

# On clusters and formations: birds flying in groups



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15 September 2009

# Abstract

Flocks of birds perform some aerial phenomena, which have amazed many of its viewers. This thesis is a literature review, which concerns the three major questions of 'When', 'How' and 'Why' birds fly in flocks. Flying flocks are roughly dividable in two types: ball shaped clusters and line formations.

Whereas cluster flying is commonly used throughout the year by groups of birds, for example while transiting between their roosting and their foraging sites, formation flight is almost specifically used for migration. The departure time of migration is a critical moment in the annual cycle of the bird. The exact moment of departure is an optimization of several external and internal factors, including migrating distance, energy reserves and weather conditions.

Clusters have a three-dimensional structure and tend to be rather disorganized. When a predator is nearby, clusters often start to perform rapid manoeuvres. Previously believed to be coordinated by telepathy or electromagnetic communication, due to high-speed filming scientists have determined that these manoeuvres are initiated by one individual bird and followed by the rest of the flock. The individual fulfilling the role of initiator changes from moment to moment. The most likely explanation for movement in a cluster is a self-organization mechanism where each bird applies a few behavioural rules in response to local information from neighbouring birds.

There are different kinds of formations, ranging from an acute V-formation to a U-shaped bow. Although the total energy saving is the same for different formations, it differs for individual birds in the group. In an acute formation, the leader gains little or no energy savings, while in a U-formation the energy savings are more egalitarian. A reason for obtaining a specific formation may be related to kin-selection or reciprocity, although no empirical evidence for this hypothesis has been found yet.

Several specific reasons have been put forward for birds to fly in clusters, mainly regarding predation prevention. These advantages include increased predator detection, a dilution effect, physical protection of neighbours and a confusion effect. Two hypotheses exist for a structured formation, like the well known V-shape. One is the aerodynamic advantage hypothesis, in which birds conserve energy by taking advantage of the upwash vortices created by the wings of the birds in front. The other is the communication and orientation hypothesis, in which birds make use of their position for their combined orientation experience and visual communication. These explanations are not mutually exclusive, and various studies have given support to both of them. However, no conclusive evidence has been found for any of the both hypotheses. There is still a debate going on between supporters and critics of both hypotheses which remains unsolved upon till now.

A review of the literature concerning the subject of flock flying shows that the use (the 'When') and the organization (the 'How') of flock flying have been thoroughly researched, which has led to a consistent view on these subjects. However, thorough research on the main reasons for flock flying (the 'Why') has not given a clear view yet. Also behavioural aspects of the organization and departure are still shrouded. These subjects still raise enough questions to provide research options for years to come.

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# Introduction

Birds are everywhere around us. Sometimes they fly alone, but often they are encountered in a group of hundreds or even thousands of birds. So there probably is an advantage to living in a group. Groups of birds display some awe inspiring phenomena. Who has not wondered why birds in a flock do not collide while making their manoeuvres of wheeling and turning? Or even how the birds decide to make a manoeuvre in the first place and in which direction? In other occasions we see birds in almost perfect V-shapes flying over high in the air. The apparent chaos has been replaced by a structured formation. This V-shape can not be a coincidence as it is also applied when military aircrafts fly together. So what are the advantages for the birds?

The subject of this thesis is the phenomenon of birds flying in groups. A group of birds is called a flock. Flocks are roughly dividable in two types: Clusters and Formations. Clusters are three-dimensional, tend to be rather disorganized with frequent break offs and shifts of positions (Heppner 1974). These flocks have dark cloudlike shapes. Formations are more two-dimensional, have fixed positions and structures like a line or row (Heppner 1974). The V-formation is the most studied example.

The thesis will address the three major questions of 'When', 'How' and 'Why' birds fly in flocks. As there is a great difference between clusters and formations concerning these questions, both types will be dealt with separately.

The goal of this thesis is to provide a clear overview of the all the literature concerning these questions. As there is a broad range of literature available, this thesis may serve as a welcome summary. It also aims to clarify and summarize which aspects are still subject to discussion. It will be shown that some of these discussions have preoccupied scientists for almost a century and still are debated.

# Chapter 1: When do birds fly in a flock?

As mentioned in the introduction, birds flying in groups can adopt clusters or formations. It should be noted that a certain group of birds does not have a fixed form. The same group of birds can fly in cluster at one time and fly in formation at another time. When a group of birds adopts cluster and when it adopts formation will be discussed in this chapter. A closer look will be taken to the departure of both clusters and formations.

## §1.1 When do birds fly in either cluster or formation?

Generally, outside the breeding season, birds living in groups use cluster flight when they fly between their feeding site and roosting site. Formation flight is a form which is generally only used during migration between their wintering grounds and their breeding grounds. Migration flight also starts in a cluster, but while gaining height the flock will gradually move into a formation to ready themselves for the long journey.

## §1.2 The departure of flocks flying in cluster

While living together in a flock, birds sometimes collectively burst into the air without an apparent cause (figure 1). Before elaborating on the reasons for cluster flight, first the departure of the flock will be addressed. Sirot (2006) constructed a model to determine general rules governing flock departures. The model makes three assumptions. First, it assumes individuals rely on others for predator detection (Lima 1995a,b, Lima and Zollner 1996, Hilton et al 1999). Second, the model assumes that the feeling of danger increases as more birds take flight (Lima 1995b, Roberts 1996, Cresswell et al. 2000).



