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Challenges and paradoxes in the companion-animal niche

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Abstract

By definition, the companion-animal niche demands merely that animals must provide companionship. At first glance, this may seem easy enough, but the forces that contribute to success in this niche are complex. Indeed, success as a companion is rarely measured in terms of biological fitness, and empirical measures of the breeding value of stock remain elusive. The challenges in the niche are manifold and reflect the need for companion animals to show behavioural flexibility, an attribute variously labelled compliance, tolerance, and even forgiveness. The borders of the niche are blurred and there is often negligible communication between buyers and suppliers of companion animals. In addition, demand for a given phenotype is subject to considerable flux. Paradoxically, companion animals may be victims of their own success. We value the social feedback they provide and yet often leave them alone for lengthy periods. There is an inherent tension between the desire to share the company of these animals and the reality that some humans find an animal's need for social contact, and indeed many species-specific behaviours, unacceptable. Also, the animal-sense of owners may be declining, reflecting reduced community exposure to animals in non-companion contexts, such as on farms and as modes of transport. Often, in the case of dogs, the companion-animal niche is occupied by a breed that was developed to work in a specific role that required endless energy and high reactivity. We select for conformation and movement in what were once working animals and yet many owners reject animals for behavioural traits that were subject to scarcely any primary selection. Since neutering of companion animals is, for many excellent reasons, now so common, the genes of outstandingly suitable pets are routinely lost to the gene pool. Companion animals may be living longer and yet, as they age, the dog-human relationship can shift diametrically. Senior dogs often become less appealing to and yet more dependent on, and needful of attention from, their owners. In Australia, urban companion-animal ownership per capita is declining in tandem with falls in living space. Despite this reduced demand, the pet industry uses positive imagery and targeted research to promote pet acquisition, helping to maintain a situation in which supply generally exceeds demand. This results in the annual euthanasia of thousands of excess animals in shelters and pounds. The pet industry also motivates owners to be consumers so it is unsurprising that expenditure on pets in Australia is rising. Sometimes food is promoted as a means of demonstrating affection. In many developed nations, unfortunately, pet owners have the resources to respond to marketing (among other forces) by overfeeding animals, often to the point of obesity. Obesity is considered to be a significant welfare problem for companion dogs. In summary, it seems that these shifts and growing paradoxes are making the companion-animal niche more challenging than ever. Perhaps science will help make the niche more predictable, but this alone will not guarantee the welfare of the animals that occupy it.

Keywords: animal welfare, breeding, cat, companion, dog, domestication

Introduction

By definition, the companion-animal niche demands merely that animals must be capable of providing companionship. This sounds simple enough, but the term 'companionship' is difficult to define. For the purposes of this article, we define a companion animal as a domestic species that provides humans with social contact, rather than having to produce a product or perform a specific task. Capturing the concept of companionship and measuring success within it are challenging; the characteristics required for an animal to function effectively as a companion to a human are poorly specified and often depend on the precise circumstances in which an animal finds itself. They are also apt to change at any moment to accord with human shifts (Herzog 2006). Even something as simple as a changing fashion trend can lead to more or less demand for a given morphological phenotype. Changing family dynamics, such as the arrival of a new child, can also markedly alter owner expectations. This lack of specificity and stability can have devastating consequences for companion-animal welfare.

On the strength of their abundance alone, companion animals seem generally successful. However, supply usually outstrips demand and a mismatch between animal



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and owner can lead to inter-specific conflict, often resulting in abandonment or death of the animal. Thousands of companion animals are euthanased annually throughout the developed world (Patronek *et al* 1995; Kass *et al* 2001), including Australia (Marston *et al* 2004, 2005). Yet, somewhat paradoxically, companion animals have a flagship role in advancing animal welfare because people often judge the impact of a given intervention on the way they would feel about it if it were to be imposed on one of the animals sharing their household.

The aim of this paper is to discuss some of the challenges and paradoxes in the companion-animal niche. Where possible, ways in which these challenges may be met are suggested. The paper's primary focus is on dogs but many of the principles described apply equally to other companion animals, particularly cats and horses.

