A

Aggregation

Quentin Fouche[1], Damien Charabidze[1] and Mathieu Lihoreau[2]
[1]CHU Lille, EA 7367 – UTML – Unité de Taphonomie Médico-Légale, Univ. Lille, Lille, France
[2]Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI); CNRS, University Paul Sabatier, Toulouse, France

Definition

An aggregation refers to both the process of grouping and the resulting spatial gathering of animals.

Introduction

Animal aggregations are the most basic form of social life, on top of which more elaborated social behaviors, such as cooperation and division of labor, have evolved. Aggregations are observed across the animal kingdom, from insects all the way to humans. Depending on the developmental stages of animals and the environmental conditions, aggregations can take various forms. They can count just a few individuals or several millions, involve physical contacts or only spatial proximity, be spatially stable or move, and last a few seconds or persist for a long time. Additionally, aggregations can have a stable composition or show a regular turnover of individuals.

Passive Versus Active Aggregations

Two broad types of aggregations are generally considered (Parrish and Edelstein-Keshet 1999). Passive aggregations refer to groups that develop in response to environmental heterogeneities (e.g., shelters, light, food sources, marine currents, or wind), while active aggregations result from inter-individual attraction (e.g., social interactions). In this case, group formation is mediated by social stimuli that are actively emitted (signals), for instance, when animals need to recruit others to a target (e.g., pheromones), or passively displayed cues (e.g., footprints). While passive aggregations always develop around environmental heterogeneities, active aggregations can also be observed in homogeneous environments (e.g., empty arena).

Mechanisms of Grouping

The mechanisms of group formation and disruption have been extensively studied since the 1980s, with the development of self-organization theory and experimental approaches combining behavioral observations, simulations of computational models, and implementation in autonomous robots (Camazine et al. 2003).

J. Vonk, T. K. Shackelford (eds.), *Encyclopedia of Animal Cognition and Behavior*,
https://doi.org/10.1007/978-3-319-47829-6_681-1

Group Formation

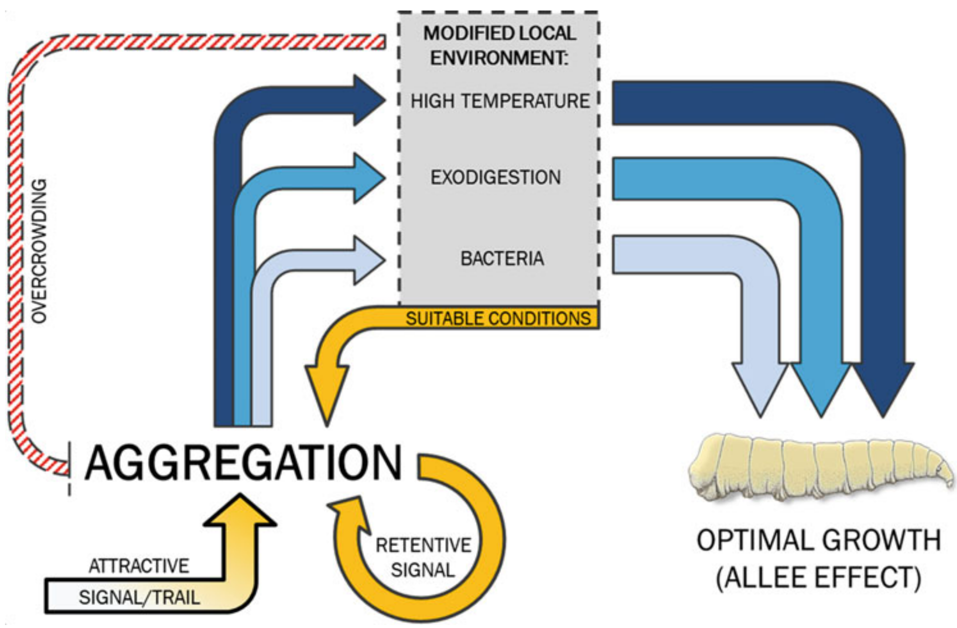
Aggregations develop based on feedback loops that influence an individual's tendency to join others and stay grouped in response to aggregation stimuli (e.g., Lihoreau et al. 2016). Long-range stimuli (e.g., volatile pheromones or visual displays) often have an attractive effect, whereas short-range stimuli (e.g., nonvolatile pheromones or contacts) tend to be retentive. These attractive and retentive effects can be additive, for example, in active aggregations of blowfly larvae where the larger the group the higher the probability that individuals join and stay (Fig. 1).

Collective Movements

Once an active aggregation is formed, various patterns of collective motion can emerge from attraction, repulsion, and alignment forces between individuals (Couzin et al. 2005). Animals can collectively rotate around an empty core (e.g., schooling fishes), dig the food substrate (e.g., drosophila larvae), or migrate to a new favorable environment (e.g., marching locusts). A general feature of these collective movements is their density-dependence. During population outbreaks of desert locusts, nymphs form marching bands that can extend over kilometers. When high densities of nymphs are reached, individuals start to align their displacements, reduce collective changes in direction, and ultimately move together in the same direction (Buhl et al. 2006).

