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Evolutionary and Behavioural Aspects of Altruism in Animal Communities: Is There Room for Intelligence?

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1. The Paradox of Altruism

An individual animal can play different roles in communities in dependence of its sex, age, relatedness, rank, and last but not least, intelligence. An individual's path to the top of a hierarchically organised community may be paved by highly developed individual cognitive skills. A classic example came from Goodall's (1971) book *In the shadow of man:* Mike, the young chimpanzee, gained top rank at once by making a terrible noise with empty metal jerricans stolen from the researchers' camp.

At the same time, the upper limit of the individual's self-expression may be specified by the specific structure of communities. There are several variants of division of social roles, from division of labour in kin groups to the thin balance between altruism and 'parasitism' within groups of genetically unrelated individuals. Task allocation in animal communities can impose restrictions on the display of members' intelligence. For instance, rodents, termites and ants condemned to digging or baby-sitting or suicide defending can not forage, scout, or transfer pieces of information even if they are intelligent enough to do this. Furthermore, subordinate members of cooperatively breeding societies sacrifice their energy to dominating individuals serving as helpers or even as sterile workers.

Lev Tolstoy in his novel *Anna Karenina* focused attention on several dramatic dilemmas in women's life and among them the dilemma: to give birth to children or to stay in a family as a perpetual helper. In many novels of the 19th century lives of members of a facultative 'sterile cast', governess, were described: intelligent but poor members of the society often devoted their whole lives to caring for offspring of rich ones (recall, for example, Charlotte Brontë's Jane Eyre). Indeed, baby-sitting is one of the most costly and essential tasks in animal communities including human ones. Some members of communities serve as helpers that are physically able to breed, but most never will.

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To be serious, analysing the problem of division of roles in animal societies, we face the paradox of *altruism* – that is, the situation in which some individuals subordinate their own interests and those of their immediate offspring in order to serve the interests of a larger group beyond their offspring. That altruistic behaviour is possible did not always seem natural for biologists. Darwin's followers, and among them Thomas Henry Huxley, the most enthusiastic populariser of natural selection as a factor of evolution, concentrated mainly on inter- and intraspecific competition, arguing that the 'animal world is on about the same level as the gladiator's show' (Huxley 1893), and thus nature is an arena for pitiless struggle between self-interested creatures. This concerns also human beings, although Darwin himself discussed the idea of how altruism can evolve in human societies in *The Descent of Man* (1871). Kropotkin (1902) was one of the first thinkers who countered these arguments and considered mutual aid as a factor of evolution, in particular of human evolution. He viewed cooperation as an ancient animal and human legacy.

In contemporary evolutionary biology, an organism is said to behave altruistically when its behaviour benefits other organisms, at a cost to itself. The costs and benefits are measured in terms of reproductive fitness, or expected number of offspring. So by behaving altruistically, an organism reduces the number of offspring it is likely to produce itself, but increases the number that other organisms are likely to produce.

Eusociality can be considered an extreme form of altruism in animal communities because sterile members of a group sacrifice the opportunity to produce their own offspring in order to help the alpha individuals to raise their young. Evolution favours individuals whose inherited predisposition enabled them to behave in ways that maximise their reproductive success. What induces individuals to be engaged in behaviour that decreases their individual fitness?

Here is one of many interesting examples of biological altruism. The trade-off between individual sacrifice and colony welfare in social insects can be easily estimated in the cases of colony defence. Thus, in the green tree ant of Australia (*Oecophylla smaragdina*) ageing workers emigrate to special 'barrack nests' located at the territorial boundary of the colony. When workers from neighbouring nests or other invaders cross the line, guards are the first to attack and to be attacked (Fig. 1). Hölldobler and Wilson (1990) joke that a principal difference between human beings and ants is that whereas we send our young men to war, they send their old ladies.

Fig. 1. A major worker *Oecophylla smaragdina* in the aggressive posture. Transferred from en.wikipedia; Author Tuan Cao (en:User:Tuancao1)

Charles Darwin saw that the paradox of altruistic behaviour of animals, in particular, social insects, was dangerous to his theory of evolution by natural selection. In his *Origin of Species* (1859) Darwin thought that sterile workers in a bee colony, being unable to transmit their genes, represent a special challenge to his theory of natural selection. This is because natural selection depends on the transmission of traits that convey selective advantages to the individuals, and these traits have to be determined genetically (so they are heritable). If workers are sterile, how can they transmit the 'helping traits' to the next generation? Even more simple cases of cooperation in animal communities which are not based on differentiation between sterile and fertile castes can be difficult for evolutionary explanation in terms of individual fitness.

Analysis of these problems became possible on the basis of ideas of gene dominance and fitness outlined by Ronald Fisher (1925, 1930). Haldane (1932, 1955) suggested that an individual's genes can be multiplied in a population even if that individual never reproduces, providing its actions favour the differential survival and reproduction of collateral relatives, such as siblings, nieces and cousins, to a sufficient degree. This hypothesis later came to be known as *kin selection*, the phrase coined by Maynard Smith (1974). These ideas can be illustrated by the following construction. Suppose an organism produces offspring some of which are reproducing, while others are non-reproducing but help greatly in caring for the reproducing ones. Compare this strategy with producing only offspring that reproduce. For an individual offspring it is advantageous to reproduce itself, but since it has the genes of its parent, it will follow the same strategy, that is, produce only reproducing offspring. Since we supposed that a non-reproducing child helps greatly in caring for the others, we can see that the average number of grandchildren will be greater if some of the offspring are non-reproducing. Note that here we assume that all offspring (reproducing and non-reproducing) have the same genes, and have shown that it can be advantageous for the population that an individual with some probability (or better to say, under some circumstances) becomes non-reproducing. In this construction altruism is directed at the certain groups or nearest relatives (parents, siblings, *etc.*). However, sometimes models of less direct altruism are also considered. A popular (although somewhat speculative) example concerns behaviour in populations of wild rabbits. It is assumed that some rabbits drum with their hind legs when they see a predator instead of running immediately to the nearest hole. Being warned by this alarm signal, other rabbits have time to flee. Of course, this does not mean that the drumming rabbit makes a decision to sacrifice its own life to the community (Fig. 2). It simply acts in accordance with its inherited behavioural program. Some members of a group of rabbits give alarm drums when they see predators (because they have a hypothetical 'drumming gene') but others (that lack such a gene) do not. By selfishly refusing to give an alarm signal, a rabbit can reduce the chance that it will itself be attacked, while at the same time benefiting from the alarm signals of others. However, it is possible to show that, under certain conditions, if there are sufficiently many relatives among the recipients of the altruistic behaviour, then altruistic behaviour is promoted within the population. For details and discussion of this model and accompanied ideas see Grafen (1984, 2007), Axelrod *et al.* (2004), and Rice (2004).

Fig. 2. A bunny preparing to sacrifice himself. Cartoon by P. Ryabko

2. The Main Evolutionary Concepts of Altruism in Animals

In the 1960s and 1970s two theories emerged which tried to explain evolution of altruistic behaviour: '*kin selection*' (or '*inclusive fitness*') theory, due to Hamilton (1964), and the theory of *reciprocal altruism*, due primarily to Trivers (1971) and Maynard Smith (1974).

The main mechanism of kin selection is *nepotism*, that is, preferential treatment for kin. Many social species including humans form nepotistic alliances to keep the flag of family interests flying. There is much evidence that animals behave nepotistically when facing vital problems in their life. For example, pig-tailed macaques, when helping group members who were attacked, do so most readily for close relatives, less readily for more distant relatives, and least readily for non-relatives (Massey 1977). To do so, animals must recognise their relatives, but there is no a strong correlation between nepotism and recognition ability. For example, Mateo's (2004) data on closely related species of ground squirrels support a hypothesis that kin favouritism and recognition capacities can evolve independently, depending on variation in the costs and benefits of nepotism for a given species. A highly nepotistic species, *Spermophilus beldingi*, produces odours from two different glands that correlate with relatedness ('kin labels'). Using these odours ground squirrels make accurate discriminations among never before encountered unfamiliar kin. A closely related species *S. lateralis* similarly produces kin labels and discriminates among kin, although it shows no evidence of nepotistic behaviour.

For kin selection to occur it is not strongly necessary for individuals to recognise their kin. Returning to the example with rabbits that alarm its neighbours by drumming, it is not that these animals must have the ability to discriminate relatives from non-relatives, less still to calculate coefficients of relationship. Many animals can in fact recognize their kin, often by smell, but kin selection can operate in the absence of such an ability. If an animal behaves altruistically towards those in its immediate vicinity, then the recipients of the altruism are likely to be relatives, given that relatives tend to live near each other.

The ability to discriminate between kin and non-kin displays in many species, and is due either to the innate recognition of character traits associated with relatedness, or to the recognition of specific individuals with whom they have grown up. Nepotism is not always clearly altruistic and does not necessarily requiring genuine cognitive skills. For instance, most young plains spadefoot toads are detritivorous and congregate with kin. Some of the tadpoles become carnivorous, and such individuals live more solitarily and at least when satiated prefer to eat non-kin than kin, reducing the damage they might otherwise do to the survivorship of their relatives. Cannibalistic tiger salamander larvae *Ambystoma tigrinum* also discriminate kin and preferentially consume less-related individuals (Pfenning *et al.* 1999). Genetic analyses of numerous fish species have shown that shoals formed by larvae often consist of closely related kin (Krause *et al.* 2000). Recent experiments have shown that juvenile zebrafish can recognise and prefer their siblings to unrelated conspecifics based on olfactory cues (Mann *et al.* 2003).

Chimpanzees possibly solve much more complex problem of kin recognition. Mechanisms underlying male cooperation in chimpanzee communities are still enigmatic (van Hooff and van Schaik 1994). Chimpanzees live in unit groups, whose members form temporary parties that vary in size and composition. Females usually leave their natal groups after reaching sexual maturity whereas males do not disperse (Ghiglieri 1984). Male chimpanzees develop strong bonds with others in their communities being engaged in a variety of social behaviour. Field observations together with DNA analysis showed that such affiliations join together males of close rank and age rather than males belonging to the same matrilines (Mitani and Watts 2005). It is worth noting that females give birth to a single offspring only once every 5–6 years, so brothers obviously should have an essential disparity in years. Do chimpanzees bias their behaviour to non-kin? Although current evidence indicates that Old World monkeys are unable to discriminate paternal relatives (Erhart *et al.* 1997), a recent study suggests that chimpanzees may be able to identify kin relationships between others on the basis of facial features alone, overmatching humans in sorting photographs by features of family relatedness (Parr and de Waal 1999). This raises the intriguing possibility that male chimpanzees might be able to recognise their paternal relatives (Mitani *et al.* 2002).

