



# CHAPTER I

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## Introduction



## Introduction

Living in groups is a widespread phenomenon throughout many animal species, including most of today's farm and companion animals. For group life to be favoured, the fitness pay-off to each group member must exceed that of living solitary (Mendl & Held 2001). Group-living increases the efficiency to detect, acquire (e.g. via group hunting), and defend food resources, and reduces the individual's risk of a predator attack compared to living individually (Mendl & Held 2001). On the other hand, single individuals or individuals in smaller groups experience less competition (Marshall et al. 2012), and a group of animals is more likely to be detected than a singleton (Krause & Ruxton 2002). An elaborate overview of benefits and cost, as well as of evolutionary and environmental considerations regarding group-living has been provided by Krause & Ruxton (2002). This chapter concentrates on mechanisms relevant in the context of group cohesion and behavioural synchronization. Examples particularly focus on farm animal species, but also include wild species for a broader overview. The term "group" is defined as a composition of multiple conspecifics which are drawn together by social attraction, sharing spatial and temporal proximity.

## Group cohesion

Group cohesion and spatial proximity are the foundation of group living. Group cohesion is often evaluated by assessing animal distribution which is influenced by environmental features, such as habitat structure or forage distribution. Cattle in open (tree-less) habitats aggregate in larger groups than in wooded communities which provide less overview (Dudziński et al. 1982). Based on similar environmental differences, highly selected lowland sheep breeds are more gregarious and disperse less than hill types (Dwyer & Lawrence 1999). Sibbald et al. (2000) observed that interindividual distances between Scottish Blackface ewes increased with plot size, but only up to a size of 133 m<sup>2</sup> per head. Above 200 m<sup>2</sup> per head, the sheep seemed to actively adjust their distances in order to maintain cohesion. Decreasing vegetation quality may increase distances especially between neighbours (Dudziński et al. 1978: free-ranging sheep; Dudziński et al. 1982: free-ranging cattle).

Collective patterns such as group cohesion are primarily observable on the group level but it is important to realize that they emerge from individual interactions (Flierl et al. 1999). From a mechanistic point of view, collective behaviour is shaped by how individuals



interact with each other and with their environment (Sumpter 2010). Interactions between group members enable individuals to gain information about space (when to go) and time (when to do something) which would exceed their own cognitive limitations (Couzin 2008). Minor changes in individual's interactions can evolve to complex group patterns (Couzin et al. 2002). Reactions to signals of peers are used for decision-making at the level of the individual (Michelena & Deneubourg 2011). Global cues may modify these interactions in some cases: during migration of ungulates, individuals may modify their local (self-organizing) interactions with others in reference to global information, such as a general desire to move in a certain direction (Couzin & Krause 2003).

How many group members influence each individual's behaviour is limited by its range of perception (Fernandez & Deneubourg 2011) and the communicative abilities of a species (Ramseyer et al. 2009). In some species such as ants or social caterpillars, cohesion relies mainly on the concept of following the direct predecessor. Individuals adjust their direction sequentially rather than synchronized. Here, cohesive behaviour at the individual level does not necessarily enhance cohesion at the collective level (Fernandez & Deneubourg 2011). Cohesive, synchronized grouping patterns, like the ones prominently exhibited by flocks of birds, fish shoals, and ungulate herds, mainly evolve from interactions with a fixed number of conspecifics, ranging between two or three (Ramseyer et al. 2009: sheep ; Rands et al. 2014: red deer), or up to six to eight topological neighbours (Ballerini et al. 2008: starlings). This assures that the same degree of cohesion is maintained irrespective of density and perturbations (Ballerini et al. 2008). Accordingly, distances between nearest neighbours in sheep tend to remain similar independent of density (Crofton 1958; Arnold & Maller 1985). Shang & Bouffanais (2014) recently used a dynamical mathematical model of locally interacting self-propelled particles (i.e. topologically interacting "particles" which are moving about a two-dimensional plane with constant speed) to reveal that irrespective of group size, a value of approximately ten topological interacting neighbours significantly accelerates the consensus reaching process to levels very close to optimal, especially in the presence of environmental disruptions.

The strength of group cohesion may also be modulated by the quality of social relationships (Michelena et al. 2008). Winfield et al. (1981) combined previously unfamiliar sheep flocks which did not readily integrate into one cohesive group, probably because of social attachment to familiar peers. Accordingly, interindividual distances vary between different dyads (Jørgensen et al. 2011: sheep), and tend to be closer between familiar conspecifics



(Boissy & Dumont 2002: sheep; Gygax et al. 2010: dairy cows). Even different personality types contribute to the maintenance of group cohesion and enable behavioural flexibility at the population level (Wolf et al. 2007: model; Michelena et al. 2010: sheep).

