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Introduction
Darwinian selection, selective breeding and the welfare of animals

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Abstract

The 150th anniversary of the publication of The Origin of Species… *is a good time to consider how selection can affect welfare — the quality of life. Darwin (1859) quoted Youatt's description of selective breeding: "…the magician's wand, by means of which he may summon into life whatever form and mould he pleases". Evolution has fairly recently included us humans in its toolbox, alongside its older instruments, such as climate and disease, as significant agents of selection. We have taken to this work vigorously and have summoned into life an extraordinary array of creatures. It is only much more recently, with the development of interest in animal welfare science, that the welfare consequences of this have begun to be critically reviewed. There are two ways that selection can affect welfare: (i) by resulting in changes that make aversive feelings more likely, eg by predisposing to disease or by altering behaviour such as to increase risk of disease or injury, and (ii) by altering sensitivity of the affect systems such that animals feel, for example, more (or less) pain or fear in response to a stimulus than their ancestors would have. Comparing natural and human selection — that is, the simultaneous scrutiny of all aspects of biology as opposed to our selection for one or two features that appeal to us — Darwin (1859) wrote: "Can we wonder, then, that nature's productions should be far 'truer' in character than man's productions; that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship". The aims of this meeting were to discuss how selection can affect welfare and how we can improve our workmanship in the interests of animal welfare.*

Keywords: *animal welfare, breeding, genetics, hereditary disease, selection*

Introduction

Even if this year was not the 200th anniversary of Darwin's birth and the 150th anniversary of the publication of *The Origin of Species*…, it would be timely to meet to review and consider how natural selection and our selective breeding of kept animals affects welfare. There has been a great deal of both scientific and public interest in this subject recently (eg see FAWC 2004; CAWC 2006; McGreevy 2007; Rooney & Sargan 2009). It has become widely apparent that, because of the major welfare impact of some conditions and the numbers of animals affected, tackling genetic welfare problems should be an important priority.

Selection is, in Youatt's words as quoted by Darwin (1859):

> "…the magician's wand, by means of which he (the farmer or breeder) may summon into life whatever form and mould he pleases".

Natural selection (including sexual selection) has been the means by which, during the last four billion years, the extraordinary diversity of life has been brought into existence. Recently (in the last few thousand years), evolution has recruited us humans as agents of selection alongside its more traditional tools, such as climate, disease and competition within and between species.

We have taken to this work vigorously and with gathering pace over recent millennia and have already 'summoned into life' a striking array of creatures: from lap dogs; guard dogs; hunting dogs and bull-fighting dogs to fantail pigeons; parlour-tumbler pigeons; hairless cats; lop-eared rabbits; cows that produce 40 litres of milk a day; chickens that reach table weight in a month; white canaries; bubble-eyed goldfish; dwarf horses and albino pythons, to mention just a very few.

Compared to the time that we have been selecting animals — hundreds or thousands of years in the cases of several farmed and companion animal species — it is only very recently that the welfare consequences of all this selection have begun to be critically reviewed. This is a reflection of the growth of scientific and public interest in animal welfare in recent decades (Fraser 2008) that roughly parallels, and which has been partly stimulated by, the developing scientific endeavour towards elucidating the neural correlates of conscious experiences.

It has become largely accepted that subjective experiences occur in, and are important to, animals other than just humans. Pursuit of the fascinating questions of how the capacity for subjective experiences (or rather its neural

correlates) evolved, what evolutionary benefits it brings, and how such feelings are generated, may prove to be very informative to our endeavours for animals' welfare. The aim of this symposium was to provide an opportunity for discussion of these topics, and of applied aspects of the subject: how anthropogenic selection for particular characters can affect welfare and how, where welfare problems have arisen, these can be tackled. My aim, in this introduction, was to sketch out some of the territory.

The territory

Natural versus anthropogenic selection

This symposium was about how selection can affect welfare. That is, how it affects quality of life as perceived by the animal itself — how it feels (see below). Selection can be natural (through survival of the 'fittest' in the evolutionary sense, including sexual selection) or it can be anthropogenic (brought about by human agency). This distinction is a helpful distinction in practice but it is arbitrary as humans and all human activity has come about through natural selection, so anthropogenic selection is ultimately a subset of natural selection.