The importance of kinship for the evolution of altruism is widely accepted today, on both theoretical and empirical grounds. However, as it has been noted before, altruism is not always kin-directed, and there are many examples of animals behaving altruistically towards non-relatives.

The theory of reciprocal altruism is an attempt to explain the evolution of altruism among non-kin. *Reciprocity* involves the non-simultaneous exchange of resources between unrelated individuals. The basic idea is straightforward: it may benefit an animal to behave altruistically towards another, if there is an expectation of the favour being returned in the future: ‘If you scratch my back, I'll scratch yours’. In his now classic paper ‘The evolution of reciprocal altruism’, Trivers (1971) argued that genes for cooperative and altruistic acts might be selected if individuals differentially distribute such behaviours to others that have already been cooperative and altruistic towards the donor. The cost to the animal of behaving altruistically is offset by the likelihood of this return benefit, permitting the behaviour to evolve by natural selection. This evolutionary mechanism is termed *reciprocal altruism*.

A study of blood-sharing among vampire bats suggests that reciprocation does indeed play a role in the evolution of this behaviour in addition to kinship (Wilkinson 1984). Vampire bats *Desmodus rotundus* typically live in groups composed largely of females, with a low coefficient of relatedness. It is quite common for a vampire bat to fail to feed on a given night. This is potentially fatal, for bats die if they stay without food for more than a couple of days. On any given night, bats donate blood (by regurgitation) to other members of their group who have failed to feed, thus saving them from starvation. Since vampire bats live in small groups within large colonies and associate with each other over long periods of time, the preconditions for reciprocal altruism – multiple encounters and individual recognition – are likely to be met. Wilkinson's study showed that bats tend to share food with their close associates, and are more likely to share with those who had recently shared with them. These findings provide a confirmation of reciprocal altruism theory.

Maynard Smith (1974, 1989) suggested that cooperative behaviour can be an evolutionary stable strategy, that is, a strategy for which no mutant strategy has higher fitness. His concept is based on game theory which, in turn, attempts to model how organisms make optimal decisions when these are contingent on what others do.

Cognitive aspects of reciprocal altruism are the source of much debate. Indeed, cooperation based on reciprocal altruism requires certain basic cognitive prerequisites, among which are repeated interactions, memory, and the ability to recognise individuals. Experimental evidence that reciprocal altruism relies on cognitive abilities, making current behaviour contingent upon a history of interaction, comes from primate studies. For example, de Waal and Berger (2000) made a pair of brown capuchins work for food by pulling bars to obtain trains with rewards. They found that monkeys share rewards obtained by joint effort more readily than rewards obtained individually. De Waal (1982) also demonstrated a strong tendency to ‘pay’ for grooming by sharing food in captive chimpanzees who based their ‘service economy’ on remembering reciprocal exchanges.

In many examples of cooperation among nonrelated animals such as grooming and food sharing behaviour in primates, or cooperative hunting in lions, wolves, hyenas and chimpanzees, it is still under discussion whether they can be interpreted in terms of reciprocal altruism. Several alternative concepts exist which explain evolution of altruistic and cooperative behaviour (Clutton-Brock and Parker 1995; Sober and Wilson 1998).

It is worth of noting that both kin- and non-kin-altruism in animal societies are based on great individual variability which includes behavioural, cognitive and social specialisation. Let us consider these aspects in more details.

3. A Harsh Environment for Pluralism in Animal Societies: Behavioural and Cognitive Specialisation

Two extreme approaches to consider species-specific behaviour exist in ecological and ethological studies: those that distinguish unique individualities of members of species and those that consider a population as a whole treating conspecific individuals as ecologically equivalent. Applying the ideas of evolutionary ecology helps to find a middle course and to reveal relatively stable fractions of populations that differ by sets of behavioural characteristics, a differentiation that covers routine differences of individuals by sex and age.

There are at least two levels of behavioural specialisation within populations. In some species members of a population comprise distinct groups that behave differently according to their evolutionary stable strategies. In some cases members of these groups can be easily distinguished by certain morphological markers. Besides, more flexible individual specialisation can be expressed in differences in diets, techniques of getting food, forming searching images, escaping predators, nestling and so on. Relatively stable groups can exist in populations that differ by complexes of behavioural characteristics.

3.1. Evolutionary Stable Strategies: A Battle of Behavioural Phenotypes

The theory of *evolutionary stable strategy* (or *ESS*) introduced by Maynard Smith and Price in 1973 is based on the concept of a population of organisms divided into several groups which use different strategies. A group is in a stable state if it is disadvantageous for any individual to change its strategy. In other terms the proportion of individuals using each strategy is optimal; natural selection suppresses any deviation from the current proportion.

Maynard Smith's best known work incorporated game theory into the study of how natural selection acts on different kinds of behaviour. He developed the idea of an evolutionary stable strategy as a behavioural phenotype that cannot be invaded by a mutant strategy. A classic example is a balance between hawks-like (aggressive) and doves-like (non-aggressive) individuals in natural populations. Maynard Smith and Price (1973) demonstrated that both carriers of aggressive and non-aggressive behavioural strategies can coexist comfortable and stable in populations for a long time, and neither aggressors nor non-aggressors can invade the population.

Males of many species are characterised by alternative mating strategies and thus compose a representative set of examples concerning distinct behavioural strategies of carriers of different ESS. These strategies are based on complex behaviour sequences and thus may give to observers the impression of deliberate choice of variants.

For instance, Sinervo and Lively (1996) revealed impressive mating strategies within populations of the side-blotched lizard (*Uta stansburiana*) native to California. These lizards have three mating strategies: distinct types of behaviour that constantly compete with one another in a perpetual cycle of dominance. Carriers of different behavioural strategies are marked by morphological signs. The researchers described the cycle of dominance in lizards in terms of ESS as the ‘rock-paper-scissors’ game.

In the side-blotched lizards males have one of three throat colours, each one declaring a particular strategy. Dominant, orange-throated males establish large territories within which live several females. Orange males are ultra-dominant and very aggressive owing to high levels of testosterone, and attack intruding blue-throated males that typically have more modest levels of testosterone. Blue males defend territories large enough to hold just one female. These males spend a lot of time challenging and displaying, presumably allowing males to assess one another. Territories of both orange and blue males are vulnerable to infiltration by males with yellow-striped throats – known as sneakers. Sneakers have no territory of their own to defend, and they mimic the throat colour of receptive females. It is interesting that yellows also mimic female behaviour. When a yellow male meets a dominant male, he pretends he is a female – a female that is not interested in the act. In many cases, females will nip at the male and drive him off. By co-opting the female rejection display, yellow males use a dishonest signal to fool some territory holding males. The ruse of yellows works only on orange males. Blues are not fooled by yellows. Blue males root out yellow males that enter their territories. Blue males are a little more circumspect when they engage another blue male during territory contests. Attack may or may not follow as blue males very often back down against other blue males. Indeed, neighbouring males use a series of bobs to communicate their identity, and the neighbours usually part without battle.

Thus, each strategy has strengths and weaknesses and there are strong asymmetries in contests between morphs. Trespassing yellows, with their female mimicry, can fool oranges. However, trespassing yellows are hunted down by blue males and attacked. While oranges can easily defeat blues, they are susceptible to the charms of yellows. In contrast, contests between like morphs (*e.g.,* blue *vs.* blue, orange *vs.* orange or yellow *vs.* yellow) are usually more symmetric. Field data showed that the populations of each of these three types, or morphs, of male lizard oscillate over a six-year period. When a morph population hits a low, this particular type of lizard produces the most offspring in the following year, helping to perpetuate the cycle. This arrangement somehow succeeds in maintaining substantial genetic diversity while keeping the overall population reasonably stable. This is a good example of genetically-based control over morphotype and behavioural type development (Sinervo and Colbert 2003).

3.2. Individual Behavioural and Cognitive Specialisation

An impressive example of behavioural specialisation came from the study on how insects of different sizes and level of intelligence catch jumping springtails, small inoffensive creatures that nevertheless are equipped with a jumping fork appendage (furcula) attached at the end of the abdomen. The furcula is a jumping apparatus enabling the animal to catapult itself (hence the common name springtail), thereby changing sharply the direction of movement and to escape attacks of predators. Reznikova and Panteleeva (2001, 2008) revealed springtail hunters in beetles of the family Staphylinidae as well as in several species of ants. Although beetles are taxonomically far from ants, there are three similar groups both in the beetles and ants: (1) good hunters that catch a jumping victim from the first spurt; (2) poor hunters that perform several wrong spurts until they catch a springtail; and (3) no-hunters that even do not display any interest to the victims (Fig. 3). Behavioural stereotypes were similar in ants and beetles, with one great difference: ants were able to bring their hunting technique up to standard of the next level whereas beetles were not.

It turned out later that hunting behaviour in ants incorporated several variants of development, one of them is based on maturation rather than learning, while others include elements of social learning and different levels of flexibility. There are three distinct types of behaviours relative to jumping victims in populations, and this is one of examples of individual behavioural specialisation.

