Livestock behavior - By what means can individual strategies be beneficial to a group?

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Abstract — Most livestock species are social, gregarious and display a hierarchical dominance within the group. Although domestication has altered some traits, behavioral strategies were not eliminated by this process. The aim of this review is to elucidate the role of individual behavioral strategies towards the group and to explain how each strategy contributes to the group fitness. Anti-predator strategies include forming large groups, vigilance behavior, gregarious nesting behavior and cooperative self-defense. Feeding strategies include flock feeding assemblies, synchronization and social facilitation. Sexual strategies depend on the species, as mating systems and group structures vary. There are many ways in which individual strategies can be beneficial to the group. Individuals may play different roles depending on its rank in hierarchical dominance. In livestock farming systems, social needs may be taken into consideration when handling the animals to avoid stress and risk of injuries. Moreover, an understanding of the behavioral strategies contributes to improve animal welfare and increase productivity.

Keywords: fitness, domestic species, anti-predator behavior, feeding behavior, sexual behavior

Introduction

Many species of vertebrates and most of domestic livestock species are social. Group confer many advantages to an individual, such as protection against predators, access to food and mates and conditions that favor the survival of the young (Arnold, 1985). However, there are also some disadvantages of living in a group: competition for food, competition for mates and susceptibility to contagious diseases (Alexander, 1974). Moreover, there is evidence that larger groups are more likely to be perceived and attacked by predators (Hebblewhite & Pletscher, 2002). Yet, when in a group, an individual is less likely to being killed by a predator since all other group members are subject to predation. Thus, it appears that to many prey species, it is more advantageous to live in a group than in solitary.

In order to maintain the group cohesion and assure its robustness, individuals adopt certain behavior strategies. These strategies may be performed by a few individuals only, or by the whole group. Nonetheless, they always have as purpose the benefice the group. By assuring the maintenance of the group, the individual is not only investing in its own survival, but also increasing its fitness. Hunt & Hodgson (2010) define fitness as "a measurable feature of alleles, genotypes or traits of individuals that predicts their numerical representation in future generations". Therefore, fitness relies not only in the individual's survival, but also in his success to reproduce and guarantee of the survival of the offspring, conditions that are favored when living in a group.

Sociality is adopted by several species as a tool to improve fitness. Group confer advantages in access to food and reduces probability of being killed by a predator, which leads to increase in rates of survival. Besides, individuals living in groups also benefit from access to mates, increasing the chances of reproducing and passing its genes. Lastly, the group provides conditions that favors the survival of the young, guaranteeing the persistence of the genes in future generations. Therefore, all of these three conditions offered by the group increase individual fitness. But when joining or staying in a group, an individual is guaranteeing the persistence of these conditions, i.e. the individual contributes to the robustness of the group.

Livestock species are known for being mostly gregarious. In fact, gregariousness was one of the major traits which favored domestication. Likewise, hierarchical dominance in the group is a desirable trait, since it allows man to take the role of the dominant animal. Other advantageous traits include short flight distance, ability to breed in captivity, precocious young and easily supplied diets. Morphological and behavioral changes can be observed in domesticated species. Small species became larger, so as to produce more meat. Large species became smaller, so they were easier to handle. Behavioral strategies such as sexual competition or anti-predator behavior have now smaller weighting in total fitness. Moreover, domestic animals show lower motivation for foraging and inferior ability to adapt their foraging strategy to the environment. All these modifications allowed livestock species to adapt to captivity. Behavior traits, however, did not disappear with domestication. Instead, the threshold to their manifestation have changed. A detailed review on how these traits have changed with domestication is given by Mignon-Gastreau et al., (2005).

It is important to remember that dominance and leadership are not synonyms. A dominant member enjoys privileged access to resources such as food, water, shelter and access to mates. Nevertheless, a dominant individual is not always the leader (i.e. the one who is followed by its companions). While in most domestic species dominance is found in males, leadership is

usually taken by older individuals. A study on sheep (Rowell & Rowell, 1993) found that in a female flock, led moves were 82% of the time performed by the oldest ewe and 16% by second oldest. Rams flock did not show clear tendency of leadership, but when both groups merged, the oldest ewe was the leader in 100% of the observations.

In farming systems, group structures is different from those found in feral animals, since they are established by man. However, the behavioral needs of a species cannot be removed so easily. As explained previously, domestication did alter the threshold for manifesting a behavior response, but it did not extinguish it. Understanding individual and social behavior strategies is fundamental to improve animal handling, attain animal welfare and assure productivity.

