and that the killing of animals can be justified. Adherents of animal rights, on the other hand, claim that the killing of a healthy animal is a violation of its right to life. (PS)

See also: Pest control – ethics of; Slaughter

Further reading

Sandøe, P. and Christiansen, S.B. (2007) The value of animal life: how should we balance quality against quantity? *Animal Welfare* 16, 109–115.

Kin recognition

Social recognition (i.e. recognition of individuals or various categories of **conspecifics**) is a necessary basis of living in stable social groups in which individuals communicate and interact. As part of this, kin recognition – that is, recognition of genetically related invividuals – has been widely studied, particularly since the work of Hamilton (1964) and his concept of **inclusive fitness**.

The concept of inclusive fitness states that the global fitness of an individual consists of his/her own reproductive success, together with the improvement in **individual fitness** that the individual can provide to related animals. Hamilton's theory, namely **kin selection**, thus suggests that helping one's relatives to reproduce benefits the helper by improving his/her inclusive fitness (proportionally to the genetic proximity of the receiver). This implies that related individuals have to be recognized and therefore makes kin recognition a prerequisite of the kin selection theory.

A large number of behaviours indicative of nepotism (i.e. preferentially helping related individuals), and supporting Hamilton's theory, have been observed across species. Parental investment, alarm calls, greater tolerance during competition, support during social interactions or **grooming**, for instance, preferentially directed towards kin, are discriminative interactions that suggest that these related individuals are recognized.

Nepotism and optimal **mate choice** are usually the two main accepted benefits of kin recognition. With regard to kin selection, being able to recognize one's relatives is clearly adaptive as it facilitates the expression of nepotism by identifying the individuals to whom this behaviour should be directed. Kin recognition can also improve direct individual fitness and be of welfare importance. For instance, recognizing one's own mother increases survival, especially among species in which only the mother takes care of her young. In the context of mate choice, Bateson's (1983) theory of optimal outbreeding hypothesized that kin recognition would prevent **inbreeding** and favour the choice of the optimal mate (i.e. neither genetically too close nor too far).

Mainly since the 1980s have the mechanisms and sensory basis underlying kin recognition been widely studied. The term 'recognition' relates to the cognitive mechanisms (i.e. neural processes) enabling animals to classify conspecifics in different categories, whereas **discrimination** corresponds to the expression of different behaviours towards different individuals. As recognition is not visible, discrimination is therefore usually used to infer it, but it should be noted that the absence of discrimination does not necessarily imply the absence of recognition. In experimental situations, the existence of kin recognition can be assessed through tests based, for instance, on the simultaneous or successive presentation of kin versus non-kin individuals. In the simultaneous choice test paradigm, it is not only the existence of recognition that is evaluated but also the existence of a preference for kin. In any case, kin discrimination is inferred through either the observation of affiliative behaviours (e.g. physial proximity, grooming, play) or the absence of **agonistic behaviours**.

Four main mechanisms of kin recognition were first proposed: spatial recognition, recognition genes, direct association and phenotype matching.

Spatial recognition is based on the geographic localization of individuals (e.g. being in the same nest). However, as animals then behave discriminatively towards kin individuals based on environmental cues and not on their individual characteristics, it has been suggested more recently that spatial recognition should no longer be considered a mechanism of kin recognition.

The existence of recognition genes was suggested by Hamilton (1964), who hypothesized that a super-gene or group of genes would code for kin recognition. This theory has been named the 'green beard effect' by Dawkins (1982), and supposes the existence of an innate reference template in the brain. The existence of such genes has been widely discussed, and candidate markers relate to histocompatibility regions of the chromosome, e.g. the major histocompatibility complex (MHC) and other genes resulting in chemical discrimination.

Direct association and phenotype matching were initially considered as two dichotomous mechanisms until the late 1980s, when Richard Porter suggested the use of the terms 'direct familiarization' and 'indirect familiarization' corresponding to a single mechanism, familiarization. Recognition through familiarization is based on experience and appears to be the fundamental mechanism of kin recognition in many species. During direct familiarization, individuals become familiar as a result of direct contact (i.e. individual characteristics are learned and memorized) and are subsequently recognized.

This mechanism is thought to be the most widely found and has been demonstrated in numerous vertebrates using, for instance, cross-fostering or embryo transfer experiments. Non-kin young raised together then behave towards each other as if they were genetic siblings. In the context of indirect familiarization, individuals that have not been previously encountered are discriminated against based upon their phenotypic resemblance to the subject animal (a process called self-matching) or to one of their relatives with whom the subject is familiar (i.e. phenotype matching). In this case it is not individual but family characteristics (which are reliably correlated to the **genotype**) that are used. It has, for instance, been demonstrated that lambs display evidence of recognizing their twins from whom they had been separated at birth, as well as the twins of familiar partners. It should be noted that the recognition mechanisms cited above are not mutually exclusive.