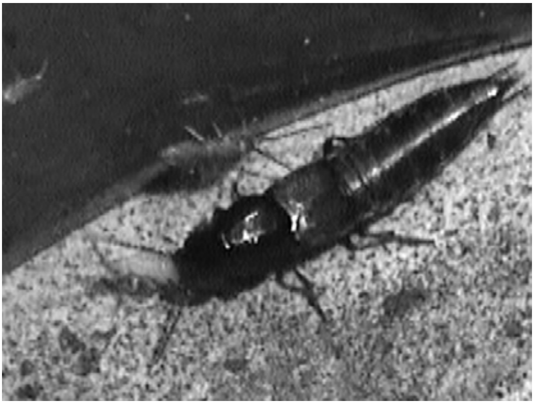

Fig. 3a

Fig. 3b

Fig. 3c

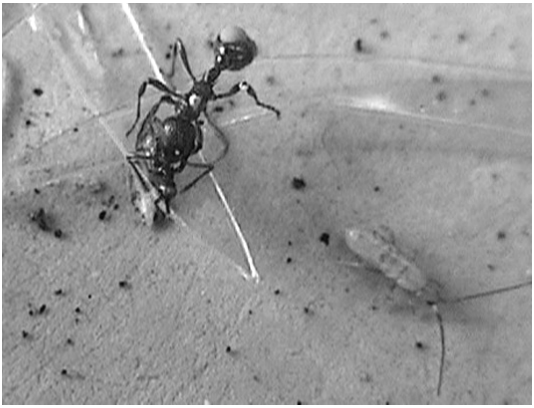

Fig. 3d

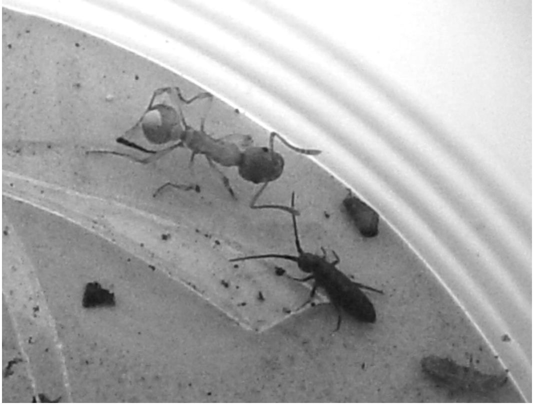

Fig. 3e

Fig. 3. Springtail hunters in beetles of the family Staphylinidae (3-a) a good hunter that catches a jumping victim from the first spurt; (3-b) a poor hunter that performs several wrong spurts until they catch a springtail; and (3-c) the no-hunter that even do not display any interest to the victim; springtail hunters in *Myrmica* ants: a good hunter (3-d) and the no-hunter (3-e). Photo by S. Panteleeva

Bolnick *et al.* (2003) present a huge collection of examples of individual behavioural and ecological specialisation for 93 species distributed across a broad range of taxonomic groups. In many species some specimens in populations are more risk-averse than others, possibly reflecting different optimisation rules. Besides, individuals vary in their prey-specific efficiency because of search image formation. Individuals also vary in social status, mating strategy, microhabitat preferences and so on. In some species individuals constitute groups on the basis of relatively stable features. Bluegill sunfish serves as a good example of differentiation of individuals relatively to their foraging strategy. When a population of bluegills was experimentally introduced to a pond, individuals quickly divided into benthic and limnetic specialists. The remanding generalists constituted 10–30 % of the population and appeared to have a lower intake rate of food.

There is an example of more complex individual specialisation in the oystercatcher *Haematopus ostralegus*. In this species individual birds specialise both on prey species and on particular prey-capture techniques such as probing mud for worms or hammering bivalves. Individuals that use bivalves tend to specialise on different hammering or stabbing techniques that reflect intraspecific variation in prey shell morphology (Fig. 4). Individuals are limited to learning a small repertoire of handling behaviours, while additional trade-offs are introduced by functional variation in bill morphology. Subdominant and juvenile birds are often restricted to sub-optimal diets rather than those they would choose in the absence of interference competition (Goss-Custard *et al.* 1984). It is interesting to note that a dabbling duck endemic to New Zealand was observed opening bivalves in a manner similar to oystercatchers'. Despite having the bill morphology of a typical dabbling duck, these birds were adept at this feeding method (Moore and Battley 2003). This enables us to suggest that behavioural specialisation could be based on highly stereotypic behaviours retained within the whole Class of animals and implemented even on the substrate of somewhat irrelevant morphology.

Fig. 4a

Fig. 4b

Fig. 4. Oystercatchers *Haematopus ostralegus* specialise on different hammering (4a) and stabbing (4b) techniques

Fig. 4c. This bird seems to find similarity between a bivalve's shell and a sheep's ear (Copyright: Omar Bronnstrom)

Fig. 4d. Oystercatchers possess enough flexibility to catch fishes as well (Copyright: Dirk Vorbusch)

In all cases described above behavioural specialisation within populations is based on intricate composition of innate predisposition and individual experience of animals to choose a way of prey handling, to avert risk or not, to dominate over conspecifics or to avoid conflicts, and so on. Some specimens can possess complex behavioural patterns that allow them to learn readily within a specific domain. This ability can be called *cognitive individual specialisation* (for details see Reznikova 2007). More exactly, cognitive specialisation in animal communities is based on the inherited ability of some individuals to form certain associations easier than others. For example, in *Myrnica* ants some members of a colony learn to catch difficult-to-handle prey much easier and earlier in the course of the ontogenetic development than others do (Reznikova and Panteleeva 2008), and in red wood ants some members of a colony display similar abilities concerning battles with enemies and competitors such as ground beetles (Reznikova and Iakovlev 2008). These individuals can serve as ‘etalons’ for those members of communities that possess poorer skills and can learn from others by means of simple forms of social learning.

4. Social Specialisation in Animal Communities

There are many gradations of social specialisation, from rigid caste division to constitutional and (or) behavioural bias towards certain roles in groups accomplishing certain tasks.

4.1. Caste Division and Polyethism in Eusocial Communities

The system of caste division was firstly described for social insects. Wheeler (1928) was the first who proposed a detailed description of caste system in social insects based on anatomy with no fewer than 30 categories. Hölldobler and Wilson (1990) define a *caste* as a group that specialises to some extent on one or more roles. *Role* means a set of closely linked behavioural acts (for example, queen care). Broadly characterised, a caste is any set of a particular morphological type, age group, or physiological state (such as inseminated *versus* barren) that performs specialised labour in the colony. A *physical caste* is distinguished not only by behaviour but also by distinctive anatomical traits. A *temporal caste*, in contrast, is distinguished by age. The term *task* is used to denote a particular sequence of acts which serves to accomplish a specific purpose, such as foraging or nest repair. Finally, the division of labour by the allocation of tasks among various castes is often referred to as *polyethism*, a term apparently first employed by Weir (1958).

A good example of division of labour in eusocial communities based on cast differentiation is existence of soldiers, that is, a specialised cast of workers that defend the colony against intruders (for a review see Judd 2000). Termites, social aphids, social thrips, and some ants produce special casts of soldiers. Some species of ants as well as eusocial shrimps and naked mole-rats show a distinct polymorphism among workers with larger individuals specialised as guards. In some species of bees and wasps guards differ from other colony members only by their aggressive behaviour but not morphologically.

Let us consider several examples of animal social systems based on caste determination and polyethism.

Eusocial insects. Eusociality is displayed in three main insect orders: Hymenoptera (ants, bees and wasps), Isoptera (termites) and Homoptera (aphids). We consider here only a rough schema. There is a great diversity of species: only ants include about 12 000 species and termites about 2 300 species. Different taxa have different numbers of castes, and different degrees of caste specification.

Ants, bees and wasps belong to the haplodiploid group Hymenoptera (it should be noted that Hymenoptera is a large group and the majority of Hymenoptera are not social). The termites, in contrast to the Hymenoptera, exhibit diploidy. The strategy of eusociality arose once in an ancestral termite, whilst it arose several times in the Hymenoptera. Recently, some species of aphids have been found to be eusocial, with many separate origins of the state. This is explicable due to their partially asexual mode of reproduction. Most aphids that are related within a colony are members of the same clone. When social aphids form a gall (a special structure of a plant) and concentrate there, some soldiers will not reproduce. This form of eusociality tends to be restricted to a few soldiers, because the sterile forms only defend and do not care for the young. Therefore, there is less potential for the development of advanced societies.

In general, in social insects most members of a community sacrifice their own reproductive potential to provide food and protection for the few reproductive members and their offspring. The so-called *primer* pheromone causes long-term physiological changes in nestmates within a colony by controlling their endocrine and/or reproductive systems. The primer pheromone is usually dispersed by only one or a few individuals (‘queens’) and may regulate sexuality and caste expression. In contrast, chemical signals that cause immediate behavioural changes in conspecifics are defined as *releaser* pheromones and are produced by numerous nestmates (Wilson 1971). The social organisation in colonies depends on the control of the proportion of different castes, and on efficient recognition and communication system.

Apis mellifera, the honey bee, has the best studied system of caste differentiation. Differences in caste-specific behaviour are understood for many years (Michener 1974), but recent molecular studies have shed new light on the mechanisms by which it occurs. In honey bees, the primary determination is between worker bees and gynes (future queens). Gynes are given a special diet that activates queen specific development. Workers assume different roles in the nest as they age, a pattern known as *temporal polyethism*. Young workers stay in the nest, and as they age they replace foragers, and are replaced by younger workers within the nest. The timing of the progression through the tasks is not fixed. The progression can be delayed, or even reversed, if young workers die. Over the winter, the progression is also delayed, so that there are workers to staff the hive early in the spring.

Some ants also have age-correlated division of labour. In ants with multiple worker castes, different morphological types assume different tasks (usually soldiers *versus* workers), but within each morphological type, work is divided in a temporal fashion.

In termites, in contrast to hymenopterans, the only adults present in colonies are the king and the queen. This one adult caste is initially winged (alate). Termite queens typically become physogastric, due to an enormous growth of the fat bodies and ovaries while the males remain relatively small. Indeed, the termite queen looks awfully fat and large in comparison to workers. For example, in the African termite, *Macrotermes subhyalinus*, the queen's body becomes so swollen with eggs that she is incapable of movement. When fully engorged, she may be 14 cm long (more than 10 times as long as a worker termite), and capable of producing up to 30 000 eggs per day.

The second true caste in termites comprises the soldiers. They are always non-reproductive and are more sclerotised and more heavily pigmented than workers. They also have highly sclerotised and powerful mundibles, which make them suitable for colony defence. Soldiers cannot feed themselves and have to be fed by workers. In some species members of the sub-cast ‘minor soldiers’ serve as scouts and leaders for workers being more sensible than workers to trial pheromones. Soldier termites can regulate their own numbers by inhibiting the larval development of other soldiers. Worker termites may be more or less differentiated, depending on the evolutionary status of the species. In primitive species, social tasks are accomplished by unspecialised larvae or nymphs. In the more highly developed Termitidae, and some other termites groups, workers constitute a true caste, specialised in morphology and behaviour and permanently excluded from the nymphal development pathway. In theory, each nymph can be developed to an alate and leave the natal colony. In some species the workers are dimorphic having large and small forms; in the Macrotermitinae the larger workers are the males and the smaller workers the females. Workers accomplish different tasks and subtasks in the colony. For example, in the termite *Hodotermes mossambicus*, one set of workers climbs up grass stems, cuts off pieces of grass, and drops them to the ground below (subtask 1) while the second set of workers transports the material back to the nest (subtask 2). Termites' lifetime is amazingly long for insects. Sterile workers live for 2–4 years while the primary sexuals live for at least 20 and perhaps 50 years (for details see Eggleton 2000)

Social aphids introduce a whole new direction in the evolution of eusociality. Like termites, they are diploid, but in contrast to termites, aphids reproduce both sexually and parthenogenetically, so they have the ability to produce genetically identical individuals. In these clonal stages large colonies are formed comprising of genetically identical individuals. Aphids are the only colonial species that exhibit eusocial behaviour (Alexander *et al.* 1991). Aoki (1977) was the first who found that the aphid, *Colophina clematis,* produced instars that defend the colony from intruders. Since then many species of social aphids have been described in the two families Pemphigidae and Hormaphididae (Stern and Foster 1996). Social aphids produce galls, which are tough pockets artificially induce in a plant by the aphids. All of the alates and reproductive destined instars are normally found inside the galls. The individuals on the outside are the soldiers which defend the gall from any predator that would destroy this nest and its contents. Stern and Foster (1996) describe several types of soldiers based on physical characteristic and behaviour.

