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Review

Hybrid vigour in dogs?

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ABSTRACT

Evidence from other species justifies the hypotheses that useful hybrid vigour occurs in dogs and that it can be exploited for improved health, welfare and fitness for purpose. Unfortunately, most of the relevant published canine studies do not provide estimates of actual hybrid vigour because of inadequate specification of the parentage of mixed-bred dogs. To our knowledge, only three published studies have shed any light on actual hybrid vigour in dogs. There are two reports of actual hybrid vigour between Labrador and Golden retrievers, the first ranging from +2.5% to –6.0% for components of a standardised applied-stimulus behavioural test, and the second being at least +12.4% for chance of graduating as a guide dog. The third study provides a minimum estimate of negative actual hybrid vigour: crossbreds between Labrador retrievers and poodles had a higher prevalence of multifocal retinal dysplasia than the average prevalence in their purebred parent breeds. The lack of estimates of actual hybrid vigour can be overcome by including the exact nature of the cross (e.g. F1, F2 or backcross) and their purebred parental breeds in the specification of mixed-bred dogs. Even if only F1 crossbreds can be categorised, this change would enable researchers to conduct substantial investigations to determine whether hybrid vigour has any utility for dog breeding.

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Introduction

> '. . . both with plants and animals, there is abundant evidence, that a cross between very distinct individuals of the same species, that is between members of different strains or sub-breeds, gives vigour and fertility to the offspring.' (Darwin, 1859a)

Evidence from other species justifies the hypotheses that useful hybrid vigour occurs in dogs and that it can be exploited for improved health, welfare and fitness for purpose. The aims of this paper are to summarise relevant evidence from other species, to review the available evidence for hybrid vigour in dogs and to suggest a change in data collection that could dramatically increase the ability of researchers to determine whether useful hybrid vigour exists in dogs.

The study of hybrid vigour, and its converse, inbreeding depression, traces back at least as far as Charles Darwin, who was the first scientist to examine the phenomenon in a systematic manner (Darwin, 1876). Hybrid vigour is synonymous with heterosis and with crossbred vigour. It is the extent to which the average performance of first-cross (F1) individuals for a specified trait is superior to the average performance of their parental strains/breeds for that same trait (Nicholas, 2010). It should be noted that it is possible for heterosis to exist for a certain trait and yet for the average performance of one of the parental strains/breeds for that trait to be greater than the average of the F1 hybrids. It should also be noted that there is variation around the F1 average for any trait, meaning that some individual F1 animals may not show any of the heterosis that exists for that trait in that cross.

Evidence of hybrid vigour in other species

Hybrid vigour is best characterised in corn (maize; *Zea mays*). The possibility of exploiting hybrid vigour in maize appears to have been first documented by Beal (1876), who was very likely influenced by Darwin's ideas through being a Harvard student of Asa Gray, one of Darwin's most intimate and long-standing correspondents. The commercial production of hybrid maize revolutionised agriculture (Troyer, 2009). One of the main reasons for this success is illustrated in Table 1, which shows that hybrid vigour results in greater than double the parental average yield (i.e. results in more than 100% increase in yield).

In livestock, the benefits of hybrid vigour are significant, but nowhere near as great as those for maize, mainly because the parental lines are only partially inbred (compared to maize parental lines, which are, in effect, 100% inbred). In poultry, for example, hybrid vigour varies from around 3–9% for egg number to around 14–23% for egg mass, with other reported traits being within that range: bodyweight at various ages (4–22%), survival (5%), egg production and age at sexual maturity (8%), and egg number (10–17%) (Flock, 2000; Ledur et al., 2003; Lalev et al., 2014). Notably, it

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Table 1
The extent of hybrid vigour for average yield (kg/ha) in maize in the 1930s and the 1980s (after Troyer, 2006). The huge increase in average yield of inbred lines between the 1930s and the 1980s is due to selection within outbred populations from which inbred lines are created, to selection among inbred lines, and to improved agricultural practice.

	Inbred parents	First-cross (F1) hybrids	Hybrid vigour	% Hybrid vigour
1930s	2027	5270	3243	160%
1980s	4506	9164	4658	103%

has been shown that hybrid vigour for egg number and egg mass increases with the extent of genetic diversity between the parental lines, as measured by tens of thousands of DNA markers covering the entire genome (Amuzu-Aweh et al., 2013).

In pigs, estimates of hybrid vigour range from around 0% for backfat thickness to around 5–6% for number of piglets weaned, weaning weight and post-weaning gain, with food conversion ratio being intermediate (around 3%).[1] The pig data underline a critical attribute of hybrid vigour, namely that it tends to decrease as heritability increases: the pig traits with greatest hybrid vigour have heritabilities in the range from around 0.10 to 0.35, while the trait with zero hybrid vigour has a heritability of around 0.55. The reason for this trend is that the extent of heterosis for a trait depends on the extent of non-additive gene action at loci affecting that trait; the higher the heritability, the lower is the relative contribution of non-additive genetic variation (Falconer and Mackay, 1996).

In sheep, typical estimates of hybrid vigour for average lamb weight per ewe vary from 15 to 20% (Shrestha et al., 1983) and for survival from 9 to 15% (Ferreira et al., 2015).