The aim of this review is to enlighten the role of individual behavioral strategies towards the group. Emphasis is given to livestock species, although wild species will also be described for comparison and understanding of domestic species.

Anti-predator behavior

One of the most important benefits provided by the group is the lower probability of being caught when encountering a predator. This is explained by a "dilution effect" due to the presence of other potential preys (Roberts, 1996). Hence, individuals benefit each other by living in a group. Furthermore, in larger groups, there is the advantage of the "many eyes effect", i.e. more individuals may be vigilant, and consequently, the chances of detecting a predator are higher (Pulliam 1973). As a consequence, individuals spend more time feeding and less time being vigilant.

A study in a wild population of Defassa waterbuck (*Kobus ellipsiprymnus defassa*) in a predation risk area revealed decrease in individual vigilance as group size increased. At the same time, collective vigilance, i.e. the proportion of time during which at least one individual was being vigilant increased significantly. The same study revealed the presence of collective waves of vigilance, which suggests that scans did not happen independently (Pays et al, 2007). In fact, coordinated vigilance is uncommon in nature, though it has been observed in some small mammals (Clutton-Brock et al., 1999) and birds (McGowan & Woolfenden, 1989). A logical explanation for this rarity is that such coordination is too costly and requires monitoring other members. Furthermore, when foraging in groups, individuals face competition for food, which could represent an obstacle to the functioning of coordinated vigilance.

Previous studies on sheep have demonstrated that when group size is increased, animals spend more time grazing (Penning et al, 1993) and less time being vigilant (Michelena et al., 2012). Penning et al (1993) have studied feeding behavior in groups from 1 to 15 and observed

that the groups of one and two individuals had significantly shorter meals than the others. Similarly, cattle display higher rates of individual vigilance in groups of less than six animals, as revealed by a study in a predation risk area (Kluever et al, 2008). Besides, the same study noticed a decrease in foraging and an increase in vigilance in cows soon after losing a calf to a predator. One possible explanation for higher rates of vigilance in groups of up to five individuals is that these animals have a perception of being in higher risk. For instance, an individual in a group of four has 25% of being killed if a predator succeeds in the attack. Instead, if this animal is in a group of 40, chances drop to 2,5%. The increased time spent feeding when in a group can also be explained by social facilitation, which will be discussed in the next topic.

Similarly to ruminants, ostriches individual vigilance decreases when group size increases. In addition, vigilant behavior is more influenced by the presence of another individual than by vigilance status of the latter (Bertram, 1980). This may be explained by a lower perception of risk or by social facilitation. These observations were recorded from groups no bigger than four individuals.

The perceived protection offered by the group can have positive impact on fitness by improving forage efficiency. Apart from the decrease in individual time spent being vigilant mentioned in the examples above, increased group size can result in larger foraging area. When in groups, European rabbits travel significantly farther distances to exploit food, as opposed to solitary rabbits who remain closer to a cover (Villafuerte & Moreno, 1997). It suggests that when solitary, rabbits perceive their risk of being predated as higher than when in a group.

By simulating predator attack on laying hens, Riber (2012) found evidence that gregarious nesting is an anti-predator strategy. During a 5 day period in which hens were exposed daily to a simulated attack, gregarious nesting was significantly more frequent than in the 5 previous and subsequent days. However, the same author states that gregarious nesting is found more frequently in commercial laying hens as opposed to feral hens.

Although rare, cooperative defense have already been observed in wild bighorn sheep (*Ovis Canadensis*) when facing attack by coyotes (*Canis latrans*) (Shank, 1977; Goodson & Stevens, 1994). Such events are rare and unexpected, since it is costly and risky. This mobbing strategy is more frequently observed in larger species of preys, such as elks.

A summary of anti-predator strategies is displayed in Table 1.

Table 1. Anti-predator strategies

Strategy	Functioning	Advantage observed	Reference
Increasing group numbers	By increasing the size of the group, individuals minimize its probability of being caught ("dilution effect") It is more likely that at least one individual is being vigilant, so the chances of detecting a predator are higher ("many eyes effect")	Decreased individual vigilance	Pays et al, 2007 (Defassa waterbuck) Michelena et al 2012 (sheep) Kluever et al, 2008 (cattle) Bertram, 1980 (ostrich)
		Increased overall vigilance	Pays et al, 2007 (Defassa waterbuck)
		Increased time spent feeding	Penning et al, 1993 (sheep)
		Larger foraging area	Villafuerte & Moreno, 1997 (rabbit)
Gregarious nesting	Laying hens share nests for oviposition		Riber 2012 (chicken)
Cooperative defense	Group members mob to defend against a predator	The predator is confronted by several individuals and is compelled to move away	Shank, 1977; Goodson & Stevens, 1994 (bighorn sheep)

Feeding behavior

Apart from profiting from the dilution effect, in some species group foraging is a main advantage in reducing the cost of food finding. Feeding assemblies operate as information centers for food finding in both fish (Pitcher et al., 1982) and birds (Ward & Zahavi, 1973). The main advantage of this strategy is reducing the cost of foraging and finding food faster than in solitary.