Eusocial rodents. In the same way as calling termites ‘white ants’ one can call naked mole-rats (*Heterocephalus glaber*) ‘mammalian termites’. These unique eusocial mammals share many features with termites. They spend virtually their entire lives in the total darkness of underground burrows, they are very small (7 to 8 cm long, and weigh between 25 and 40 g), and, what is the most important, they are eusocial. Besides, like in termites, in mole-rats high-cellulose diet is also rather hard to digest, and their stomachs and intestines are inhabited by bacteria, fungi, and protozoa that help break down the vegetable matter. Similarity with insects intensifised with the fact that the naked mole-rat is virtually cold-blooded; it cannot regulate its body temperature at all and requires an environment with a specific constant temperature in order to survive. These eusocial rodents cooperate to thermoregulate. By huddling together in large masses, they slow their rate of heat loss. They also behaviorally thermoregulate by basking as needed in their shallow surface tunnels, which are warmed by the sun.

These amazing creatures are neither moles nor rats. Like rats, they are rodents, but they are more closely related to porcupines and chinchillas. *Heterocephalus glaber* is known since 1842, but only in 1981 Jarvis discovered their eusocial organization system that is believed to be unique among mammals. Since that, this species has been intensively studied (see Jarvis 1981; Sherman *et al.* 1991; Bennett and Faulkes 2005). There are essential ecological reasons for which naked mole-rats have broken many mammalian rules and evolved an oddly insect-like social system. These animals are ensconced in the arid soils of central and eastern Ethiopia, central Somalia, and Kenya, where they must continually dig tunnels with their enlarged front teeth, in search for sporadic food supplies and evade the deadly jaws of snakes.

Naked mole-rats live in well-organized colonies, with up to 300 members in a group (20 to 30 is usual). A dominant female (the queen), who outweighs the others by up to 20 g, leads a colony. The queen is the only female that breeds, and she breeds with one to three males. When a female becomes a queen she actually grows longer, even though she is already an adult, by increasing the distance between the vertebrae in her spine. These animals are extremely long living; in captivity some mole-rats have lived to 25 years old. One naked mole-rat queen, as the breeding females are called, produced more than 900 pups in her 12-year lifetime at a laboratory colony. The young are born blind and weigh only about 2 g. The queen nurses them for the first month, and then the other members of the colony feed them by faeces (again like termites) until they are old enough to eat solid food (Fig. 5).

Fig. 5. Naked mole-rat (*Heterocephalus glaber*). Images from Bioimages home. Copyright: 2003 Steve Baskauf http://www.cas.vanderbilt.edu/bioimages/animals/mammalia/naked-mole-rat.htm

The breeding female (the queen) suppresses the breeding of all the other females in the colony. She sometimes leaves her nest chamber to check on her workers and to keep them unfertilized by pheromone control as well as by swoops and bites thus demonstrating that they should not ‘think’ about anything but digging tunnels and defending a colony from snakes and newcomers. The worker males are also suppressed, although they do produce some sperm. When the queen dies, several of the larger females fight, sometimes to death, to become a queen. They can regain their fertility quickly.

The majority of workers (both males and females) spend their entire lives working for the colony. Workers cooperate in burrowing, gathering food, and bringing nest material to the queen and non-workers. They use their teeth to chisel earth and to create piles of soil. There is a great deal of branching and interconnection of tunnels, with the result that a colony's total tunnel length can add up to 4 km. Tunnels connect nest chambers, toilet areas, and food sources. Burrowing is the only way these animals find food, since they do not travel above ground. Some colony members ‘farm’ succulent tubers that are formed by many of the plant species that grow in arid areas. They generally bore through the tuber, eating mainly the interior flesh while leaving the thin epidermis intact. This behaviour may allow the plant to remain healthy for some time, indeed even to continue growing, thereby providing a long-term food resource for the colony. Judd and Sherman (1996) studied captive colonies in order to determine whether successful foragers recruit colony mates, like many eusocial insects do. It has been revealed that individuals that found a new food source typically give a special vocalisation on their way back to the nest, wave the food around once they got there, and lay odour track for other nestmates to follow.

Whilst most offspring become workers, some continue to grow and become colony defenders. Their main duty is to defend the colony against predators. In particular, rufous-beaked snakes (*Rhamphiophis oxyrhynchus rostratus*) are attracted to the smell of freshly dug soil and will slither into burrows through mole hills in search of a rodent meal. Soldier mole-rats fight back with their teeth and attempt to block the entrance with dirt. If everything fails, a soldier will directly attack the snake, sometimes sacrificing its own life while others escape.

Should a breeder die, just one of defenders will become reproductive to replace it. They can occasionally disperse to found a new colony with an unrelated member of the opposite sex.

In general, caste differentiation in mole-rats bears a strong resemblance (of course, merely superficial) with termite's one. The sterility in the working females is only temporary, and not genetic. Like in termites, there are castes of fertilised queens and kings and unfertilised workers and soldiers, and workers descend from ‘nymphs’, that is, under-grown members of the colony. The life span of mole-rats is unprecedented among small rodents just like the life span of termites is unprecedented among insects. It is possible that these long living animals will surprise experimenters with their cognitive abilities.

Eusocial shrimps. Tiny marine coral-reef Crustacea offer a new data about the ecology and evolution of eusociality. Colonies of the social snapping shrimp *Synalpheus regalis* share several features with those of eusocial insects and cooperatively breeding vertebrates (Duffy 1996). *Synalpheus regalis* inhabits internal canals of tropical sponges, living in colonies of up to a several hundreds of individuals. Colonies consist of close kin groups containing adults of at least two generations which cooperatively defend the host sponge using their large and distinctive snapping claws, and in which invariably only a single female breeds. Irreversible caste differentiation is governed by the queen that typically sheds her large snapping claw and re-grows a second minor-form chela, rendering her morphologically unique among the members of the colony. It is still not completely known how the queen accomplishes social control over sexual maturation of other colony members. Both genetic data and colony structure confirm that many offspring remain in the natal sponge through adulthood. Colonies consist largely of full-sib offspring of a single breeding pair which ‘reigns’ for most or all of the colony's life. In captive colonies researchers have regularly observed a large male in association with the queen behaving aggressively with other large males approach her. The inference of monogamy from genetic data suggests that the queen associates with a single male for a prolonged period. There is a strong competition for suitable nest site and a shrimp attempting to disperse and breed on their own would have low success. Colony members discriminate between nestmates and others in their aggressive behaviour. Laboratory experiments revealed behavioural division of labour within colonies. Large males shoulder the burden of defence, leaving small juveniles free to feed and grow, and the queen free to feed and reproduce (Fig. 6). Such size- and age-related polyethism in shrimps has many similarities with poyethism in social insects (Duffy *et al.* 2002).

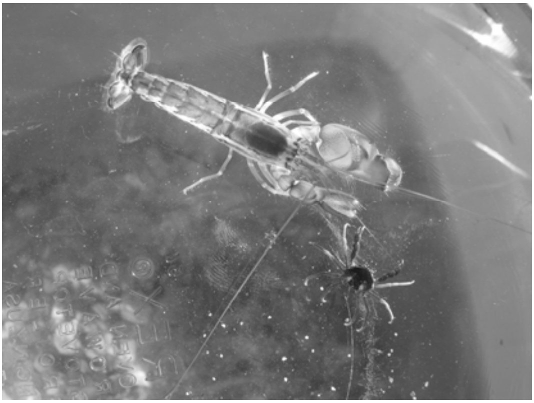

Fig. 6. Defending snapping shrimp. Photograph by A. Bray. Courtesy of A. Bray

Considering intellectual potential of social shrimps, Duffy (2003) refers to Darwin's (1871) note that ‘the mental powers of the Crustacea are probably higher than might be expected’. Social shrimps demonstrate coordinated behaviour. For example, they pick up dead colony members and push out of their sponge dwelling. Recent experiments suggested coordinated snapping, during which a sentinel shrimp reacts to danger by recruiting other colony members to snap intruders. The phenomenon of ‘mass snapping’ begins by rhythmic snapping of one individual, following by rapid recruitment of many others. The initial one-to-one confrontation elicited a snap response from the defender. Colony members joined in with a cacophony of snapping thus providing an unequivocal signal that the sponge is already colonized. This distinctive behaviour is the first evidence for coordinated communication in the social shrimp and represents yet another remarkable convergence between social shrimps, insects and vertebrates (Tóth and Duffy 2005).

Summarising the data on caste division of labour within communities of eusocial organisms we have to admit that the correlation between cognitive and morphological specialisation in these animals is not yet completely described. Even in ants and bees which have been intensively studied for more than hundred years, it remains unclear what effect does the caste determination has on their intelligence. Further we will consider a more gentle system of division of labour in animal societies that perhaps leave more room for intelligence.

4.2. Division of Labour in Cooperative Breeders

Eusociality can be considered an extreme of cooperative breeding systems being based on irreversible caste determination. However, many vertebrate species possess more flexible social systems which are based on facultative division of labour and temporal limits on breeding for some members of communities. In cooperative breeding vertebrates, a dominant pair usually produces the majority of the offspring, whereas the cost of caring for offspring is shared by non-breeding subordinates. In certain cooperative breeding animals one or a few dominant females are the only capable of breeding; the subordinates do not have the proper hormone levels to be fertile although they are physiologically equipped for the task.

There is still a great controversy in literature about to what extent cooperative breeding can be explained in terms of kin selection theory. Results so far are mixed: while some studies have produced evidence supporting the association between kinship and contributions for cooperative activities, others have found no consistent association between contributions to helping behaviour and variation in relatedness (for reviews see Clutton-Brock *et al.* 2002).

