2 Quantitative trait loci (QTL) and association mapping

QTL mapping is now a very well-established technique, first becoming popular in the 1990s (Lander and Botstein, 1989). The first major step in increasing its use came with microsatellite markers. More recently, Single Nucleotide Polymorphism (SNP) markers and resequencing technology have increased the number of molecular markers available exponentially. These advances are enabling the step to gene discovery to be performed (previously a major failing with this approach). In essence, QTL mapping is the crossing of two distinct populations that differ for one or more traits of interest. This creates an inter-cross population containing a large degree of genetic variation (containing alleles that both increase and decrease the trait under examination). QTL mapping involves mapping the loci that differ between the two parental populations that are crossed. Thus, this technique is particularly amenable for domestic animals,

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where extremely large phenotypic differences frequently occur between wild and domestic populations (Andersson and Georges, 2004), with this extreme phenotypic diversity providing excellent power for gene mapping. After the intercross is continued to either an F_2 or backcross generation, the intercross individuals are then genotyped for multiple markers spread throughout the genome, with the genotype information correlated with the phenotypic data. This enables the identification of the number of loci affecting the traits that differ between the two populations, their effect size in terms of the variation present in the intercross that they explain, and their genomic location.

The QTL can be defined in terms of their additive and dominance components, while pleiotropy (one locus affects multiple different traits) and epistasis (when multiple genes are interacting with one another) can also be identified. As stated previously, the major issue in standard QTL mapping is one of resolution of the detected loci (with very large confidence intervals generally being the norm), while the sample sizes that are required for the detection of small effect loci may also be large (Beavis, 1998). The issue of the resolution of the detected loci is limited by the number of recombinations present in the test cross (Darvasi, 1998, Lynch and Walsh, 1998). Typically, as the number of recombinations in a backcross and F2 are rather restricted, this means in turn that the resolution of each QTL is rather low, covering several megabases (Mb), and relatively few QTL have been refined to the causative gene (QTG/ QTN).

Association mapping is a similar, but more recent, application. This typically uses a single outbred population in combination with high-density SNP genotyping per individual. The difference with this technique is that by using a single large, outbred population, many more recombinations are present in comparison to a standard QTL intercross population, and therefore the the resolution is far greater due to the smaller haplotype blocks. This does therefore require far more markers per individual, while population substructure can be an issue. Additionally, in such large populations, the genetic architecture can be very complicated. Far more polymorphisms and alleles are contained in the natural population as compared to a standard QTL cross which typically utilises inbred populations/individuals and most commonly only two different populations with a limited number of founder individuals. Results with association mapping in large populations in humans tend to show that very few QTLs with large effects are present, and relatively little of the variance present can be explained by the loci which are discovered (Carlson et al., 2004). However, the power of this approach is that rather than being constrained by a precise cross, natural populations can be used far more easily.

In the case of domestic animals, the possess many features that make them more amenable to this type of analysis (Goddard and Hayes, 2009). Firstly, the strong directional effects of domestication selection often mean that fewer markers are required as haplotype blocks are larger (for instance

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in the case of the dog (Karlsson et al., 2007)). The chicken itself has several highly advantageous genomic features when it comes to these types of linkage mapping and association studies. They have a rather compact genome (just over 1Gb in length, as compared to around 3Gb for humans – (Wallis et al., 2004)). Not only that, but they also have a higher recombination rate (one recombination every 350kb, as opposed to one recombination every 1Mb in humans and mice (Groenen et al., 2000)). This increased recombination rate translates into a higher resolution due to more recombinations accruing over a given area, as compared to mammals. Therefore, they are highly amenable to these forms of genetic mapping and can yield excellent results with a higher resolution, meaning far narrower confidence intervals are generated.

3.1.3 Selective sweep mapping

The identification of selective sweeps is potentially an extremely powerful tool for the dissection of genetic architecture, and can be particularly relevant for domestic populations (Andersson and Georges, 2004). The basis of selective sweep mapping occurs when a new mutation arises in a population and is then selected upon via strong directional selection. In this case, not only the mutation but also the neighbouring polymorphisms (i.e. the haplotype in which the mutation arose) will also go to fixation. Thus, the surrounding SNP markers will 'hitch-hike' along with the mutation (Smith and Haigh, 1974). Once the new mutation is in full fixation, relating to the strength of selection and the time that has elapsed since fixation, this signature of selection will then be slowly eroded. In the case of domestic populations, the strength of selection is often high, which in turn increases the likelihood of such sweeps occurring. However, these sweeps are also dependent on the genetic architecture of the trait (Pritchard and Di Rienzo, 2010). In particular if many genes of small effect are responsible for the bulk of trait variation, selective sweeps may be less prevalent due to polygenic adaptation (where small changes in allele frequency can have a large cumulative effect). Such small changes in allele frequency will not lead to the characteristic regions of fixation that are detected by selective sweep mapping. Selective sweeps have been observed in domestic chickens, where around 50 40kb regions were putatively identified as being under selection in one study (Rubin et al., 2010), while a more recent study also found a number of further broiler and layer-specific sweeps (New Leif ref). This approach is particularly powerful when multiple domestic populations are analysed, with shared regions of identity-by-descent identified over multiple different population types. It has been used to locate both discrete mutations (for example, the pea comb (Wright et al., 2009) and yellow skin (Eriksson et al., 2008) mutations in chickens) and, for mutations affecting quantitative traits (QTNs), see comb size in chickens (Johnsson et al., 2012).

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