Group Disruption

In most cases groups erode from the independent leaving events of individuals (e.g., animals on a food source become satiated and leave). However, quick synchronized dispersion can also result from social interactions, for instance, in response to a stressing event (e.g., predators). In fruit fly aggregations, the number of immobile individuals



Aggregation, Fig. 1 Mechanisms of group formation and fitness consequences in necrophagous blowfly larvae (Diptera: Calliphoridae). Positive feedbacks are represented by orange arrows. Negative feedbacks are represented in red. Larvae leave a chemical trail as they move on the substrate. These cuticular cues, along with thigmotactism, maintain larvae densely aggregated, which results in deep modifications of the environment. First, the metabolic heat emitted by larvae increases temperature up to 45 °C in large maggot-masses. Second, the exodigestives enzymes and the mechanical action of the hundreds of mouth-hooks break muscular fibers and liquefy fleshes, while highly efficient antimicrobial compounds control the growth of yeast, fungi, and bacteria. The combination of these effects favors the fast development of larvae (Allee effect). In case of overcrowding (e.g., food depletion or overheating), larvae move to the periphery, resulting in a self-regulation of the aggregation has an inhibitory effect on the probability of leaving. But following exposure to an aversive odor (e.g., CO_2), contacts between moving individuals that start fleeing and stationary individuals that did not yet respond to danger trigger collective escape behaviors (Ramdya et al. 2015).

Costs and Benefits of Grouping

Aggregations provide a range of fitness benefits to individuals that typically increase with population density and peak at a critical density. This pattern is known as the "Allee effect."

Predation Risks

Aggregations can reduce predation risks through several mechanisms (Krause and Ruxton 2002). At the most basic level, for any one predator attack, the larger the group of prey animals, the lower the chance that any particular individual will be the victim (i.e., dilution effect). Grouping can also augment the efficiency of vigilance behaviors through information transfer (i.e., many-eyes effect) or distract predators that have more difficulties to focus and catch any single prey (i.e., confusion effect). In conditions of overcrowding, however, aggregations may attract more predators and parasitoids, as well as favor the spreading of diseases and pathogens among group members.

Modifications of Local Conditions

The group itself can have an effect on local conditions and help individuals to cope with natural variations of the environment. Some animals protect themselves from cold by rising temperature above ambient. For moving aggregations, grouping can also reduce energetic expenditure during flight or swim, a benefit resulting from particular group structures (e.g., V formation in birds) that improve the aero- or hydrodynamism of individuals (Weimerskirch et al. 2001). Other animals, such as necrophagous blowfly larvae, modify their food resource by releasing metabolic heat and accumulating exodigestive enzymes that speed up food liquefaction and create favorable conditions for larval development (Fig. 1). At high densities, however, these group effects can become deleterious, leading to self-pollution (e.g., waste accumulation) or thermic stress.

Information Transfer

Grouping may enables individuals to obtain important information about the environment that would otherwise be costly to acquire (Sumpter 2010). In active aggregations, information transfer can lead to collective decision-making whereby individuals agree on an option to take among other alternatives (e.g., a food source, a shelter, a direction). When some individuals detect a suitable option, their change of behavior is perceived by the others that tend to follow their choice. The probability of an individual to follow can depend on a quorum, i.e., a threshold in the number of individuals displaying the behavior. Through this process, large groups have lower probabilities to reproduce "mistakes" (i.e., non-adaptive behaviors) expressed by a single or few individuals. Such collective responses often improve the speed and accuracy of decision-making.

Mixed Species Aggregations

Although less studied, several animals form interspecific aggregations (Boulay et al. 2017). This is the case in birds, where "follower" species can join "leader" species. In such mixed-species flocks, followers can benefit from the anti-predator vigilance of leaders, and thus re-allocate their energy to foraging. If resources are sufficiently abundant for limiting interspecific competition, benefits can be equally distributed between species (e.g., dolphins, seabirds, and sharks aggregating to concentrate large amount of preys), suggesting that the benefits of grouping can also drive the evolution of mutualistic associations.

Conclusion

The benefits of aggregations, their emergent patterns, and their ubiquity among animal species have made them the subject of numerous studies in past and recent decades. While most research has focused on describing the general mechanisms leading to group formation and maintenance across a wide diversity of species, still little is known about the evolutionary processes that drive gregarious behaviors. Future developments in comparative quantitative research and evolutionary modeling are promising avenues to fill this gap.

Cross-References

- ▶ Benefits of Group Living
- ▶ Chemical Cues
- ▶ Costs of Group Living
- ▶ Group Living
- ▶ Group-Spacing and Coordination
- ▶ Optimal Group Size
- ▶ Recruitment
- ▶ Social Behavior

References

Boulay, J., Aubernon, C., Ruxton, G. D., Hédouin, V., Deneubourg, J. L., & Charabidzé, D. (2019). Mixed-species aggregations in arthropods. *Insect science, 26*, 2–19.

Buhl, J., Sumpter, D. J., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., & Simpson, S. J. (2006). From disorder to order in marching locusts. *Science, 312*, 1402–1406.

Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Bonabeau, E., & Theraula, G. (2003). *Self-organization in biological systems* (538pp.). Princeton: Princeton University Press

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature, 433*, 513.

Krause, J., & Ruxton, G. D. (2002). *Living in groups* (210pp.). Oxford: Oxford University Press.

Lihoreau, M., Clarke, I. M., Buhl, J., Sumpter, D. J., & Simpson, S. J. (2016). Collective selection of food patches in *Drosophila*. *Journal of Experimental Biology, 219*, 668–675.

Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science, 284*, 99–101.

Ramdya, P., Lichocki, P., Cruchet, S., Frisch, L., Tse, W., Floreano, D., & Benton, R. (2015). Mechanosensory interactions drive collective behaviour in Drosophila. *Nature, 519*, 233–236.

Sumpter, D. J. (2010). *Collective animal behavior* (312pp.). Princeton: Princeton University Press.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., & Jiraskova, S. (2001). Energy saving in flight formation. *Nature, 413*, 697.