Cognitive aspects of cooperative breeding are intriguing and have not been studied enough. Serving as helpers for the ‘royal family’ young animals gain experience that can be useful for them in future when they establish their own families. Nevertheless, in many cases helpers have no chance to have their own offspring. Somehow or other, cooperative breeding system enables helpers to sacrifice their intelligence for other members of the community. It is possible that helping individuals accomplish a wider variety of tasks and under more risky circumstances than those who have the opportunity to raise their young being given every support by helpers. Several examples will give us an impression of how division of labour occurs within communities which are based on communal breeding.

In birds about 3 percent (approximately 300 species) of species are known as cooperative breeders. Helpers (also called auxiliaries) at the nest were first described by Skutch in 1935. It was not until the mid-1960s, however, with the advent of modern behavioural ecology, that widespread attention began to focus on cooperatively breeding species (Emlen 1995).

Cooperative systems often appear to arise when environmental constraints force birds into breeding groups because the opportunities for younger birds to breed independently are severely limited. Limitations may include a shortage of territory openings, a shortage of sexual partners, and unpredictable availability of resources. That cooperative breeding is a common strategy in arid and semi-arid portions of Africa and Australia lends strong support to this line of reasoning. For some species the role of ecology is not completely clear (Arnold and Owens 1999).

Cooperative breeding may be viewed primarily as a means by which young adults put off the start of their own breeding in order to maximize their lifetime reproductive output, and in the process occasionally promote genes identical with their own via kin selection. There are two types of cooperative arrangements: those in which mature nonbreeders help protect and rear the young, but are not parents of any of them, and those where there is some degree of shared parentage of offspring. Cooperative breeders may exhibit shared maternity, shared paternity, or both.

The best-studied North American cooperative breeders, the Scrub-Jay, Gray-breasted (Mexican) Jay, Groove-billed Ani, and Acorn Woodpecker provide good examples of communal breeding (see Ehrlich *et al.* 1988). Scrub-Jays in Florida reside in permanent, group-defended territories. Woolfenden and Fitzpatrick (1984) have found that groups consist of a permanently bonded monogamous pair and one to six helpers, generally the pair's offspring of previous seasons. About half the territories are occupied by pairs without helpers, and most other pairs have only one or two helpers. Although pairing and breeding can occur after one year spent as a helper, birds often spend several years as non-breeding auxiliaries. Males may remain in this subsidiary role for up to six years; females generally disperse and pair after one or two years of helping. Helpers participate in all non-sexual activities except nest construction, egg lying, and incubation. Pairs with helpers are more successful – they fledge one and a half times younger than pairs without helpers. Like the Florida Scrub-Jays, the closely related Gray-breasted Jays live in permanent group-defended territories, and breeding adults are monogamous. Brown (1974) has shown that the cooperative system of this species is more complex than that of its south-eastern relative in several ways. Gray-breasted Jay groups are much larger, ranging from 8 to 18 individuals; thus, they usually include offspring from more than just the preceding year. Within each group, two and sometimes three breeding pairs nest separately but simultaneously each season, and some interference among them often occurs. Interference usually involves theft of nest-lining materials, but can include tossing of eggs from nests by females of rival nests. Although the laying female does all the incubating, she is fed on the nest both by her mate and by auxiliaries. Nestlings receive more than half of their feeding from auxiliaries.

Acorn Woodpecker group of communal breeders is composed from up to 15 members whose territories are based on the defence and maintenance of granaries in which they store acorns (Koenig and Dickinson 2004). Groups consist largely of siblings, their cousins, and their parents. Some of the sexually mature birds are non-breeding helpers. Within each group, up to four males may mate with one (or occasionally two) females, and all eggs are laid in a single nest. Thus paternity and sometimes maternity of the communal clutch is shared.

In mammals more than 100 species have been described as cooperative breeders, and among them are cooperative carnivorous, mongooses (meerkats, dwarf mongooses), primates (marmosets and tamarins), as well as several species of rodents and shrews. As it was noted before, some rodent species possess facultative communality in dependence of their habitat and many ecological factors.

The painted hunting dog (African wild dog) *Lycaon pictus* provides a good example of obligate cooperative breeding. These dogs live in packs of up to 20 adults, in which most of the time only the alpha pair breeds. The remaining adults are reproductively suppressed and help to raise the pups; they must wait to breed until their circumstances improve, either through the death of a higher-ranking female or by finding a mate with an unoccupied territory (Fuller *et al.* 1992). Baby sitting is a costly task and this includes: watching pups to prevent loss, alerting them to danger (lions, hyenas), protecting them from smaller predators or alien dogs, and moving them under cover in heavy rain. Other members of the pack are also involved in caring for common babies: they feed pups with regurgitated meat when return from successful hunting. Baby sitting is not an obligatory load for pack members, as they can choose between hunting and guarding young. Researchers observed situations where a dog returned to a den to baby-sit after encountering a predator close by (Malcolm and Marten 1982). At the same time, *Lycaon* hunt cooperatively and baby sitting draws a member of a pack away from hunting where both efficiency and the risk to lose prey for kleptoparasites depend on the size of the party (Gorman *et al.* 1998). It is worth to note that in contrast to queens in eusocial communities that are specialised baby-machines, the breeding female in wild dogs, as in other cooperative carnivorous, is often an experienced hunter, and her presence in the hunting pack may increase efficiency of enterprise. Besides, there is a threshold for the group size to survive. Smaller packs need to hunt more often to feed their pups, especially when using a pup guard (Courchamp *et al.* 2002).

Another impressing example of obligatory communal breeding in mammals comes from small arboreal monkeys, marmosets and tamarins of the family Callitrichidae endemic to the Northern half of South America. Within the family, cooperative breeding strategies are widespread and virtually all species are characterised by small territorial groups of approximately 4–15 individuals, where reproduction is monopolised by one or a small number of dominant individuals. Typically one dominant female breeds, normally producing dyzigotic twins. An important role of helpers in the group is to assist in the care of the dominant female's offspring. This is principally by sharing the burden of carrying the relatively bulky twin infants around their arboreal habitat. Each group member helps rear the young, which involves food sharing, caring and defence against predators (Snowdon and Soini 1988).

Life history of Callitrichidae can serve as an example of cooperative breeding in groups consisting both of related and unrelated individuals. Helping behaviour in these primates is thus possibly governed by mechanisms of reciprocal rather than kin altruism. This raises a question to what extend cognitive abilities allow these small primates to calculate reciprocity in their groups. Hauser *et al.* (2003) have conducted experiments on food sharing within groups of cotton-top tamarins (*Saguinus oedipus*) concentrating on psychological mechanisms of reciprocity. The design of experiments was based on animals' tool-using abilities. The apparatus consisted of a tray with an inverted L-shaped tool. When food was on the actor's side, pulling the tool's stem brought the food within rich. Similarly with experimental paradigm used in many experiments on social learning (for details see Reznikova 2007) where researchers trained several animals to be the demonstrators of new skills, here again stooge ‘altruists’ and ‘defectors’ were specially trained to pull pieces of food to their partners or to themselves. Results clearly showed that tamarins discriminate between altruistic and selfish actions, identify and recall conscpecifics by their cooperativeness and give more food to those who give food back. Special series of experiments also demonstrated that tamarins give food to genetically unrelated conspecifics even though they obtain no immediate benefit from doing so. Tamarins therefore have the psychological capacity for reciprocally mediated altruism.

The ability to estimate partner's cooperativeness and remember the history of inter-individual relationships is particularly important for those communal breeders that incorporate both kin and non-kin into their communities, and whose altruistic acts are costly. This is well illustrated by experiments of Clutton Brock *et al.* (2000) on individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*.

Meerkats (suricates) are desert-adapted animals living in groups of 3–25 animals that typically include a dominant female that is responsible for more than 75 % of all breeding attempts, a dominant male that fathers most of the offspring born in the group and a number of helpers of both sexes. A dominate female controls the presence of subordinate adult females in the group. During the first month of pup's life babysitters usually remain at the burrow with young for a full day while the rest of the group is foraging and feed little or not at all during their period of babysitting. Clutton-Brock *et al.* (2000) have shown how costly babysitting is: helpers suffer substantial weight losses. It is important that large differences in contribution exist between helpers. These differences are correlated with such characteristics of group members as age, sex, and weight, but, surprisingly, not with their kinship to the young raising. In field experiments researchers regularly provided some group members with food (boiled eggs) matching them with controls of the same sex and age. It turned out that feeding essentially increased contribution of helpers to babysitting. So a regular salary may increase and equalise individual contributions of co-operators. However, in natural situations meerkats cannot rely on donations from above, they rather depend on their ability to distinguish between more and less conscientious cooperators (Fig. 7).

Fig. 7. A daily procedure of feeding and weighing meerkats. Photograph by L. Hollén. Courtesy of L. Hollén

4.3. Teams in Animal Societies

In group living animals division of labour is sometimes based on coordinated activities of group members. In relatively rare cases individuals form groups in which the members stay together for extended periods to accomplish a certain task. Such groups are called teams or cliques (Hölldobler and Wilson 1990; Anderson and Franks 2001).

For example, when working together to dig tunnels, naked mole-rats line up nose-to-tail and operate like a conveyor belt. A digger mole-rat at the front uses its teeth to break through new soil. Behind the digger, sweepers use their feet and the fine hairs between their toes to whisk the dirt backwards. At the back of the line a trailing member of the group kicks the dirt up onto the surface of the ground, creating a distinctive volcano-shaped mole hill. One of folk names of naked mole-rats is ‘sand puppies’. There are several other creatures that join efforts of group members to survive in the running sand. Desert ants *Cataglyphis pallida* demonstrate the same manner of coordinated working digging tunnels like a conveyor belt.

There are several examples of hunting teams in vertebrates. Usually individuals coordinate efforts so that one or more individuals chase the prey, or flush it from hiding, while others head off its escape. For instance, in chimpanzees (*Pan troglodytes*), some group members chase and surround the prey (usually juvenile baboons) forcing it to climb a tree while at the same time other chimpanzees climb adjacent trees ready to capture the prey when it attempts to leap across to escape. In African wild dogs (*Lycaon pictus*) some individuals chase the prey, and can change leaders during the chase (van Lawick-Goodall, Hugo and Jane 1970).

The most organised teams in animal societies are based on discrete division of labour that may be called ‘professional specialisation’. Stander (1992) has shown that lion teams can be particularly organized in that an individual will tend to stick to a particular position (subtask) during the hunting on successive hunts. That is, some lions can be classed as ‘wingers’, individuals who always tend to go around the prey and approach it from the front or from the side, while others are better classified as ‘centres’, individuals who remain chasing directly behind the prey. Perhaps the most organized hunting teams in vertebrates occur in Galapagos and Harris' Hawks (Faaborg *et al.* 1995). Hawks hunt cooperatively with several birds simultaneously swooping on their prey on such animals as wood rats, jackrabbits and other birds. However, if the prey item finds cover, some birds land and surround it, while one or two hawks will walk or fly into the vegetation to kill the prey. Once the prey is killed, all the birds feed together on the prey.