In beef cattle, hybrid vigour ranges from around 1% for carcass grade to around 6% for post-weaning gain (Long, 1980; Williams et al., 2010). The extent of hybrid vigour is similar in dairy cattle, ranging from around 2–4% for production of milk, fat and protein and for response to treatment for reproductive diseases, to around 10–15% for fertility and longevity (Van Raden and Sanders, 2003; Sørensen et al., 2008; Buckley et al., 2014).

Many of the traits mentioned above are, of course, not relevant to dog breeding. They have been included in this review to illustrate the following principles of hybrid vigour that apply to all animal species.

Principles of hybrid vigour

Four compelling generalisations emerge from scrutiny of the livestock literature on hybrid vigour.

First, the lower the heritability of a trait, the greater is the expected hybrid vigour. Since fitness traits tend to have low heritability, hybrid vigour tends to be greatest in traits most closely associated with fitness (i.e. reproduction and viability). This is potentially good news for dog breeders because fitness traits (e.g. disease resistance and longevity) are of value in companion dogs.

Second, the greater the genetic diversity between the parental populations, the greater is the expected hybrid vigour in crosses between them. As explained by Nicholas (2010), the theoretical expectation is that the greater the difference in gene frequencies between the two populations being crossed, the greater is the hybrid vigour in the F1 offspring. Compelling evidence to support this expectation includes the comparison between the extent of hybrid vigour in crosses from inbred maize lines (that have the maximum difference in allele frequency between lines at a large proportion of loci, namely those for which they are homozygous for different alleles) and from breeds of livestock (that have far smaller difference in allele frequency at many loci, namely those loci at which the same alleles are segregating in more than one breed); and the evidence in chickens of greater heterosis in crosses between more genetically-divergent breeds. Strictly speaking, this principle applies to genetic diversity at only the loci that contribute to variation in the trait of interest. In practice, genomic estimates of genetic diversity are a very useful proxy.

Third, breeding from hybrids dissipates hybrid vigour. For example, offspring of two F1 animals are expected to have only half the hybrid vigour of the F1 animals themselves (Nicholas, 2010). In other words, for any trait, the expected average performance of the offspring of two F1 animals is halfway between the expected average performance of the F1 animals and the average of the performance of the two parental populations.

Fourth, the more inbred the parents, the greater the hybrid vigour in their crossbred offspring, i.e., hybrid vigour is the mirror image of inbreeding depression (Nicholas, 2010). This is well illustrated by the large difference in the level of hybrid vigour summarised above for maize (more than 100%) and livestock (less than 25%, and often less than 10%).

The inbreeding coefficient (F) of an individual is the probability that the two segments of DNA present at a site on a pair of chromosomes in that individual are identical by descent. It can be calculated as one half of the relationship between the parents of the individual. Contrary to popular belief, the inbreeding coefficient is *not* a measure of the extent to which an individual is homozygous. It is actually a measure of the extent to which an individual is *less heterozygous* than individuals in a reference (base) population assumed to be unrelated with zero inbreeding (Nicholas, 2010). The inbred lines used in the breeding of F1 hybrids in maize are, in essence, completely inbred, i.e. have an F of around 1 (Fig. 1). In contrast, results of pedigree analyses suggest that the average inbreeding coefficients of parental lines used in the production of livestock hybrids are far closer to zero than to 1. As shown in Fig. 1, pig breed-average F ranges from 0.01 in Czech Pietrain (Krupa et al., 2015) to 0.18 in US Landrace (Welsh et al., 2010); sheep breed-average F ranges from 0.01 in Navajo-Churro (Maiwashe and Blackburn, 2004) to 0.08 in Iran Black (Mokhtari et al., 2014); cattle breed-average F ranges from 0.01 for Brown Swiss (Worede et al., 2013) through 0.03 for UK Holstein-Friesian (Kearney et al., 2004) to 0.08 for Canadienne (Melka et al., 2013). It is obvious that livestock are at the other end of the inbreeding spectrum compared with inbred lines of maize. Such relatively low breed-average inbreeding coefficients of livestock parental strains explain why the gains

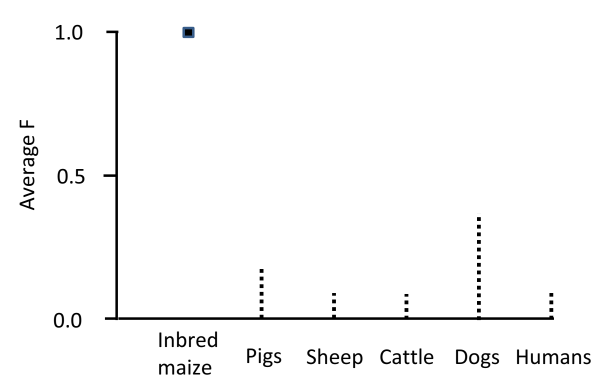

Fig. 1. A comparison of the range of average breed or population inbreeding coefficients (average F) in inbred maize and in pigs, sheep, cattle, dogs and humans. References for each of the ranges are cited in the text.

[1] See: Department of Agriculture, Fisheries and Forestry, 2010. Improving your herd with genetics. http://www.daff.qld.gov.au/animal-industries/pigs/improving-your-herd-with-genetics/heterosis (accessed 26 January 2016).

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