by a species that would prevent total adaptation. This is illustrated by the development of ever more elaborate and precise displays by many species living in relatively stable tropical environments, and the conservation of variation in animals living in more variable environments. Individual differences may also arise as a result of the advantages associated with **kin recognition** and the communication of individual identity (e.g. to prevent unnecessary **agonistic behaviour**).

The importance of individual differences in animal management, **conservation** and **welfare** is increasingly recognized as increased emphasis is focused on the importance of the individual's welfare and its value as a genetic resource. Different individuals may respond to a similar disease challenge or load from a **stressor** differently as a result of individual differences (personal risk factors), and so the physical and psychological **health** of an individual cannot be understood fully without an appreciation of the individual that is affected.

Recognition and appreciation of this is one of the essential skills of a good clinician. One of the challenges of medicine and the development of good husbandry practices is the identification of significant risk factors of clinical relevance relating to individual differences, i.e. those factors that are of real importance, and this will vary with the condition under consideration. For example, in the case of a potentially fatal problem, small risk factors relevant to small individual differences are important but, in the case of less serious conditions, such variation may be of less relevance.

To date, most work has focused on physical differences, e.g. skin colour and the risk of squamous cell carcinoma in cattle and cats, with less attention generally paid to behavioural and psychological differences, despite their potential importance in susceptibility to even infectious disease. The notable exception to this is the study of individual differences in behaviour as a risk of behavioural problems, e.g. **aggression** and the risk of **cannibalism** in chickens, attachment behaviour and the risk of **separation anxiety** in dogs, etc.

An appreciation of the importance of individual differences in behaviour is therefore important to many aspects of applied animal behaviour and welfare. (DSM)

References and further reading

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Individual fitness

Evolution by natural selection is a potent force of adaptive change. Simply put, those individuals whose genes spread through the population have greater **fitness** than those whose genes do not. An individual's genes can spread directly and/or indirectly, and this distinction is important. **Charles Darwin** recognized possible ways that his hypothesis of natural selection could be challenged if individuals did things that directly benefited others at some cost to themselves. For instance, we often see animals helping feed or care for others or emitting potentially costly alarm calls. How could these potentially costly behaviours be adaptive to individuals? The solution is that individuals share genes with relatives (they share more genes with close relatives and fewer with more distance relatives (**see: Kinship**) and, by helping relatives survive and reproduce, individuals are helping their own genes survive and reproduce.

The British geneticist J.B.S. Haldane once said that he'd be willing to sacrifice his life for two brothers or eight first cousins. Working though the maths, we see that saving two brothers will generate 1 fitness unit (2 brothers × 0.5, the coefficient of relationship between an individual and a full sibling), as will saving eight first cousins (8 × 0.125, the coefficient of relationship between an individual and his first cousin). Thus, Haldane's back of the envelope calculation was correct.

There are a number of common confusions about the term fitness. Darwinian fitness is often mistakenly confused with physical condition. Evolution by natural selection does not inevitably select those in the best condition to reproduce; rather, those that reproduce have the highest Darwinian fitness. Envision an elephant seal. We typically think that large-bodied males are better able to defend harems and therefore have higher reproductive success. In most years this is certainly so, and we see the largest males obtain the most copulations and sire the most young in a colony. However, what happens when insufficient food is available? We know that, in such conditions, females of some species may save energy by not breeding. Because large-bodied individuals require absolutely more energy than smaller-bodied ones, large males may be the most vulnerable individuals when food is drastically restricted. In this case, small-bodied individuals might survive and be alive to reproduce the following year. Thus, the largest animals, in apparently the best physical condition, might not have the highest fitness.

Elephant seals also illustrate another strategy. Large males exert a lot of energy defending their harems and fight viciously with other large males. Smaller male elephant seals look more like females. Because they have no chance of winning a fight with a large male, they do not try. Rather, on occasion, smaller males will try to mate with a female in a large male's harem. These males are referred to as 'sneakers', and this illustrates a condition-dependent strategy whereby large males fight for reproductive success and smaller males try to steal it. Such condition-dependent strategies are common and illustrate another way that 'being in the best physical condition' may not necessarily translate to having the highest fitness.

Fitness is a relative concept. Fitness will not lead to the best conceivable individuals or traits. Rather, heritable traits will evolve so that populations consist of individuals with those beneficial traits. When conditions change, what determines the best trait might change, and thus we will have selection for another trait. Moreover, traits do not evolve to some '**optimal** fitness'; rather, traits evolve such that individuals with them do better than individuals without them.

Fitness is constrained in many ways. The fluctuating selection described above, whereby large animals might be favoured in years of plenty and smaller animals might be favoured in sparse years, will maintain heritable variation and prevent fixation of a particular trait. Additionally, if there are genetic correlations among traits, selection for a particular trait may be constrained by its correlated trait. Since we expect traits to be correlated, and since linkage is common, 'optimal fitness' will not be seen.