Until recently, the existence of teams within insect colonies, possibly based on individual identification, has not been known. According to Hölldobler and Wilson (1990), ants do not appear to recognise each other as individuals. Indeed, their classificatory ability is limited to recognition of nestmates, different castes such as majors and minors, the various growth stages among immature nestmates, and possibly also kin groups within the colony. There are, however, several examples showing elements of team task distribution. In swarm-raiding army ants, large prey items are transported by the structured teams which include members of different castes (Franks 1986). In the desert ant *Pheidole pallidula* Ruzsky, minor workers pin down intruding ants and later major workers arrive to decapitate the intruders (Detrain and Deneubourg 1997). Robson and Traniello (2002) found complex relations between discovering and foraging individuals in group retrieving ant species; removal of the discovering ant during the process of recruitment led to dissolution of the retrieval group.

The question of constant membership and individual recognition within group of workers in ant colonies has been so far obscure. Reznikova and Ryabko's (1994, 2003) findings on teams in ants are connected with the discovery of the existence of complex communicative system in group retrieving ant species by means of the special maze called ‘binary tree’ (for details see Ryabko and Reznikova 2009). Such communication system is based on scouts-foragers informative contacts where each scout transfers messages to a small (5 animals in average) constant group of foragers and does not pass the information to other groups. The ants thus work as co-ordinated groups which may be called teams. Does this necessarily mean that they recognise each other as individuals? Indeed, it is possible that the animals presume on recognition of specialists' roles rather than their personal traits.

Donald Michie (personal communication) has referred to his experience as a Rugby player. Being a scrum half, he was always confident on his ability to spot his opposite number (that is, another scrum half) when meeting an opposing team socially before the game. To be adapted to the scrum half's specialist role, one must typically be small, resilient, agile, not necessarily a fast runner. The only other typically agile team member is the fly half, but he has also to be a fast accelerator and need not be resilient. A year later he might still recognise one of that same team's forwards, for example, but not remember the face of the scrum half.

One can find it hard to say that ants are able to recognise each other personally. That a scout can distinguish members of its own team from members of another team is not the same thing as individual recognition. Continuing the use of the metaphor from football, one can imagine a team manager who might be able to distinguish players of his own team from those of a different team (for example by the patterns of their shirts), and this is yet not to distinguish same-team players one from another.

We have not yet distinguished reliable behavioural signs in ants indicating personal recognition like the well-knowing ‘eyebrow flash’ in humans (see Eibl-Eibesfeldt 1989); neither are we able to train ants for distinguishing between pictures of different individuals like in Kendrick *et al.'s* (2001) experiments with sheep (for details see Reznikova 2007). Nevertheless, we can be confident on at least circumstantial evidences that group-retrieving ant species possess personalised teams as functional structures within their colonies.

The first evidence comes from ontogenetic studies. Reznikova and Novgorodova (1998) observed the ontogenetic trajectories of 80 newly hatched *F. sanguinea* ants in one of laboratory colonies and watched the processes of shaping of teams. There were 16 working teams in that colony which mastered the ‘binary tree’ maze. From 80 individually marked naive ants, 17 entered 7 different working teams, 1 to 4 individuals in each. Only 3 became scouts, 2 of them starting as foragers joining 2 different teams and 1 starting as a scout at once. The 3 new groups were composed of workers of different ages, mainly from reserve ones. The age at which the ants were capable to take part in the working groups as foragers ranged from 18 to 30 days, and the ants could become scouts at the age of 28 to 36 days. Constancy of membership was examined in two colonies of *F. sanguinea* and *F. polyctena.* In a separate experiment researchers isolated all team members from 9 scouts. 3 scouts appeared to mobilize their previous acquaintances and attract new foragers, 4 scouts were working solely, and 2 ceased to appear on the arenas. In another experiment we removed scouts from 5 *F. polyctena* teams. It was possible to see foragers from those groups on the arenas without their scouts. 15 times different foragers were placed on the trough with the food, but after their return to home they contacted other ants only rarely and occasionally. These results suggest that formation of teams in group retrieving ants is a complex process which is based on extensible relations and possibly include individual identification.

Another evidence of existence of teams in ants is based on division of labour within groups of aphid tenders discovered in red wood ants. It is well known that ants look after symbiotic aphids, protect them from adverse conditions, and in return, ants ‘milk’ the aphids, whose sweet excretions are one of the main sources of carbohydrate for adult ants. In an ant family, there is a group of ants dealing with aphids (aphid-milkers), which has a constant composition. Reznikova and Novgorodova (1998) were the first to describe a system of intricate division of labour (professional specialisation) in aphid milkers: ‘shepherds’ only look after aphids and milk them, ‘guards’ only guard the aphid colony and protect them from external factors, ‘transit’ ants transfer the food to the nest, and ‘scouts’ search for the new colonies (see Fig. 8). This professional specialisation increases the efficiency of ant-aphid mutualistic relations. When ants were experimentally forced to change their roles, much food was lost. The ants belonging to the same aphid tending group, distinguish at least 2–3 shepherds from 2–3 guards within this group. Such professional specialisation was only found in the same species that exhibited the complex communication system in experiments of Reznikova and Ryabko (1994, 2003).

Fig. 8a. ‘Shepherd’ milking aphids and a ‘guard’ (with open mandibles) protecting an aphid colony

Fig. 8b. 'Transit' ant is receiving the food from a shepherd in order to transport it to the nest; a 'guard' is also present here. Photographs by T. Novgorodova

5. Social Intelligence in Animals

Since the second part of the twentieth century a growing body of field data about wild social life have led researchers to the idea that social animals should display advanced cognitive abilities within specific domains related to social living and that intelligence is not a monolithic functional entity but includes a number of specialised mental abilities to cope with life in complex and changeable social environment. Thus, to the primary components of intelligence, such as the ability for flexible problem solving and the ability to cope with novel situations, we can add the ability for solving social problems.

According to the *social intelligence hypothesis,* which was first articulated by Jolly (1966) and Humphrey (1976), complex social interactions (including cooperation, competition, manipulation, and deception) can occur when animals live in large and stable social groups. After spending three months with Dian Fossey and her gorillas in Rwanda (see Fossey 1983), Humphrey wrote a review essay in 1976 titled 'The Social Function of Intellect' on the evolution of cognitive skills. He argued that primate and human intelligence is an adaptation to social problem-solving, well suited to forward planning in social interaction but less suited to non-social domains. These subforms of intelligence assumed the name 'Machiavellian intelligence' after the 16th century Italian politician and author, Niccolò Machiavelli. It provides individuals or groups with a means of social manipulation in order to attain particular goals. In 1532 Machiavelli published his book *The Prince.* Giving somewhat cynical recommendations to an aspiring prince, he was prescient in his realisation that an individual's success is often most effectively promoted by seemingly altruistic, honest, and prosocial behaviour. According to Machiavelli's *real politic,* a popular leader had to give the impression of being sincere, trustworthy, and merciful. To retain his power, however, a prince can set himself above all moral rules and use cunning, lies, and force. Skill in deception and maintaining alliances are two of the prince's most important properties. ‘Machiavellian intelligence’ seemed an appropriate metaphor that inspired primatologists to explicit comparison between the animal social strategies and some of the advice offered five centuries earlier.

De Waal, in his book *Chimpanzee Politics* (1982), describes how clever high-ranking chimpanzees are at manipulating others. Byrne and Whiten (1988) propose that the ability to use other individuals as tools, manipulating the social environment in order to meet preconceived goals, is an important factor in the evolution of primate intelligence. In order to compete successfully within groups, apes and monkeys have to recognise who outranks whom, who is closely bonded to whom, and who is likely to be allied to whom.

Skilfulness in navigating social landscape is based on the advanced ability that seems to be unique to primates, that is the ability to keep track of how other animals relate to each other and thus to recognise the close relationships that exist among individuals (Cheney and Seyfarth 2003; Kitchen *et al.* 2005).

Experimental evidence for animals' ability for tracking social and kin relations came from the laboratory study performed by Dasser (1988) on captive longtail macaques *Macaca fascicularis.* The monkeys were shown a pair of slides of members of the group, and their task was to identify another pair of photographs which ‘matched’ the first one. The first pair could be, for example, a mother and a daughter, two sisters, or two unrelated individuals. The macaques quickly learned to identify the right kinship patterns. The experiment indicates that they do not just recognise their own offspring and siblings, but that they also keep track of other individuals' kinship relations. For example, in one test, Dasser trained a female to choose between slides of one mother – offspring pair and slides of two unrelated individuals. Having been trained to respond to one mother – offspring pair, the monkey was then tested with 14 novel slides of different mothers and offspring paired with an equal number of novel pairs of unrelated animals. In all tests, she correctly selected the mother – offspring pairs. Dasser suggests that the monkeys can use the abstract category to classify pairs of individuals that was analogous to our concept of ‘mother – child affiliation’.

The experiments of Parr and de Waal (1999) demonstrated chimpanzees as being able to judge about mother – offspring relationships by comparing pairs of photographs of mothers and sons and mothers and daughters. Surprisingly, within mother – offspring category, the chimpanzees could find similarities between mothers and sons much better than between mothers and daughters. The authors suggest that facial similarities are more noticeable to chimpanzees in males in view of their male philopatric society and the tendency towards ‘political’ alliances in which males incur great risk on behalf of other males (de Waal 1982). Phenotypic matching might assist the recognition of subsets of related males who tend to support each other.

A number of naturalistic studies have suggested that monkeys recognise the close associates of other group members. For example, play-back experiments using the contact calls of rhesus macaques have demonstrated that females not only distinguish the identities of different signallers but also categorise signallers according to matrilineal kinship (Rendall *et al.* 1996). In play-back experiments with vervet monkeys Cheney and Seyfarth (1990) found that when females were played the scream of an unrelated juvenile, they were more likely to look towards that juvenile's mother than towards other females. Also Cheney and Seyfarth (1990, 2003) argue that vervets can perform vendettas: they prefer to attack relatives of the individuals who have attacked their own relatives.