Domestic ruminants tend to synchronize behaviors within the herd or flock. Grazing activity occurs mainly during the day, normally with two important periods around sunrise and sunset (Arnold, 1985). Behavior synchronization has been proved on sheep (Rook & Penning, 1991) and cattle (Rook & Huckle, 1995). Although there is a physiological component influencing circadian rhythms (Dukes, 2006), the behavior synchronization can also be explained by social facilitation. Clayton (1978) defines social facilitation as "an increase in the frequency or intensity of responses or the initiation of particular responses already in an animal's repertoire, when shown in the presence of others engaged in the same behavior at the same time." Indeed, synchronization is shown to be stronger in the beginning than in the end of behavior bouts (Rook & Penning, 1991).

A study on vertical social learning in piglets (Oostindjer et al., 2011) have evaluated the influence of observation and participation of the sow in the piglets' feeding behavior. Both treatments showed significantly higher intake of food than control group, who could neither see nor participate in the mothers' meal. There was no significant difference in food intake between the two treatments, which suggests that visual contact is enough for the piglets copy their mother's behavior.

In stabled ponies, social facilitation occur when visual contact with the neighbors is allowed (Sweeting et al., 1985). The ponies spent significantly more time standing non-alert when visual contact was blocked. Differently, when visual contact was allowed, they spent significantly more time eating. Interestingly, in this study animals were not prevented from auditory and olfactory contact. Similarly, sheep spend significantly more time eating when in groups (Penning et al., 1993).

Group members' influence on feeding behavior is not restrict to time spent eating and food intake. By demonstrating which foods are safe to eat and which are not, individuals help naïve companions to improve their diet selection. In an experiment on sheep, Chapple et al. (1987) has observed significant increase in the intake of a new food (wheat) by naïve individuals in the presence of experienced sheep. Experienced individuals then take the role of the teachers in this situation. When it comes to feeding, learning by observing a companion is less costly and less risky than learning through trial and error. Therefore, experienced individuals contribute to improve the fitness of the group by teaching naïve individuals.

A study on sheep (Thorhallsdottir et al., 1990) have tested social influence on individuals conditioned to avoid an experimental food (calf-manna pellets). In addition to the new food, the treatment group was given lithium chloride (LiCl) which causes indigestion, whereas control group was given sodium chloride (NaCl). When exposed with untrained sheep to alfalfa and experimental food, conditioned ewes kept avoiding the latter. Contrarily, in the same situation, lambs have increased ingestion of experimental food from roughly 1% to 12% of that ingested by controlled lambs. This experiments measured animals in pairs, ewes with ewes and lambs with lambs. Lamb increase in consumption of the experimental food could have been even more significant if they were paired with control ewes. In the same study, when given no option but the experimental food, both lambs and ewes have increased significantly the intake of it. Such finding may suggest that conditioned food aversion can be reversed by social influence when no other food is available. Nonetheless, care should be taken on this assumption, since this trial lasted five days. As the cost for eating was no more than an indigestion, animals chose to assume the risk, given that the other option was hunger. Using the same aversion

training with lithium chloride (LiCl), a study on heifers have demonstrated extinction of the aversion by social facilitation (Ralphs & Olsen, 1990). It is possible that conditioned individuals note the absence of poisoning in the companions, and then resume eating.

When grazing on heterogeneous pastures, sheep use spatial memory to locate preferred food patches (Edwards et al., 1996). Experience in diet selection and knowledge of the territory may explain why older individuals frequently take the role of the leader (Rowell & Rowell, 1993). A summary of the influence of the group on feeding behavior is shown in Table 2.