Anthropogenic selection for particular traits can be deliberate (as by strategies, such as measuring milk yield in cattle and breeding from the highest producers) or it can be unintentional — as was probably the case when humans first began to keep animals and bred from their favourites. It can be direct, by pairing selected animals, or indirect as, for example, when animals adapt to an anthropogenically modified environment — as in the famous story of the rise of dark-coloured (melanistic) peppered moth morphs as an adaptation to the industrial smoke-blackening of trees (Steward 1977). It seems likely that there are currently very strong selection pressures for adaptation to anthropogenically altered habitats and niches and that our effects on the genetics of other animals extend way beyond the deliberate shaping of breeds of farmed and pet animals.

Animal welfare and subjective feeling

There is a large consensus amongst welfare scientists that, in line with the general public view, concern for an animal's welfare is concern, mostly (or at least partly), for its feelings. Some argue that health is part of what 'welfare' means but I think it is helpful to distinguish between the concepts of health and welfare, particularly in the context of this symposium. The focus of this meeting is not on the impact of selection on health or evolutionary fitness *per se*, a subject that has received a vast amount of attention since 1859, but on welfare/quality of life as experienced by the animal which, in contrast, has not. Of course, health has a very major influence on welfare.

I have suggested that welfare is:

> "the balance, now or through life, of the quality of the complex mix of subjective feelings associated with brain states induced by various sensory inputs and by cognitive and emotion processes" (Kirkwood 2004).

We are all very familiar, from personal experience, with what seems an effective system of sticks and carrots to reward us with pleasant feelings for actions that increase our chances of evolutionary success and punishes us with unpleasant feelings, such as fear and pain, if we put the survival of our genes at risk. How the machinery — the brain circuitry — that results in feelings (and I mean consciously, subjectively experienced feelings throughout) works, and when, and why, it evolved, remain great puzzles.

It seems likely that the states of the brain that embody the intensity and duration of unpleasant feelings, such as fear and pain, are closely regulated through evolutionary scrutiny because, for example, being either too fearful or not fearful enough would be detrimental to evolutionary fitness. Likewise, we might expect that the brain states that correlate with positive feelings will be under close scrutiny also. What happens to these apparently finely engineered sticks and carrots — whose effects and interactions amount to welfare (quality of life) itself — when selection is not for evolutionary fitness but for traits we prefer in pursuit of ideal companion or laboratory animals, or of greater farm animal production?

What are the ways in which selection could affect welfare?

I suggest that there are two ways that selection can affect welfare. (i) The first is if it results in changes that make it more likely that the brain will receive aversive signals. For example, if selection increases predisposition to painful disease or if it results in behavioural changes that increase the likelihood that the brain will receive aversive signals. For example, if increased frequency of a behaviour makes a painful disease or injury more likely. And, (ii), if it results in brain changes such that there is increased sensitivity to incoming aversive signals. That is, if it results in animals that experience greater fear or pain in response to a stimulus than would have been experienced by their ancestors.

The above points address how selection can adversely affect welfare but they can all be turned around to illustrate, equally, how selection could have positive effects: decreasing the likelihood or intensity of aversive feelings or increasing the likelihood or intensity of positive feelings.

Is natural selection good for welfare?

This symposium includes mention of many cases in which anthropogenic selection has adversely affected welfare. In *The Origin of Species*…, Darwin (1859), contrasting natural selection — which constantly scrutinises every aspect of an animal's biology — with our efforts which typically focus on one or very few traits, wrote:

> "But Natural Selection… is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art".

And,

> "Can we wonder, then, that nature's productions should be far 'truer' in character than man's productions; that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship".

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There is no question that natural selection acts so that organisms tend to increasingly exquisite adaptation to their environments, but does that mean it is generally good for welfare? Under stable conditions, we might expect that, as animals become ever more finely adapted to their environments, their welfare might, in some ways, improve. For example, that they are less likely to feel thermal stresses because they are well adapted to the climate (eg polar bears), they are less likely to be poisoned by toxic plants because they will either have adapted to avoid them or to deal with the toxins (eg rabbits can eat deadly nightshade), they will tend not to be debilitated by parasitic infestations because they will have evolved to prevent their harmful effects, and so on. However, as Darwin argued, the most intense competition is between individuals of the same species. Because all are well adapted does not mean that a larger number will survive to breed, because population sizes are limited by space, food or other factors. The other side of the coin of survival of the fittest is the not-survival of the much larger numbers of less fit and their demise in many, often unpleasant, ways.