Knowledge of the relationship between other group members, the so-called *third-party relationships,* play a particular important role in formation of coalitions, helping individuals to predict who will support or intervene against them when they are fighting with particular opponents, and to assess which potential allies will be effective in coalitions against their opponents (Tomasello and Call 1997). There is much evidence that monkeys and apes cultivate relationships with powerful supporters. Silk (1999) has demonstrated that male bonnet macaques put their knowledge of their own relationships with other males and their knowledge of relationships among other males to good use when they recruit coalitions. By selectively soliciting males that most frequently supported them and animals that outranked them and their opponents, males focused their recruitment efforts on the candidates that were most likely to intervene on their behalf and those whose support was most likely to be effective in defeating their opponents. They avoided soliciting top-ranking males that were more loyal to their opponents than to themselves. For this they have to have some knowledge of the pattering of support amongst other individuals, another kind of third-party knowledge.

Although not so well studied as monkeys and apes, several non primate species also show the ability to acquire information about many different individual social relationships. Male dolphins form dyadic and triadic alliances when competing over access to females, and allies with the greatest degrees of partner fidelity are most successful (Connor *et al.* 1992). Analysis of patterns of alliance formation in hyenas suggests that they do monitor other individuals' interactions and extrapolate information about other animals' relative ranks from their observations. During competitive interactions over meat, hyenas often solicit support from other, uninvolved individuals. When choosing to join ongoing skirmishes, hyenas that are dominant to both of the contestants almost always support the more dominant of the two individuals. When the ally is intermediate in rank between the two opponents, it inevitably supports the dominant individual. These data enable researchers to suggest that hyenas are able to infer transitive rank relations among other group members. However, unlike monkeys, they showed no evidence for recognising third-party relationships (Engh *et al.* 2005).

Conclusion

Altruistic behaviour of animals is still enigmatic for evolutionary biologists in many aspects, although a great deal of data have been analysed and rational concepts have been developed such as the theory of inclusive fitness and the theory of reciprocal altruism. Altruistic behaviour in animal societies is based, to a greater or lesser extent, on the division of roles between individuals in dependence of their behavioural, cognitive and social specialisation. There are many gradations of social specialisation, from rigid caste division to constitutional and (or) behavioural bias towards certain roles in groups accomplishing certain tasks. In some situations behavioural, cognitive and social specialisation can be congruent; maybe this is the formula for happiness in animal societies.

To navigate social landscape, animals need a surplus of intelligence that overcomes the immediate survival needs, such as eating, avoiding predators, feeding offspring, *etc.*, and this surplus intelligence might have been advantageous for social manipulation. There is much work to be done to evaluate the role of intelligence in maintaining cooperative behaviour. We can assume that cooperation that is based on reciprocal altruism requires more advanced cognitive skills than altruism towards kin because reciprocity demands remembering and discounting levels of cooperativeness among individuals. Specific cognitive adaptations can be expected in some species such as specific concentration of attention and calculation of mutual aids.

However, we should not expect to find a linear correlation between social complexity and levels of intelligence in non-human species. Although experiments based on pair comparison of intellectual abilities in group-living and solitary species have brought some positive results, we should take into consideration that animals that live in solitary in complex and risky environment relay on their own memory and learning skills and may enjoy freedom of restrictions and obligations imposed upon them by their possibly narrow roles within a community.

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References

Alexander R. D., Noonan K. M., and Crespi B. J. 1991. The Evolution of Eusociality. *The Biology of the Naked Mole-Rat* / Ed. by P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, pp. 3–44. Princeton, NJ: Princeton University Press.

Anderson C., and Franks N. R. 2001. Teams in Animal Societies. *Behavioral Ecology* 12: 534–540.

Aoki S. 1977. Colophina Clematis (Homoptera, Pemphigidae), an Aphid Species with Soldiers. *Kontyu* 45: 276–282.

Arnold K. E., and Owens I. P. F. 1999. Cooperative Breeding in Birds: The Role of Ecology. *Behavioral Ecology* 10: 465–471.

Axelrod R., Hammond R. A., and Grafen A. 2004. Altruism via Kin-Selection Strategies that Rely on Arbitrary Tags with which They Coevolve. *Evolution* 58/8: 1833–1838.

Bennett N. C., and Faulkes C. G. 2005. *African Mole-Rats Ecology and Eusociality* (with the foreword of J. Jarvis). Cambridge: Cambridge University Press.

Bolnick D. I., Svanback R., Fordyce J. A., Yang L. H., Davis J. M., Hulsey C. D., and Forister M. L. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. *American Naturalist* 161: 1–28.

Brown J. L. 1974. Alternate Routes to Sociality in Jays – with a Theory for the Evolution of Altruism and Communal Breeding. *American Zoologist* 14: 63–80.

Byrne R. W., and Whiten A. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Claredon Press.

Cheney D. L., and Seyfarth R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species.* Chicago: University of Chicago Press.

Cheney D. L., and Seyfarth R. M. 2003. The Recognition of Other Individuals' Social Relationships. *Kinship and Behavior in Primates* / Ed. by B. Chapais and C. M. Berman, pp. 347–364. Oxford: Oxford University Press.

Clutton-Brock T. H., Brotherton P. N. M., O'Rian M. J., Griffin A. S., Gaynor D., Sharpe L., Kansky R., Manser M. B., and McLlarth G. M. 2000. Individual Contributions to Baby-Sitting in a Cooperative Mongoose *Suricata suricatta*. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 267: 201–205.

Clutton-Brock T. H., Russell A. F., Sharpe L. L., Young A. J., Balmforth Z., and McIlrath G. M. 2002. Evolution and Development of Sex Differences in Cooperative Behavior in Meerkats. *Science* 297: 253–256.

Clutton-Brock T. H., and Parker G. A. 1995. Punishment in Animal Societies. *Nature* 373: 209–216.

Connor R. C., Smolker R. A., and Richards A. F. 1992. Two Levels of Alliance Formation among Bottlenose Dolphins (*Tursiops* sp). *Proceedings of National Academy of Science* 89: 987–990.

Courchamp F., Rasmussen G. S. A., and Macdonald D. W. 2002. Small Pack Size Imposes a Trade-off between Hunting and Pup-Guarding in the Painted Hunting Dog. *Lycaon pictus*. *Behavioural Ecology* 13: 20–27.

Darwin C. 1859. *On the Origin of Species*. Facsimile reprint with an introduction by Ernst Mayr (1964). Cambridge, MA: Harvard University Press.

Darwin C. 1871. *The Descent of Man, and Selection in Relation to Sex*. 2 vols. London: John Murray.

Dasser V. 1988. A Social Concept in Java Monkeys. *Animal Behavior* 36: 225–230.

Detrain C., and Deneubourg J. L. 1997. Scavenging by *Pheidole pallidula*: A Key for Understanding Decision-Making Systems in Ants. *Animal Behaviour* 53: 537–547.

Duffy J. E. 1996. Eusociality in a Coral-Reef Shrimp. *Nature* 381: 512–514.

Duffy J. E. 2003. Eusociality in Sponge-Dwelling Shrimps. *Genes, Behavior, and Evolution in Social Insects* / Ed. by T. Kilkuchi, N. Azumi, and S. Higashi, pp. 217–252. Sapporo: Hokkaido University Press.

Duffy J. E., Morrison C. L., and Macdonald K. S. 2002. Colony Defense and Behavioral Differentiation in the Eusocial Shrimp. *Synalpheus regalis*. *Behavioral Ecology and Sociobiology* 51: 488–495.

Eibl-Eibesfeldt I. 1989. *Human Ethology*. New York: Aldine de Gruyter.

Ehrlich P. R., Dobkin D. S., and Wheye D. 1988. *The Birder's Handbook*. New York: Simon and Schuster, Inc.

Emlen S. T. 1995. An Evolutionary Theory of the Family. *Proceedings of the National Academy of Science* 92: 8092–8099.

Engh A. L., Siebert E. R., Greenberg D. A., and Holekamp K. E. 2005. Patterns of Alliance Formation and Post-Conflict Aggression Indicate Spotted Hyaenas Recognize Third Party Relationships. *Animal Behaviour* 69: 209–217.

Eggleton P. 2000. Global Patterns of Termite Diversity. *Termites: Evolution, Sociality, Symbioses, Ecology* / Ed. by T. Abe, D. E. Bignell, and M. Higashi, pp. 25–51. Dordrecht: Kluwer Academic Publishing.

Erhart C., Coelho A., and Bramblett C. 1997. Kin Recognition by Paternal Half-Siblings in Captive. *Papio cynocephalus*. *American Journal of Primatology* 43: 147–157.

Faaborg J., Parker P. G., Delay L., De Vries Tj., Berdnarz J. C., Paz S. M., Naranjo J., and Waite T. A. 1995. Confirmation of Cooperative Polyandry in the Galapagos Hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology* 36: 83–90.

Fisher A. R. 1925. *Statistical Methods for Research Workers.* New York: Hafner Publishing Company.

Fisher A. R. 1930. *The Genetical Theory of Natural Selection.* Oxford: Claredon Press.

Fossey D. 1983. *Gorillas in the Mist.* Boston, MA: Houghton Mifflin Company.

Franks N. R. 1986. Teams in Social Insects: Group Retrieval of Prey by Army Ants. *Behavioral Ecology and Sociobiology* 18: 425–429.

Fuller T. K., Kat P. W., Bulger J. B., Maddock A. H., Ginsberg J. R., Burrows R., McNutt J. W., and Mills M. G. L. 1992. Population Dynamics of African Wild Dogs. *Wildlife Populations* / Ed. by D. R. McCullough and R. H. Barrett, pp. 1125–1139. Amsterdam: Elsevier.

Ghiglieri M. P. 1984. *The Chimpanzees of Kibale Forest*. New York: Columbia University Press.

Goodall J. 1971. *In the Shadow of Man*. Boston, MA: Houghton Mifflin Publishing.

Gorman M. L., Mills M. G. L., Raath J. P., and Speakman J. R. 1998. High Hunting Costs Make African Wild Dogs Vulnerable to Kleptoparasitism by Hyenas. *Nature* 391: 479–481.

Goss-Custard J. D., Clarke R. T., and Durell, S. E. A. le V. dit 1984. Rates of Food Intake and Aggression of Oystercatchers. *Haematopus ostralegus* on the Most and Least Preferred Mussel *Mytilus edulis* Beds of the Exe Estuary. *Journal of Animal Ecology* 53: 233–235.

Grafen A. 1984. Natural Selection, Kin Selection and Group Selection. *Behavioural Ecology* / Ed. by J. R. Krebs and N. B. Davies, pp. 62–84. 2nd ed. Oxford: Blackwell Scientific Publications.

Grafen A. 2007. Detecting Kin Selection at Work Using Inclusive Fitness. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 274: 713–719.