Behaviour of individual group members is highly interdependent (Krause & Ruxton 2002). As a result, cohesion depends on the activities of group members. Usually, group members disperse more widely when grazing, and aggregate more when resting (Le Pendu 1996; Broom & Fraser 2010). As a consequence, distances between resting and migrating individuals could lead to a breakdown of the group. Michelena et al. (2008) demonstrated that groups of sheep with grazing as well as resting members were less aligned than groups exhibiting full behavioural synchronization. The importance of behavioural states for group cohesion becomes evident each time grouped animals abandon a resting place, stop migration to rest, or start to flee. Because behavioural synchronization can be considered a driving force of group cohesion, the following sections further explore its definition, relevance, underlying mechanisms, and mathematical determination.



## Behavioural synchronization

### Definitions

Behavioural synchronization is a common collective phenomenon which occurs in animal aggregations when multiple individuals perform the same activity at the same time. Many collective processes are examples for synchronization, such as synchronous oscillations in neurons (Whittington et al. 1995), synchronized flashing in fireflies (Buck 1988), activity synchronization in ants (Boi et al. 1999), synchronized hatching in some reptile species (Doody 2011), simultaneous clapping in human audiences (Néda et al. 2000). Activity synchronization in farm animals has been described for cows (Rook & Huckle 1995), pigs (Hsia & Wood-Gush 1983), chicken (Collins & Sumpter 2007), sheep (Rook & Penning 1991; Gautrais et al. 2007), or horses (Rifá 1990; Boyd & Bandi 2002).

The terms behavioural “synchronization”, “synchrony”, “synchronicity”, “social facilitation” and “allelomimetic behaviour” have been used interchangeably to describe such phenomena. Definitions are reviewed in Table 1. *Social facilitation* originates from social psychology studies in humans and initially describes the effect that individuals perform better in simple tasks when other individuals are present. Thus, social facilitation originally occurs in the absence of competition, reinforcement, or cooperation (Guérin 1993). Thorpe (1963) describes social facilitation even as “contagious behaviour”, which performed by one individual will act as a releaser for the same behaviour in other individuals, resulting in synchronous behaviour. One of the most popular definitions is the one by Clayton (1976) who characterized social facilitation as an increase of a familiar behavioural trait in the presence of others displaying the same behavioural trait at the same time. In general, social facilitation does not describe the phenomenon of synchronization itself but rather its social causes. Because of terminology inconsistencies, the term social facilitation is not used during the course of the current study.

Similarly, the term *allelomimetic behaviour* does not describe the phenomenon of synchronization itself, but an underlying mechanism or motivation resulting in mutual synchronization between group members. A classic example for allelomimesis is recruitment in social insects, when a forager discovers a food source, and recruits others which in turn recruit more foragers (Deneubourg & Goss 1989). According to Vogel et al. (1950), a species can either be generally characterized as allelomimetic (e.g. dogs, fish, chickens) or non-allelomimetic (e.g. rats). They state that under certain circumstances,



allelomimetic behaviour can lead to social facilitation, e.g. if two animals move towards the same goal, and the slower animal speeds up. In non-allelomimetic animals, social facilitation of feeding may occur in the presence of competition (Harlow 1932: rats).

The dictionary defines *synchrony* as a state which results when things happen, move, or exist at the same time (Merriam-Webster 2014). According to this definition, behavioural synchronization seems like a static entity, which once evolved remains stable. But behavioural synchronization in ungulate groups is a collective process, characterized by spontaneous switches and flexible adaptation to environmental or social factors.

The term *synchronicity* originates from Jung's psychology in the 1950s. It describes external incidents which are coincidentally connected in a meaningful way to an individual's internal experiences. Therefore, it describes a psychic factor, which can be realized subjectively, but which usually cannot be proven objectively (Jung 1952). One example for synchronicity is the seemingly telepathic transmission of thoughts or emotions. In this sense, synchronicity was originally used to explain incidents which could not be explained by direct linking physical mechanism. Recently, occurrence of synchronicity has been clarified as due to moments of mental and physical order that emanate from a seemingly chaotic underpinning of unconscious factors (Cambray 2002). While this appropriately implies interplay of a variety of factors leading to synchronous behaviour (see section *Influential factors*), the term synchronicity still emphasizes the psychological component. Thus, the term *synchronicity* is not properly transferable from human psychology to synchronized behaviour in group living animals.