Natural selection is for evolutionary fitness and is blind to everything else. A long and pure ancestry of natural selection does not, in any way, guarantee a life of good welfare in the wild. Through the struggle for existence, the bar is always being raised and, in a competitive, challenging and changing environment (as environments are), successfully overcoming one hurdle means surviving to struggle with the next. Natural selection cannot address the problems that occur late in life, after reproduction and contributions to rearing offspring, so even the fittest tend to run into welfare problems at this stage (eg through degenerative diseases).

As animals evolve to become ever more finely adapted to their environments, they may 'solve' some of the problems that used to adversely affect their welfare but, in so doing, survive to encounter others — so it is hard to conclude that natural selection generally tends to improve welfare. However, for those species in which a major cause of mortality is being killed by a predator (eg many small rodents), evolution acts in the direction of keeping them fit and in a state of good welfare until that moment (although welfare environmental challenges are likely often to compromise welfare). Also, where protected from competition and other risks in an environment to which they are adapted, animals shaped by natural selection tend to have the capacity for good welfare. How does anthropogenic selection compare?

Anthropogenic selection and its welfare consequences

> "Within the boundaries of modern human ecology there are niches, which do not exist otherwise, for all manner of animal types from achondroplastic dogs to red canaries, bubble-eyed goldfish and albino corn snakes. In one sense, what we see is that the process of evolution, being constantly 'on the look out' to fill all possible niches, has begun to 'explore' these new ones; and with its inherent disregard of whether or not they are pleasant 'places' to be" (CAWC 2006).

Evolution abhors a vacuum. Every new generation of replicating organisms is a set of variants so that, by chance, individuals arise that can survive and breed in places or under circumstances in which their ancestors could not. In this way, life constantly 'tries' to populate all possible niches.

The evolution of humans has opened up many new creeks and channels for evolution to explore and, through human agency, it has engineered many new varieties of plants and animals to fit niches that did not exist before. Evolution has included humans, in its toolbox alongside all its other instruments of selection, such as climate, geography and disease, in 'probing' and 'trying to fill' all available niches. But, in the context of deliberate anthropogenic selection, 'the fittest', as in survival of the fittest, are those that conform most closely to our whims or strategies, and this kind of 'fitness' is very different from the traditional sort. Those breeds that best fit anthropogenic niches (such as poultry houses, urban sitting rooms, pig farms or pigeon lofts) tend to be found unfit by natural selection — although there have been countless opportunities to 'escape' and establish in the wild (as many non-indigenous species, eg the grey squirrel, have successfully done), very few anthropogenic breeds establish wild populations.

During the last twenty-five years, there has been a very great increase in the range of species of animals kept and bred in captivity as companion animals (CAWC 2006), and there is considerable interest amongst pet keepers in selection for preferred colour and other traits in these animals. Unless efforts are made to avoid it, it is likely that this will result in many genetic welfare problems.

What are the welfare consequences of anthropogenic selection? When farmers first started selecting for hens that tended to continue to lay a few more eggs instead of brooding them once a usual clutch had been laid, we can suppose that there would have been no apparent welfare consequences to the birds. Changes in farmed animals have generally been gradual — too slight during any one breeder's lifetime to be likely to prompt much pondering about how they may have affected the animals' welfare. But, knowing as we do now, that all the varieties of domesticated animals are derived from a common wild ancestor — that all pigeon breeds are descendents of rock doves and that all dogs are descendents of the wolf — the great scale of the morphological, functional and behavioural changes brought about over time have become clear. How do we assess the welfare consequences of these?

Assessment of the welfare consequences

If welfare is defined as being about quality of life — how animals feel — then assessment of welfare is a two-stage process (Kirkwood *et al* 1994). The first stage involves observations and measurements of clinical, pathological or behavioural parameters. The second involves making judgements, based on these findings, about their impact on the animals' feelings — are the signs observed likely to be indicative of, for example, pain? And, if so, can an assessment be made as to whether this is mild, moderate or

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severe? We have no direct access to other animals' feelings and cannot avoid subjectivity in making such inferences. For this reason, opinions sometimes differ considerably about the welfare significance of clinical and behavioural signs. However, the difficulties associated with this can be minimised by making clear the bases of such judgements.