Individuals act in many other ways to maximize their individual fitness. Any time we see animals acting in ways that favour their personal survival, we see evidence of animals behaving in ways that suggest that individual fitness is important. Consider a fight between two male bull elk (a large deer). These opponents have a formidable set of weapons – large, multi-pronged antlers. When two opponents meet they engage in a complex assessment ritual. They bugle, because the lowest frequency of an individual's **vocalization** is directly related to body size (larger animals produce lower-frequency vocalizations). This is an unbluffable display, and many potential competitors simply avoid larger opponents. They engage in parallel walks whereby opponents 'size each other up'; they lock antlers and push a bit. Only if very well matched will individuals initiate full-scale combat, because combat is risky. Animals could break a leg by falling, or be skewered with an antler. If an individual is small, and therefore likely to lose, it is much better to run away and come back and fight another day.

Fatal fighting is thus rare, and the conditions under which we see it are revealing. Fatal fighting is seen when the magnitude of direct benefit is large, and there is considerable skew in who obtains it (meaning that not all individuals will be able to obtain a needed resource) and when individuals have only a limited period of time to obtain it. In a mating context, we expect to see fatal fighting among animals with little residual reproductive value (i.e. among older ones that will die soon). We also expect to see more fatal fighting in species that have extremely short lives with a very circumscribed mating period. (DTB)

Infanticide

Infanticide is 'a behaviour that makes a direct and significant contribution to the immediate death of an embryo or newly hatched (born) member of the performer's own species' (Mock, 1984). Infanticide by males and non-relatives occurs in many species, generally serving to increase the fitness of perpetrators (e.g. male lions have been reported to kill nursing cubs after a pride take-over in order to trigger females' return to receptivity). The phenomenon of mothers killing their own infants has been documented in diverse mammalian species including humans, **elephants**, silver foxes, **rodents** and domestic **dogs** and **cats**. Mothers of other species, including those commonly kept on farms, as companions, in laboratories or otherwise in association with humans, occasionally display violent behaviour towards their newborn.

Domestic ruminant mothers such as cows and ewes are rarely overtly violent, but neglect or abandonment will lead to the death of a minority of infants. Perhaps because it is so unpleasant, infanticide has frequently been described as an **abnormal** behaviour, but is probably more accurately characterized as a normal response to a particular set of circumstances. Sarah Blaffer Hrdy (1979) suggested that mothers might increase their **inclusive fitness** by killing their infants because of their low social status, in response to lack of resources, due to disturbance or because infants were abnormal or too numerous. All of these factors decrease the probability of offspring surviving to sexual maturity, and killing infants reduces the mother's investment where the probability of successful rearing is low.

The maternal repertoire of the domestic **pig** includes some of the most violent acts of any seen in commonly farmed species. The phenomenon was referred to in the 1920s as 'parturient psychoneurosis', and as 'hysteria' as recently as the 1980s. In pigs, 'savaging' starts during or soon after farrowing. The sow, which may or may not be generally restless, threatens and may attack piglets that are close by. The attacks can result in injury or death of one or more piglets, or occasionally of a whole litter. Savaging episodes can be very brief, consisting of a single or a few snaps, or continue for several hours in the absence of intervention. **Aggression** may spontaneously cease at any time, or may stop once piglets start to suckle. Savaging is not generally followed by **cannibalism** of dead piglets.

Reports of the frequency of savaging have varied widely: levels may change with time and it has been reported to be a 'contagious' behaviour, occurring in sporadic outbreaks. A large-scale Canadian survey of commercial hybrid pigs reported that 3.4% of gilts (first-parity sows) and 1.2% of multiparous sows killed one or more piglets. Counting dead piglets alone will certainly underestimate the magnitude of aggressive behaviour: studies involving videotaping of farrowing in farmed wild boar and domestic gilts observed that 30% displayed some aggression towards their newborn, although few attacks resulted in **injury** or fatality. In common with many species where **mis-mothering** is more common in young females, savaging occurs more frequently in sows having their first litters, and there is some evidence that sows which savage their first litters are more likely to be infanticidal with subsequent litters. Gilts that savage at their first parity may not be kept by farmers for a second farrowing.

Traditionally, pig farmers might treat the savaging sow with a diverse range of home remedies, which included giving her beer, perhaps due to the now discredited belief that the behaviour arose due to extreme thirst, smearing her face and the backs of the piglets with a kipper, smacking her with the body of a dead piglet or the application of a rubber boot top, secured with string, around her snout. Modern treatments include the administration of sedatives such as azaperone and/or temporarily removing the litter until the sow has calmed down.

Wild boar farrow in secluded nests under dense cover; hence, the degree to which they or free-living sows giving birth in semi-natural conditions are infanticidal (if at all) is unknown. While it is unlikely that savaging is a **captivity**-induced behaviour, intensive production might increase its occurrence. The effect of the farrowing environment is unclear – it has recently been reported both that the behaviour is more frequent in open pens than in **farrowing crates** and that there is a tendency for more savaging when gilts farrow in crates.