*Synchronization* describes the maintenance of two processes in step with each other (McGraw-Hill 2003). This definition includes that adaptations are necessary to maintain synchronization. The term *synchronization* seems to best illustrate the processual nature of the emergence of simultaneous behaviour in animals. Therefore, it is consistently applied in the current study. In this study, behavioural synchronization is defined as the non-random, temporally synchronized occurrence of the same activity in multiple members of an animal group.



**Table 1:** Terms used to describe the simultaneous occurrence of the same activity in animal groups or pairs.

Term	Definition	Original source	Context	Source
<b>Synchronization</b>	“The maintenance of one process in step with another” (McGraw-Hill 2003)	mid-19th century: from Greek <i>sun-</i> , together + <i>khronos</i> , time	Behavioural switches resulting in synchronization of behaviour in pairs of animals	Dostálková & Špinková (2007)
<b>Synchrony</b>	“a state in which things happen, move, or exist at the same time” (Merriam Webster 2014)	mid-19th century: from Greek <i>sun-</i> , together + <i>khronos</i> , time	Emergence of synchronized behaviour in groups of sheep	Gautrais et al. (2007)
<b>Synchronicity</b>	Events which coincidentally occur simultaneously in a meaningful way (Jung 2010)	1952: Human psychology, C.G. Jung	Synchronous occurrence of flashing in fireflies	Moiseff & Copeland (1994)
<b>Social facilitation</b>	An animal increases or decreases its behaviour in the presence of another individual even if the other individual does not exhibit the same behaviour (Guérin 1993)	Human social psychology, first studied by Tripplet (1898)	Simultaneous occurrence of grazing, moving, standing, and resting in a herd of horses	Boyd & Bandi (2002)
<b>Allelomimetic behaviour</b>	Any behaviour in which animals do the same thing with some degree of mutual stimulation and consequent coordination (Scott 1956)	From Greek <i>allemo</i> , mutual + <i>mimetikos</i> , imitative	Simultaneous attendance of a functional area by both cows of a dyad	Neisen et al. (2009) Gygax et al. (2010)
			Increase of preening in the common tern in the presence of preening neighbours	Palestis & Burger (1998)
			Allelomimetic feeding in fowl	Hughes (1971)
			Allelomimetic behaviour switches in sheep	Gautrais et al. (2007)



## Evolutionary relevance

Describing a theoretical model on synchronous behavioural interactions among animals, Walker et al. (2010) summarized that the relevance of behavioural synchronization to survival lies in the flexibility of behavioural responses to a changing environment. Rapid synchronized decisions about direction of movement and behavioural switches are crucial for grouping animals (Couzin & Krause 2003). Therefore, behavioural synchronization is frequently acknowledged as a requirement (Clayton 1978; Conradt & Roper 2000; Favreau et al. 2009) or even an indicator (Miller & Wood-Gush 1991; Van Dierendonck et al. 1996; Souris et al. 2007; Michelena et al. 2008) for group cohesion. However, synchronization might be costly to achieve; it implies that all group members have to switch behaviours at the same time. Accordingly, some individuals have to compromise their own activity decisions, including abruption of foraging bouts or resting periods, and possible fitness consequences. The bigger interindividual variations in timing of events, the more costly synchronization becomes for the individual which finally result in spatial group segregation (Ruckstuhl 1998; Conradt & Roper 2000). Conversely, Pérez-Barbería et al. (2007) found high synchronization values before group segregation occurred which led them to propose that group segregation actually succeeded an increased synchronization. However, their results made it impossible to clearly separate if high synchronization induced segregation or if grouping mechanisms amplified synchronization.

Conradt & Roper (2000) hypothesize that many benefits of group-living only apply if group members synchronize their behaviour. Examples are facilitation of social information transfer about direction of movement or location of feeding resources (Bailey et al. 2000; Couzin et al. 2002; King & Cowlshaw 2007), or reduction of predation risk by synchronization of vigilance behaviour (Pays et al. 2007; Sirot & Touzalin 2009). Aggregation, e.g. during synchronized resting, is known as a defence against flying insects (Rutberg 1987: feral horses; Mooring et al. 2003: bighorn sheep) or as a means to regulate body temperature (Huynh et al. 2005: huddling in pigs). Studies on sticklebacks have shown that simple synchronized interactions can reduce predations risk by more than 50% and are therefore relevant for survival and evolutionary processes, like reciprocal altruism (Axelrod & Hamilton 1981; Milinski 1987). However, for some behavioural patterns, a certain degree of desynchronisation might be preferable: sleeping rather occurs in collective waves, which means that the proportion of sleeping group members rises and declines systematically. This





increases the chances for predator detection, and therefore survival, compared to perfect synchronization (Beauchamp 2011).