Examples of genetic welfare problems

Anthropogenic selection has resulted in many welfare problems. Examples include:

- High prevalence of lameness in dairy cattle (Webster 2005);
- Chronic hunger in broiler breeders because of the need to restrict their food intake in order to avoid the leg abnormalities that would occur if they were fed to appetite (FAWC 1998);
- High prevalence of hip dysplasia in Golden Retrievers (and various other breeds) (Paster *et al* 2005; Rettenmaier *et al* 2005);
- Prevalence of skin-fold dermatitis in Sharpei dogs (CIDD 2004);
- Prevalence of otitis in spaniels (Baba & Fukata 1981) and;
- Predisposition to flystrike in sheep (Phillips 2009).

As CAWC (2006) argued, genetic welfare problems can be of a major scale in that they can affect many animals, cause serious discomfort or pain, sometimes for prolonged periods (months or years), and can do so generation-after-generation.

The welfare consequences of the cases listed above are readily apparent, but there is a need for research into, and assessment of the welfare consequences of, very many other phenotypic modifications. For example, although the pelage of many animals has been modified — there are long-haired strains of many animals: eg dogs, rabbits, cats, sheep — the consequences of this on quality of life (through, for example, possible impacts on thermoregulation, changes in prevalence of skin infections, ingestion of hair leading to occurrence of gastric hair balls) has received little direct attention. Similarly, research is needed into the welfare consequences of behavioural changes such as increased fearfulness.

Tackling the problems: treatment or prevention?

Considerable veterinary effort is involved in dealing with the problems that have arisen through anthropogenic selection. For example, interventions necessary due to difficulties at parturition in various farm and companion animal breeds, and the deployment of a wide range of surgical and medical treatments for problems arising because of morphological or other changes. Surgical methods have been developed, for example, for correcting or ameliorating many problems including excision of the lateral wall of the ear canal to treat chronic otitis in dogs, surgical correction of entropion (inversion of the eyelid) in various breeds, surgery on the skull to relieve the effects of syringomyelia in Cavalier King Charles spaniels (Rusbridge *et al* 2006), and 'mulesing' (surgical alteration of the conformation of the perineum) in sheep to reduce the likelihood of flystrike (Phillips 2009). Similarly, many pharmacological therapies are used in treatment of problems arising from anthropogenic selection (eg antibiotics in the treatment of otitis or skin-fold dermatitis in dogs).

From the welfare perspective, it is crucially important that as much effort as is directed to development and application of treatments, if not very much more, should be put into prevention. That is, into developing breeding strategies to tackle these problems. It is good to see many such initiatives gaining momentum (eg in this volume, Conington & Dwyer 2010; Lewis *et al* 2010; Rodenburg *et al* 2010). Increasingly, modern molecular genetic technology is being used to identify animals for breeding that are free of genes known to cause diseases. Often, such technology is not available but, whilst, in some cases this may constrain improvements, progress is frequently possible through selection based on phenotypic characters.

There is no doubt that this preventative approach — selection to eliminate or reduce the prevalence or severity of problems — can often work extremely effectively (given time). Whereas, if the focus is on treatment and breeding continues from animals that have been treated, prevalence and severity will tend to increase with time.

This is not an argument against treatment of genetic welfare problems. There is no down side to treatment of animals that are not going to become breeding stock or which can be constructively used in breeding strategies to tackle problems. What it does argue for, is harnessing evolution's power in tackling these problems at source through appropriate breeding strategies. A simple, low-tech approach would be simply to breed only from animals that have not needed any treatments — or, at the very least, being duly circumspect and cautious about breeding from (or, in the case of wildlife casualties, of releasing to breed) animals that have needed treatments. Where genetic tests are available for the detection of potentially harmful alleles or where several hereditary problems have to be tackled simultaneously, more sophisticated approaches may be possible, through detection of unaffected carrier animals, and advantageous.

Conclusion

Anthropogenic selection for particular traits, in pursuit of various economic or aesthetic interests, has resulted in many changes away from ancestral morphology, function and behaviour in domesticated animals. Recently, a very wide range of species has come to be kept and bred as pets and selection for arbitrary traits is gathering pace in these also. Selection can have profound adverse welfare consequences. Growing recognition of this is stimulating efforts to develop breeding strategies aimed at tackling some of the problems but much more needs to be done both to address existing problems and to prevent new ones arising.

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