The neural mechanisms on which kin recognition is based are still not exactly known. It is supposed that the animal builds templates that are memorized and against which a comparison of the characteristics of the individuals encountered can be made. But how these templates are built, where they are stored and how the matching is evaluated remain uncertain, even though some decision-making models have been suggested (Tang-Martinez, 2001).

Kin recognition depends on learning the phenotypic characteristics of kin individuals. This implies that those individuals have to: (i) wear labels giving information about their individual identity or the family group to which they belong; (ii) be able to perceive their conspecifics' labels and form an internal representation based upon them (i.e. a template comprising the traits of kin individuals) and to which the subsequently perceived labels will be compared; and (iii) evaluate the kinship of the individuals encountered thanks to a decision rule.

Complex phenotypical traits that are, to a certain extent, individually distinctive and will be used for recognition are called 'signatures'. The sensory basis used for kin recognition tends to depend on those that are predominant for communication in the species concerned (e.g. **olfaction** in rodents). Recognition can depend mainly on a single sensory basis or on several. In rodents, for instance, anosmic animals (i.e. those deprived of olfaction) are no longer able to discriminate their brothers from strangers. By contrast, in sheep, several studies have demonstrated that visual as well as acoustic cues and **odours** play a role in twin recognition and that the suppression of only one of those sensory cues does not disrupt recognition.

It has been shown that phenotypic signatures have a genetic basis and can thus indeed be used for kin recognition. However, such signatures, especially olfactory cues, can also be modulated by environmental factors such as the diet or maternal olfactory labelling (e.g. licking in the **cat**), which can then influence recognition. The development of kin recognition, its efficiency and the mechanisms used can also vary depending on several factors such as the learning period (e.g. pre- and postnatal learning), the kin individual's relationship (e.g. mother versus siblings), the **ecology** of the species and whether it shows temporal variation. (SL)

References and further reading

Bateson, P. (1983) Optimal outbreeding. In: Bateson, P. (ed.) *Mate Choice*. Cambridge University Press, Cambridge, UK, pp. 257–277.

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Hepper, P.G. (ed.) (1991) *Kin Recognition*. Cambridge University Press, Cambridge, UK.

Tang-Martinez, Z. (2001) The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behavioural Processes* 53, 21–40.

Kin selection

The term 'kin selection' is often used synonymously with the term 'indirect selection', but its original definition embraced the evolutionary effects of both parental care and descendent offspring and **altruism** directed at non-descendent kin (i.e. relatives other than offspring). Indirect selection encompasses only the latter. This definition recognizes that the evolutionary consequences of a parent helping a descendent offspring are in fact genetically identical to the 'parent' helping a full sibling. Thus kin selection is a process in which genes may increase in frequency when bearers help close relatives produce additional offspring, so long as the benefits of giving aid to relatives outweigh the genetic costs of giving up the chance to produce descendent kin themselves (i.e. Hamilton's rule is obeyed; **see: Inclusive fitness**). (PE)

Kinship

Animals may benefit from behaving preferentially towards their kin, and this simple insight has revolutionized the study of animal behaviour. One solution to the apparent paradox of **altruism** is that animals benefit not only by obtaining direct **fitness**, but also by helping relatives obtain fitness (**see: Kin selection**). Because relatives share genes, helping kin can help spread an individual's genes. This insight, solidified by the evolutionary biologist W.D. Hamilton, created the important aim of quantifying kinship.

Kinship, the probability that genes are identical by common ancestry, can be calculated from detailed genealogies or from molecular techniques that focus on estimating those identical alleles shared by descent. In diploid organisms, the sperm and egg each contain a single strand of DNA that are combined during fertilization and first expressed in the **zygote**. Because each individual in a litter or clutch obtains half its DNA from its mother and half from its father, parents and offspring have a coefficient of relationship (often abbreviated r) of 0.5. Within a litter, the exact genes passed on to an individual are likely to be different, but the coefficient of relationship between full siblings is 0.5. Grandparents and grandchildren similarly share a 0.25 coefficient of relationship, while first cousins have a 0.125 coefficient of relationship.

A general method of calculating the coefficient of relationship is to draw a genealogy and then sum the pathways by which two individuals could share genes. Each generational link is counted, and r = the number of pathways $\times\ 0.5^{L}$, where L is the number of generational links. (DTB)

Further reading

Krebs, J.R. and Davies, N.B. (1993) *An Introduction to Behavioural Ecology*, 3rd edn. Blackwell Scientific Publications, Oxford, UK.

Knowledge

Knowledge refers to that which is known; but the basis on which we know, as opposed to simply believe in, something is a source of considerable debate among philosophers. The philosophical study of knowledge is called **epistemology**. (DSM)

Kwashiorkor

Kwashiorkor is a type of **malnutrition** thought to be caused by insufficient protein consumption. It usually affects younger animals, especially when switching from a high-protein milk diet when nursing to a high-carbohydrate and -starch diet after weaning, and is most prevalent after famine or when the majority of the diet is uncharacteristically made up of starchy vegetables. Kwashiorkor is characterized by a swollen abdomen, alternating bands of light and dark hair and weight loss. (LMD)