Conradt & Roper (2007) argue that any synchronous shared decision to switch behaviours was evolutionary stable, because the benefits from acting together outweigh the benefits from more suitable individual timing. Dostálková & Špinka (2010) modelled the probabilities and costs of perfect synchronization, partial synchronization, no synchronization, and splitting into subgroups. While a lower than perfect degree of synchronization was the most stable solution, full synchronization is usually the optimal solution in terms of costs and benefits for the group. Obviously, certain mechanisms ensure that full synchronization is maintained during repeated synchronization challenges (Dostálková & Špinka 2010). The following section provides an overview of mechanisms known to affect synchronization.

## **Influential factors**

Behavioural synchronization is triggered by reactions to various external (temporal and spatial) stimuli and internal factors (hunger, fatigue, health), as well as by reactions to conspecifics based on social interactions. Social and environmental factors are probably interwoven and to separate them is a big challenge in the study of collective movement (Pillot et al. 2011).

### *External influences*

Individuals temporally synchronize their behavioural patterns with external events such as circadian rhythms, the phenology of plants as a food resource, or attacks of predators (Engel & Lamprecht 1997; Walker et al. 2010). In most organisms, the light cycle serves as a primary *zeitgeber*, i.e. temporal entraining agent which synchronizes an individual's behavioural rhythm with the external world (Davidson & Menaker 2003). Even when the same light cycle is maintained daily rhythms can be modified by stabling conditions (Piccione et al. 2008). Although milking or feeding times can act as artificial synchronizers on behavioural synchronization (Miller & Wood-Gush 1991: dairy cows), synchronization has been shown to vary with time of day even in the absence of milking-times (Stoye et al. 2012: beef cattle).



Also spatial factors (habitat type, forage abundance) can have an impact on the degree of synchronization (Ruckstuhl & Neuhaus 2001; King & Cowlshaw 2009). Whereas spatially similar conditions stimulate synchronization (Engel & Lamprecht 1997), group synchronization might be difficult to preserve in heterogeneous habitats which prohibit visual contact between group members or aggregated presence at the same location, or which even induce monopolisation of resources and competition (Ruckstuhl & Neuhaus 2001; Vahl et al. 2007). Focardi & Pecchioli (2005) hypothesize that synchronization of movement is lower in habitats which are 'open', i.e. provide a vast view and facilitate group cohesion. Accordingly, in baboons synchronization was lower in 'open' desert habitats than in woodland habitats with an obstructed view where cohesion was probably more difficult to preserve (King & Cowlshaw 2009). However, studies comparing group synchronization under different farm management conditions are scarce. In laying hens, overall synchronization has been shown to increase with cage size (Jenner & Appleby 1991). Cows have been observed to exhibit more behavioural synchronization outdoors than in a barn, probably due to lack of circulation space indoors (Miller & Wood-Gush 1991). Limited lying space has been shown to reduce synchronization of lying in dairy cows (Krohn et al. 1992: tie stall vs. pasture; Nielsen et al. 1997: pens with lying areas of 1.8 m<sup>2</sup>, 2.7 m<sup>2</sup>, or 3.6 m<sup>2</sup>; O'Driscoll et al. 2008: free-stall vs. out-wintering pad) as well as in sheep (Bøe et al. 2006: stable with 1.0 m<sup>2</sup> vs. 0.5 m<sup>2</sup> lying space). Neither pen shape (Bøe et al. 2006: pen width 0.45 m/ head vs. 0.90 m/ head) nor different types of pen partitions (Jørgensen et al. 2009: 1.5 m<sup>2</sup>/ head) modified lying synchronization in sheep.

In herbivores, feed intake and digestion represent the predominant behavioural traits which are strongly affected by ultradian rhythms and seasonal variability of the vegetation (Scheibe et al. 1999). Boulos & Terman (1980) argue that the periodic expression of most behavioural patterns might be linked to the externally restricted periodicity of food intake. Brouns & Edwards (1994) compared two groups of pigs fed once daily with two groups of pigs fed *ad libitum* and discovered that synchronization was actually reduced in the *ad libitum* diet, probably because the food induced competition although it was abundant. Not surprisingly, also the number of troughs can affect synchronization. Ingrand et al. (2001) observed in dairy cows kept in a loose-housing system that feeding synchronization decreased when one manger was available compared to two, probably due to competition. However, sheep used feeding space more synchronously when it was reduced (Bøe & Andersen 2010: 1:1 vs. 1:3 animals per feeding space).