Defining successful companionship traits

The well-being of companion animals is profoundly dependent on their being able to fulfill the requirements of a specific human owner. This sounds simple enough but the factors that contribute to success in the companion-animal niche are so complex and idiosyncratic that it is difficult to predict, other than at the species level, which animals will be most effective. The niche has blurred rather than defined boundaries and flux in demand effectively renders the niche a moving target to those who aim to fill it. This is most apparent in relation to dogs, the companion animal species most commonly kept by households in Australia (Headey 2006) and the US (American Pet Products Association 2008). As Darwin (1889) intimated in his work on animal emotional expression, dogs have, through many generations of close collaboration with humans, acquired some humanlike capacities (Helton et al 2009). Perhaps as a consequence of this, the wide range of human personality types known to exist seems to be matched by those reported in dogs (Lev et al 2009). Alternatively, it could be argued that this is only because work on assessing temperament in animals has focused predominantly on companion animals and that, rather than being a product of the dog's relationship with humans, the traits reported for these animals may simply reflect general traits shared by most social animals.

Some dog owners prefer to have their companionship provided by large dogs, some small; some like particularly active animals, others prefer those that barely move; some like those willing to confront a stranger, others would be horrified by any sign of aggression, no matter what the provocation. Colour and coat length can make a difference to the perceived appeal of a given dog, as do less tangible characteristics, such as whether a dog is submissive, biddable or cute. A recent study indicates that some behavioural features are highly valued by almost all companiondog owners. These include the dog being safe with children, fully house-trained, friendly and obedient (King et al 2009). According to this study, most owners also want their dog not to escape from their property, to enjoy being petted and to display affection to their owners. Even if scientists were able to identify genes contributing to these features, it is unlikely that a rigid, one-size-fits-all approach to fulfilling the requirements that must be met by companion dogs will ever be successful.

Other companion-animal species face issues that are similar although often less marked. The demands placed on goldfish, rabbits and some pet birds tend to be minimal since, being confined to the house, they do not generally have to behave according to societal norms, but horses and cats are also subject to rejection if their individual behavioural traits are not well matched with owner requirements, expectations and handling and training abilities; all characteristics that are difficult to evaluate in advance.

To address this situation it is critical that we clearly define what behavioural and morphological features are desirable in our companion animals so that we can select for these features in intentional breeding programmes (as distinct from accidental and random matings, such as occur when owners fail to de-sex (neuter) their animals and manage them appropriately). It is also imperative that we clearly describe breed and species differences, so that purchasers can make informed purchasing decisions. An equally important approach is to use education to shape the expectations of companion animal owners. For example, those who do not expect a specific breed of dog to display behaviours typically exhibited by members of that breed should perhaps be dissuaded or even prevented from purchasing one.

Companion animal production

Assuming that we can identify a workable number of characteristics associated with success as a companion for a human, it should be possible to breed selectively for these characteristics in the species we choose to keep as companions. In non-companion domesticated species, selection of breeding animals most suited to the roles their offspring will be expected to perform has resulted in enhanced adaptation, reduced stress and, hence, improved welfare (Nicholas 2003). In most animal industries, breeding choices are determined by market forces and informed by advanced genetic sciences, such that social pressure to improve the welfare of animals can lead to the selection of traits desired by consumers. Unfortunately, this is not the case with companion animals, for three reasons.

First, breeding decisions are only rarely, if ever, adequately informed by feedback about how well an animal's progeny fulfill the companionship role. The sophisticated science that leads to the development of estimated breeding values in other domesticated animal species depends on feedback being received in relation to large numbers of animals kept within reasonably uniform environments (Nicholas 2003). Compare this with the companion-animal industry, characterised by thousands of small-time hobby breeders, many with no scientific training and limited experience, breeding a variety of diverse animals within totally unregulated environmental constraints. The numbers of animals owned by such breeders is often small, limiting breeding choices, and increased experience is not always accompanied by a sustained rise in the skill base of owners. There may also be few opportunities for breeders to obtain feedback about the

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Demographic group	Selection for good health	Selection for longevity	Selection for physical phenotype	Selection for behavioural phenotype	Likelihood of de-sexing	Likelihood of providing optimal healthcare
Responsible pet owner	$\uparrow \uparrow \uparrow$	↑ ↑	↑ ↑	$\uparrow \uparrow \uparrow \uparrow$	$\uparrow \uparrow \uparrow$	$\uparrow \uparrow \uparrow \uparrow$
Less responsible pet owner	↑	↑	1	↑	↑	1
Show owner/breeder	$\uparrow \uparrow \uparrow$	1	$\uparrow \uparrow \uparrow \uparrow \uparrow$	$\uparrow \uparrow \uparrow$	\downarrow	$\uparrow \uparrow \uparrow$
Commercial breeder	↑ ↑	1	$\uparrow \uparrow \uparrow \uparrow$	↑ ↑	$\downarrow\downarrow\downarrow$	$\uparrow \uparrow$
Working dog owner/breeder	$\uparrow \uparrow \uparrow$	↑ ↑	↑ ↑	$\uparrow \uparrow \uparrow \uparrow$	↑ ↑	↑ ↑
Accidental (backyard) breeder	↑	↑	$\uparrow \uparrow$	↑	↑	1
Responsible pet breeder*	$\uparrow \uparrow \uparrow \uparrow$	$\uparrow \uparrow \uparrow$	$\uparrow\uparrow\uparrow$	$\uparrow \uparrow \uparrow \uparrow$	$\uparrow \uparrow \uparrow$	$\uparrow\uparrow\uparrow$
* This could be commercial, show or hobby breeder.						