Haldane J. B. S. 1932. *The Causes of Evolution*. London: Longmans and Green.

Haldane J. B. S. 1955. *Population Genetics*. *New Biology*. New York: Penguin Books.

Hamilton W. D. 1964. The Genetical Evolution of Social Behaviour: I, II. *Journal of Theoretical Biology* 7: 1–52.

Hauser M. D., Chen K., Chen F., and Chuang E. 2003. Give unto Others: Genetically Unrelated Cotton-Top Tamarin Monkeys Preferentially Give Food to Those Who Give Food Back. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 2363–2370.

Hölldobler B., and Wilson E. O. 1990. *The Ants*. Cambridge: The Belknap Press of Harward University Press.

Hooff J. van, and Schaik C. van 1994. Male Bonds: Affiliative Relationships among Nonhuman Primate Males. *Behaviour* 130: 309–337.

Humphrey N. K. 1976. The Social Function of Intellect. *Growing Points in Ethology* / Ed. by P. P. G. Bateson and R. A. Hinde, pp. 303–317. Cambridge: Cambridge University Press.

Huxley T. H. 1893. *Evolution and Ethics*. London: Macmillan.

Jarvis J. U. M. 1981. Eusociality in a Mammal: Cooperative Breeding in Naked Mole-Rat Colonies. *Science* 212: 571–573.

Jolly A. 1966. Lemur Social Behaviour and Primate Intelligence. *Science* 153: 501–506.

Judd T. 2000. Division of Labour in Colony Defence against Vertebrate Predators by the Social Wasp. *Polistes fuscatus*. *Animal Behaviour* 60: 55–61.

Judd T. M., and Sherman P. W. 1996. Naked Mole-Rats Recruit Colony Mates to Food Sources. *Animal Behaviour* 52: 957–969.

Kendrick K. M., Leigh A., and Peirce J. W. 2001. Behavioral and Neural Correlates of Mental Imagery in Sheep Using Face Recognition Paradigms. *Animal Welfare* 10: 89–101.

Kitchen D. M., Cheney D. L., and Seyfarth R. M. 2005. Male Chacma Baboons (*Papio Hamadryas Ursinus*) Discriminate Loud Call Contests between Rivals of Different Relative Ranks. *Animal Cognition* 8: 1–6.

Koenig W. D., and Dickinson J. L. (eds). 2004. *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge: Cambridge University Press.

Krause J., Hoare D. J., Croft D., Lawrence J., Ward A., Ruxton G. D., Godin J. G. J., and James R. 2000. Fish Shoal Composition: Mechanisms and Constraints. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 2011–2017.

Kropotkin P. 1902. *Mutual Aid: A Factor of Evolution.* Reprinted in 1998. London: Freedom Press.

Lawick van H., and Lawick-Goodall van J. 1970. *Innocent Killers*. London: Collins.

Malcolm J. R., and Marten K. 1982. Natural Selection and the Communal Rearing of Pups in African Wild Dog (*Lycaon pictus*). *Behavioural Ecology and Sociobiology* 10: 1–13.

Mann K. D., Turnell E. R., Atema J., and Gerlach G. 2003. Kin Recognition in Juvenile Zebrafish (*Danio Rerio*) Based on Olfactory Cues. *Biological Bulletin* 205: 224–225.

Massey A. 1977. Agonistic Aids and Kinship in a Group of Pigtail Macaques. *Behavioural Ecology and Sociobiology* 2: 31–40.

Mateo J. M. 2004. Recognition Systems and Biological Organization: The Perception Component of Social Recognition. *Annales Zoologici Fennici* 41: 729–745.

Maynard Smith J. 1974. The Theory of Games and Animal Conflicts. *Journal of Theoretical Biology* 47: 209–221.

Maynard Smith J. 1989. *Evolutionary Genetics*. Oxford: Oxford University Press.

Maynard Smith J., and Price G. R. 1973. The Logic of Animal Conflict. *Nature* 246: 16–18.

Michener C. D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Cambridge, MA: Harvard University Press.

Mitani J. C., Watts D., Pepper J., and Merriwether D. A. 2002. Demographic and Social Constraints on Male Chimpanzee Behaviour. *Animal Behaviour* 63: 727–737.

Mitani J. C., and Watts D. 2005. Correlates of Territorial Boundary Patrol Behaviour in Wild Chimpanzees. *Animal Behaviour* 70: 1079–1086.

Moore S. J., and Battley P. F. 2003. Cockle-Opening by a Dabbling Duck, the Brown Teal. *Waterbirds* 26(3): 331–334.

Parr L. A., and de Waal F. B. M. 1999. Visual Kin Recognition in Chimpanzees. *Nature* 399: 647–648.

Pfennig D. W., Collins J. P., and Ziemba R. E. 1999. A Test of Alternative Hypotheses for Kin Recognition in Cannibalistic Tiger Salamanders. *Behavioral Ecology* 10: 436–443.

Rendall D., Rodman P. S., and Emond R. E. 1996. Vocal Recognition of Individuals and Kin in Free-Ranging Rhesus Monkeys. *Animal Behaviour* 51: 1007–1015.

Reznikova Zh. 2007. *Animal Intelligence: From Individual to Social Cognition.* Cambridge: Cambridge University Press.

Reznikova Zh., and Iakovlev I. 2008. Development of Aggression as a Possible Basis of ‘Professional’ Specialization in Ants. *Doklady Biological Science* 418: 56–58.

Reznikova Zh., and Novgorodova T. 1998. The Importance of Individual and Social Experience for Interaction between Ants and Symbiotic Aphids. *Doklady Biological Sciences* 359: 173–175.

Reznikova Zh., and Panteleeva S. 2001. Interaction of the Ant *Myrmica rubra* L. as a Predator with Springtails (Collembola) as a Mass Prey. *Doklady Biological Sciences* 380: 475–477.

Reznikova Zh., and Panteleeva S. 2008. An Ant's Eye View of Culture*:* Propagation of New Traditions through Triggering Dormant Behavioural Patterns. *Acta Ethologica* 11(2): 73–80.

Reznikova Zh., and Ryabko B. 1994. Experimental Study of the Ants Communication System with the Application of the Information Theory Approach. *Memorabilia Zoologica* 48: 219–236.

Reznikova Zh., and Ryabko B. 2003. In the Shadow of the Binary Tree: Of Ants and Bits. *Proceedings of the 2nd Internat. Workshop of the Mathematics and Algorithms of Social Insects* / Ed. by C. Anderson and T. Balch, pp. 139–145. Atlanta: Georgian Institute of Technology.

Rice S. H. 2004. *Evolutionary Theory. Mathematical and Conceptual Foundations*. Sunderland, MA: Sinauer Associates, Inc. Publishers.

Robson S. K., and Taniello J. F. A. 2002. Transient Division of Labour and Behavioral Specialization in the Ant. *Formica schaufussi*. *Naturwissenschaften* 89: 128–131.

Ryabko B., and Reznikova Zh. 2009. The Use of Ideas of Information Theory for Studying ‘Language’ and Intelligence in Ants. *Entropy* 11/4: 836–853.

Sherman P. W., Jarvis J. U. M., and Alexander R. D. (Eds.) 1991. *The Biology of the Naked Mole-Rat*. Princeton, NJ: Princeton University Press.

Silk J. B. 1999. Male Bonnet Macaques Use Information about Third-Party Rank Relationships to Recruit Allies. *Animal Behaviour* 58: 45–51.

Sinervo B., and Colbert J. 2003. Morphs, Dispersal, Genetic Similarity and the Evolution of Cooperation. *Science* 300: 1949–1951.

Sinervo B., and Lively C. M. 1996. The Rock-Paper-Scissors Game and the Evolution of Alternative Male Reproductive Strategies. *Nature* 380: 240–243.

Skutch A. F. 1935. Helpers at the Nest. *Auk* 52: 257–273.

Snowdon C. T., and Soini P. 1988. The Tamarins, Genus *Saguinus*. *Ecology and Behaviour of Neotropical Primates.* Vol. 2 / Ed. by R. A. Mittermeier, A. F. Coimbra-Filho, and G. A. B. da Fonseca, pp. 223–298. Washington, D.C.: World Wildlife Fund.

Sober E. R., and Wilson D. S. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behaviour*. Cambridge, MA: Harvard University Press.

Stander P. E. 1992. Cooperative Hunting in Lions: The Role of the Individual. *Behavioural Ecology and Sociobiology* 29: 445–454.

Stern D. L., and Foster W. A. 1996. The Evolution of Sterile Soldiers in Aphids. *Biological Review* 71: 27–79.

Tomasello M., and Call J. 1997. *Primate Cognition*. Oxford: Oxford University Press.

Tóth E., and Duffy J. E. 2005. Coordinated Group Response to Nest Intruders in Social Shrimp. *Proceedings of the Royal Society of London*. *Series B*, *Biology Letters* 1: 49–52.

Trivers R. L. 1971. The Evolution of Reciprocal Altruism. *Quarterly Review of Biology* 46: 35–57.

Waal F. B. M. de. 1982. *Chimpanzee Politics. Power and Sex among Apes*. New York: Harper and Row. (Republished in 2000, Baltimore: Johns Hopkins Universitry Press.)

Waal F. B. M. de, and Berger M. L. 2000. Payment for Labour in Monkeys. *Nature* 404: 563–563.

Weir J. S. 1958. Polyethism in Workers of the Ant *Myrmica*. *Insectes Sociaux* 5: 97–128.

Wheeler W. N. 1928. *The Social Insects: Their Origin and Evolution*. London: Kegan Paul.

Wilkinson G. S. 1984. Reciprocal Food Sharing in the Vampire Bat. *Nature* 308: 181–184.

Wilson E. O. 1971. *The Insect Societies*. Cambridge, MA: Belknap Press.

Woolfenden G. E., and Fitzpatrick J. W. 1984. *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton, NY: Princeton University Press.

Abstract

Altruistic behaviour of animals is still enigmatic for evolutionary biologists in many aspects, although a great deal of data have been analysed and rational concepts have been developed such as the theory of inclusive fitness and the theory of reciprocal altruism. Altruistic behaviour in animal societies is based, to a greater or lesser extent, on the division of roles between individuals in dependence of their behavioural, cognitive and social specialisation. It is a challenging problem to find room for intelligence within the framework of social specialisation in animal communities. In this review characteristics of different levels of sociality are considered, and the role of flexibility of individual behaviour in functional structure of animal communities is analysed. In some situations behavioural, cognitive and social specialisation can be congruent; maybe this is the formula for happiness in animal societies.