Table 2. Influence of group companions on feeding habits and diet selection

Species	Increase in food intake when with others (SF)	Increase in time spent feeding when with others (SF)	Increased intake of a novel food when with others (SF)	Extinction of CFA by SF	Extinction of CFA when no other option	Reference
Pig	X					Oostindjer et al., 2011
Horse		X				Sweeting et al., 1985
Sheep		X				Penning et al., 1993
Sheep	X		X			Chapple et al., 1987
Sheep				X	X	Thorhallsdottir et al., 1990
Cattle				X		Ralphs & Olsen, 1990

CFA = Conditioned food aversion; SF = Social facilitation

Sexual behavior

When it comes to reproduction, one of the main improvement in fitness by living in a group is the increased probability of survival of the offspring. Although young animals are more susceptible to predator attacks, the group confer an extra protection because of the dilution effect.

While female reproductive success depends on access to environmental resources (e. g food, shelter or nesting sites); males depend solely on access to females. Consequently, males invest in competition strategies for breeding (Mendl & Held, 2001).

Most mammals, including livestock species, are polygamous with female-only parental care. When female groups are relatively small and defendable by one male, polygyny occurs. This social structure is observed in horses, where a single stallion defends a group of mares and foals. When females form large groups, defending it becomes too costly. In this case, the mating strategy is to compete for females during the breeding season. This system observed in cattle and sheep. The occurrence and establishment of mating systems in mammals are detailed in the review of Clutton-Brock (1989).

In feral cattle, three types of groups have been observed. The first one is composed of females with young calves and sub-adult males. The second one consists of adult and sub-adult males. Finally, the third one is a mixed sex group that forms essentially during the breeding season, when males join the first group (Daycard, 1990). Similarly, in sheep, flocks of females and young males are joined by adult males during the breeding season. In these species, breeding season is known as rut, or rutting period. In this period, males display series of fight to establish dominance and thus privilege in breeding. Females, however, get to choose their mates, mostly based on courtship performance and dominance status (Shackleton & Shank, 1984).

Horses live in harem system groups, which means one male has exclusive mating privilege. In this society, colts disperse and form temporary groups of bachelor males. Females also disperse, which may be a strategy to prevent inbreeding. Although harems are supposedly polygamous system, it has been proved that the dominant male may not always have exclusive breeding when it dominates too many females. In this situation, it becomes more difficult to prevent mares from mating with rival stallions (Kaseda & Khalil, 1996).

Because dominance leads to privileged access to food and greater success in breeding, individuals within the same group may have different values of fitness according to their ranking. Low ranking males, for instance, have limited access to mates and very little access to food when compared to higher ranks. Such inequalities bring up the question of why low ranking individuals remain in the group in spite of all its disadvantages.

In fact, reproduction is not the only way to improve individual fitness. If fitness is the capacity of passing its genes to future generation, it can also be achieved by helping kin survival and reproduction. This explains the role of low ranking individuals in the fitness of the group. Moreover, despite inequalities, it may be more advantageous to a low ranking individual to remain in the group than assuming the risk of deserting.

Applications in livestock farming

In livestock farming systems, groups are established by man and often consist of individuals of the same age and/or sex. In order improve grazing exploitation of a paddock, it is interesting to combine experienced with naïve individuals. Experienced animals will lead naïve through the territory, showing the location of better patches and teaching which plant species are edible. Nonetheless, when in a paddock infested by poisonous species, care should be taken, as there is evidence that social facilitation can extinguish food aversion.

Young animals should not be deprived from seeing the mother when feeding, as visual contact is vital to learning. Besides, in stabled animals visual contact can allow social facilitation to increase food intake.

In free ranging herbivores, however, it is in small groups that individuals have higher rates of vigilance and lower food intake. In order to achieve better performances, groups larger than six should be considered for sheep and cattle.

Reproduction in livestock systems is frequently controlled by man. In these cases, individuals do not get to chose their mates. However, attention should be paid when putting dominant males together, as there is a risk of competition fights resulting in injuries.

Conclusion

There are many means by which individual strategies are favorable to the group. When an animal chose to join or remain in a group, the probability of each member to being killed by a predator is reduced. In addition, individual vigilance rates decrease, and social facilitation leads animals to spend more time eating. Besides vigilance, some other anti-predator strategies can help the group, such as gregarious nesting and cooperative defense.

Flock feeding is advantageous because it reduces time searching for food. Social facilitation also plays as important role in the food intake and diet selection.

Domestic species show differences in group structure and mating systems. Generally, access to mates is a privilege of the dominants, which result in unequal fitness values between individuals of the same herd. However, low ranking individuals enjoy other advantages of the group and play a different role than the dominants.

Although domestication have diminished the importance of once vital traits for fitness, it did not extinguish the expression of behavioral strategies. It is important to take into consideration the social needs of animals in order to achieve a better productivity. Therefore, understanding individual and group strategies is necessary in livestock farming systems.

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