Table I Hypothesised importance of various characteristics to different dog-owning and dog-breeding groups (the more arrows, the more important we believe the characteristic may be to that group).

quality of the puppies they produce. In the short term, feedback, when it is provided, comes primarily in the form of puppy sales for some breeders and show-ring performances for others. Neither of these measures is necessarily related to long-term performance as a companion animal, since this is impossible to assess in the show ring or in immature animals. Only the most reputable breeders track their puppies' health and welfare for life and so obtain more comprehensive feedback. Even then, this may not be available until after a bitch has produced several litters.

This situation is at odds with basic Darwinian principles dictating that reproductive success should be determined by biological fitness - the degree to which an organism 'fits' its biological niche. The extraordinary lack of feedback on an animal's success as a companion is one of the greatest challenges for success in the companion-animal niche (McGreevy & Nicholas 1999). Rather than evolving to live with a specific group of familiar conspecifics, it could be said that, with domestication, dogs have developed the ability to live successfully with many other dogs, including both familiar and unfamiliar animals, and with familiar and unfamiliar humans. Doing so successfully previously had a profound impact on which dogs successfully reproduced (those perceived to be safe and with the reduced flight distance necessary to gain access to human food scraps). However, despite the continued importance of this trait, almost no selection pressure currently comes to bear on the ability of animals to cope with the transition from litter to inter-specific living.

Related to this challenge is the second problem, a lack of accountability. A pig or hen producer who produces defective stock quickly loses repeat business and soon runs out of customers. Not so for breeders of companion animals. Rarely is there a link between breeder and product sufficient to hold the breeder accountable if the animal is defective as a companion. Instead, there is often negligible communication between demanders (owners) and suppliers (breeders). In addition, most people own only a few companion animals during their entire lifetime, so repeat business is inconsequential in determining the success or failure of a breeding enterprise. This is important because many of the animals currently used as companions were traditionally produced for another reason, with quite different specifications. With dogs, for example, the companion-animal niche is often occupied by a breed that was developed for a specific type of work. It has been argued that Darwinian selection should promote the regulation of brain states associated with *pleasant* feelings such that activities that advance biological fitness are rewarded (Kirkwood 2010). This probably explains why many breeds of dogs appear to enjoy the work for which they were bred (Kirkwood 2010). The problem is that the working niche differs so radically from the emergent companion niche. In an effort to preserve traditional breed features, breeders select for conformation and movement in what were once working animals and yet owners generally reject animals for behavioural traits that were subject to scarcely any primary selection. So, for example in Briards, selection pressure may be applied for a harsh coat and the mandatory double dewclaws mounted low on each rear leg (morphological features considered suitable for herding and guarding sheep) but some dogs may fail to succeed in the companion niche because they develop separation anxiety, a trait not tested for. Unless producers are held accountable for their failures, this situation is not likely to change.

A third challenge relates to the fact that companion-animal neutering is, for many excellent reasons, now extremely common in most developed countries (see Table 1). This means that the genes of outstandingly suitable pets are routinely lost to the gene pool. Whether purebred or not, those animals undergoing the most informative test of their ability to be good companions (ie, being road-tested in responsible homes over a relatively long period of time) are presumably those most likely to be de-sexed. Unfortunately, far too much of what remains are animals owned by irresponsible owners who fail to conform to social norms, and those owned by breeders who may make breeding decisions on the basis of show-ring performances or commercial demand for puppies as potential companions. As described previously, neither judges nor puppy buyers are in a position to identify or reward breeders who select for good 'companionship' traits. Further, in our opinion, some of the most difficult animals to manage (eg so-called status or macho dogs such as pit bull terrier types) tend to be owned by the least skilled humans with the worst reasons for keeping animals. The trend for these animals to enter the shelter population after having been bred, due to ignorance and reluctance to de-sex on the part of such owners, is troubling since it seems to be increasing the frequency with which this type of dog is presented for purchase or adoption (F McMillan, personal communication 2009). Shelters and pounds provide a filter before unwanted animals are returned to the public but may call upon humans with the best motives to deal with the behavioural legacies from someone else's training and management mistakes. This sector's inclination to adopt may wane as the shelter population morphs towards dogs of fighting types.

The challenges presented by the mismatch between current companion animal production and the traits needed for success in the companion-animal niche can be addressed only by radical restructuring of companion-animal breeding industries. The advent of microchips means that progeny should be traced more easily back to breeders, who could then be held accountable for producing animals with predictable faults (eg inherited disorders as the result of mating diseased parents). But, clearly, it depends upon a central record being kept, matching breeders with microchips for this to occur. Developing behavioural and genetic methods of assessing breeding stock for their suitability as companions will be critical in providing buyers with the tools they need to demand better quality animals, rendering companion-animal breeders subject to the same market forces that have led to changes in other animal groups.

Companion-animal socialisation and training

Two characteristics likely to rate highly on the list of features desired in companion animals are docility and behavioural flexibility, an attribute variously labelled compliance, tolerance, and even forgiveness. Yet, selection that concerns itself solely with either of these traits may have paradoxical effects. Selection for docile animals may be accompanied by low central and circulating concentrations of androgenic steroid and high HPA-axis reactivity (Korte *et al* 2010). This may increase susceptibility to distress through, for example, separation from an attachment figure. There is an inherent tension between the desire to share the company of these animals and the reality that

some humans find an animal's need for social contact and indeed many species-specific behaviours unacceptable (McGreevy 2009). We value the social feedback they provide and their apparent dependence on us as attachment figures, yet often leave them alone for lengthy periods likely to challenge their capacity to adapt (Masters & McGreevy 2007; McGreevy & Masters 2007).

Selection for behavioural flexibility may also be inherently risky if it increases the importance of early experiences in shaping the adult animal. The behaviourist, JB Watson (1930) famously claimed that he could take any human child and create an adult with characteristics of his choosing, purely by manipulating environmental contingencies. With advances in our knowledge of behavioural genetics very few scientists would now endorse the view that human behaviour is quite as malleable as Watson believed. Nevertheless, we acknowledge that poor or abusive parenting during critical developmental periods can lead to ongoing difficulties for children (Hoeve et al 2009). The more flexible the behavioural repertoire of a species, the more critical it is to ensure that developmental opportunities are carefully designed to equip the animal for its adult life. Yet, even if they have acquired companion animals during their socialisation period, modern owners are likely to lack the discretionary time required to socialise their animals adequately, and also (due to the urban nature of most developed countries) typically have far less 'animal-sense' since they lack exposure to animals on farms and in other contexts to inform their socialisation and training practices.

Ideally, we should perhaps be aiming not for behavioural flexibility but for animals suited primarily to the companionship role even in the absence of absolutely optimal training and socialisation. Unfortunately, achieving this aim is made difficult by the previously mentioned reality that, within this niche, the demand for animals of a given phenotype is subject to considerable flux. For example, technology is shifting to the extent that it is difficult for some humans, let alone non-humans, to keep up. The responses of dogs when first encountering glass barriers and mirrors illustrates this point (McGreevy 2009). Social circumstances are also increasingly dynamic. Whereas it was previously common for a family to occupy a single residence for many years, modern living is characterised by smaller dwellings, higher density living and frequent relocation. Companion animals are expected to cope with constant change and most do so admirably. However, this flexibility may come at the expense of behavioural predictability if, as the animal becomes more flexible in its behaviour, we become less able to predict how it will behave in any given circumstance. This may lead to ongoing adaptation challenges for some animals and their owners.

Health and longevity

Desirable behavioural characteristics may be fluid and difficult to identify, but surely we can at least agree that companion animals should be healthy and long-lived? Or perhaps not! As discussed previously, people who breed companion animals are often influenced by fads and

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fashions (for certain breeds and even types within breeds) rather than by forces that will determine the long-term welfare of the animals they produce (Herzog 2006). This has resulted in the creation of numerous animal breeds that are inherently defective (McGreevy 2007).

Living in spaces with humans can be associated with health risks (to the animals themselves) from allergies (Walton 1967) and even neoplasia (eg from exposure to tobacco smoke) (Milberger *et al* 2009). To give a related feline example, the companion-animal niche brings cats far closer to motor vehicles than would otherwise be the case. This increases the risk of injury and death. Similarly, where anthropogenic food sources are abundant, the niche may facilitate dense populations (Case 2003) that permit the spread of pathogens such as Feline Immunodeficiency Virus (FIV) and *Mycoplasma haemofelis* (formerly known as *Haemobartonella felis*).

Paradoxically, poor breeding choices often provide work for the veterinary profession (McGreevy & Nicholas 1999) such that the nature of the profession has undergone a wholesale change and, some would argue, it is losing its *raison d'être* and perhaps even its credibility in the eyes of governments (Leighton 2004). Using advanced technologies (such as caesarean sections) to enable reproduction in animals that would not otherwise be fit to reproduce in biological terms (such as bulldog females with narrow pelvises) merely perpetuates the genetic problems currently observed in some popular companion-animal species.

Using advanced veterinary techniques to keep animals alive can also have deleterious effects on animal welfare. For example, companion animals may be living longer and yet old age is a time when dog-human relationships can shift diametrically. As they age, dogs become less appealing to owners and yet more dependent on and needful of attention from their humans. Specifically, Marinelli et al (2007) showed that as the length of the relationship increased, owners tended to pay less attention to their dogs, while dog attachment to the owner increased. Thousands of adult dogs and cats are euthanased in shelters and pounds annually in Australia (Marston et al 2004, 2005) and elsewhere (Patronek et al 1995; Kass et al 2001) because the benefits they provide to owners are no longer seen to justify the costs. It is possible that the socalled throw-away society has rendered keeping an animal for many years and maintaining it during the aging process no longer a realistic proposition for many people. The need for education of people considering acquisition of a companion animal is clear. This should permit a costbenefit analysis of companion animal keeping, although who should develop and provide the education, and how it should be paid for, remain unknown.

While the increased availability of resources and veterinary therapeutics may enable many much-loved pets to receive the veterinary care they require, it may also have had the paradoxical effect of rendering health problems less serious from the owner's perspective — again taking the pressure off breeders, owners and pet food companies, all of whom should be taking measures to prevent health problems from arising in the first place.

The veterinary industry is not the only one perpetuating some of the problems confronted by our companion animals. In Australia, urban companion-animal ownership per capita is declining (Australian Companion Animal Council [ACAC] 2009) in tandem with falls in living space. Despite this reduced demand, the pet industry uses positive imagery and targeted research to promote pet ownership and breeding, helping to maintain a situation in which supply generally exceeds demand, resulting in the annual euthanasia of thousands of excess animals in shelters and pounds (Patronek et al 1995; Kass et al 2001; Marston et al 2004, 2005). The pet industry also motivates owners to be consumers so it is unsurprising that expenditure on pets in Australia is rising (ACAC 2009). Sometimes food is promoted as a means of demonstrating affection. In many developed nations, unfortunately, pet owners have the resources to respond to marketing (among other forces) by overfeeding animals, often to the point of obesity (McGreevy et al 2005, 2008). Obesity is considered by some authors to be one of the most significant welfare issues confronted by companion dogs (Robertson 2003; Colliard et al 2006).

The luxury of companion-animal ownership is more affordable for many, but increased affluence has been accompanied by a sharp fall in the time available to be spent with animal companions. As far as horses are concerned, the increased demand for leisure horses that amount to companions has been accompanied by declines in the availability of peri-urban pasture and in the average skill set of owners. As a result, horses are stabled unnecessarily and often become unmanageable for novices (McGreevy & McLean 2007). In addition, there is tension between the need for horses to be reactive athletes and the danger that this reactivity brings to the humans who ride them (McGreevy 2007).

Animal welfare implications

In summary, companion animals are successful in spite of, rather than because of, recent trends in selection practices that operate in competitions for excellence in conformation. It is remarkable that both pedigree and non-pedigree dogs so often fit the companion-animal niche without intentional selection for temperament. Furthermore, it seems that growing paradoxes are making the companion-animal niche more challenging than ever. Perhaps science will help make the niche more predictable, but this alone will not guarantee the welfare of the animals that occupy it.

There is a need for better education of potential companionanimal purchasers so that their expectations are realistic and their skills are adequate; this will improve their ability to meet the behavioural needs of their animal companions. This need is matched by the necessity for improved and more frequent feedback between companion-animal purchasers and breeders and increased accountability of breeders.

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