Figure 1: A cluster of thousands of Starlings

The third assumption is that the perception of predation risk is influenced by the level of vigilance of its flock mates, although evidence for this is mixed (Caraco et al. 1980, Caraco and Bayham 1982, Lima 1995a). Birds are less vigilance while foraging (Lima 1995a). When they forage, birds benefit from the vigilance of the whole group. As more birds become satisfied, the vigilance of the group increases. Birds will adopt alert postures without necessarily perceiving danger (Gill et al. 1996, Riddington et al. 1996). Based on assumption three, these alert postures will increase the vigilance of nearby flock mates, increasing the vigilance of the group as a whole even more. Sirot (2006) suggests that this increase in vigilance may lead to a reaction on other reasons than predation risks, like unusual noises and strange objects. When they depart, the rest of the flock will stop feeding and take flight based on assumption two. Although this behaviour is not optimal because it sometimes leads to premature departure, it is evolutionary stable because an individual bird ignoring the signals would also be the last one to depart when a real attack occurs. It is better to depart unnecessarily sometimes which means energy costs, than to depart to late once which means a bird becomes a victim. Thus, a group of birds generally departs collectively and may do so very often even though there is no predation risk.

## §1.3 The departure of flocks flying in formation

Several species of birds migrate long distances every year between their southern wintering grounds and their northern breeding grounds. The timing of departure for the journey of several thousands kilometres is very important. The actual departure is quite a happening, but also during migration birds face multiple challenges. Therefore in this paragraph not only the departure will be described, but also some of the challenges during migration.

### §1.3.1 The timing of departure

Migration is a fitness maximizing strategy in seasonal environments (Alerstam 1990). In the northern breeding grounds birds can profit from long summer days and high abundant food supply to maximize reproductive output (Piersma et al. 2005). During northern winter they migrate to their southern wintering grounds to take advantage of the favourable climates to maximize their own survival (Piersma et al. 1994).

To be on time at their breeding grounds in summer, birds start their migration in spring (Piersma et al. 1990a; McNamara et al. 1998). To be back in time at their wintering grounds, they leave their breeding grounds in autumn.

There are multiple factors that influence the exact date of departure to the breeding or wintering grounds. First of all, distance is a factor (Piersma et al. 1990a). Because birds migrate as fast as possible, the actual flying time of the migration distance consists of several days. A longer distance takes longer to fly so the greater the distance the birds have to travel, the earlier they have to depart. However, this difference is only a matter of days. A factor which has more impact on the departure time is the amount of energy that is needed for the journey (Piersma 1987). Migrating birds mostly visit stop over sites on their way from the wintering to the breeding ground and vice versa, because they cannot make the journey without replenishing energy reserves (Piersma 1987, Corven 1998). Birds who have to migrate longer distances have to stopover more often and/or stay at a stop over site longer to be able to refuel enough to finish their migration. Because fuelling up takes several weeks, this factor has a great influence on the departure time (Piersma 1987). Another factor which has influence on the departure time is the settling time on both the stopover sites as the final destination. Each time the birds arrive at a new site they have to invest time and energy into finding food and safe places (Alerstam and Lindström 1990, Gudmundsson et al. 1991, van der Kam et al. 2004). This means that birds that have to fly greater distance and therefore have to stopover more often, also have to depart earlier to compensate for this settling time. Piersma et al. (1990a) investigated the relation between departure time and distance to the breeding site. They found a migratory departure delay of approx. 2 days per ° breeding latitude.

These factors discussed above determine the departure for migration to a certain time of the year, this is referred to by Piersma et al. (1990b) as the correct seasonal timing. A bird has to make sure that it has enough energy reserves to be able to start the journey. The fuel of the birds is reserved in body fat (Rayner 2001). A bird has to have enough body fat at the correct seasonal timing.

Although the correct seasonal timing is internally controlled, the specific day to depart within the correct period of time may be determined by external causes. Piersma et al. (1990b) indicate several of these external causes, like the possibility for a last-minute top-up, the favourability of winds and other weather conditions and the availability of flock mates. These causes are not confirmed by all studies, for example Piersma et al. (1990a) showed little evidence for adjustments in response to wind conditions. However, Åkesson and Hedenström (2000) confirm the theory that wind conditions do not influence the seasonal timing of departure, but do influence the day of departure. They stated that there is a final day when birds will depart regardless of wind conditions, but there was a significant correlation with favourable wind conditions and departure days.

When the day for migration departure is optimal, birds have to choose a departure time. Research has shown that the most optimal moment is just before sundown (Henshaw 1910, Drost 1931, Dick et al. 1987, Meltofte 1988, Lank 1989, Alerstam et al. 1990, Åkesson and Hedenström 2000). There are several reasons for this. One reason is that day and night provide different orientational cues (Emlen 1975). During the day, the sun is the orientation point and in the night the stars. Just before sundown, birds can use both the sun as well as the stars for orientation. A research by Piersma et al. (1990b) analysed 277 departures and in spite of a 60% average cloud cover, the sun was always visible at the departures.

Sandberg and Gudmundsson (1996) found that on heavy clouded evenings birds did not show migration behaviour. Also wind currents play a role because at night the atmosphere is calmer and more predictable (Kerlinger and Moore 1989). Another reason could be a possible breakfast at the destination. Because it is easier and safer for birds to feed during the day, it seems better to fly at night (Zwarts et al 1990). Prevention of heat stress could also be a reason, because the lower temperature at night decreases the risk of overheating and losing moisture (Kerlinger and Moore 1989, Klaassen 1996). Most flocks depart at moving tides (Lank 1989, Piersma et al. 1990b). It is suggested that when birds move because of the water level change, this may serve as the actual trigger for departure (Piersma et al. 1990b).

The exact moment of departure probably is an optimization of all these reasons. All the factors can be summarized in a checklist for a migration bird as shown in figure 2 (Piersma et al. 1990b). When all conditions are met, a bird is ready to leave.

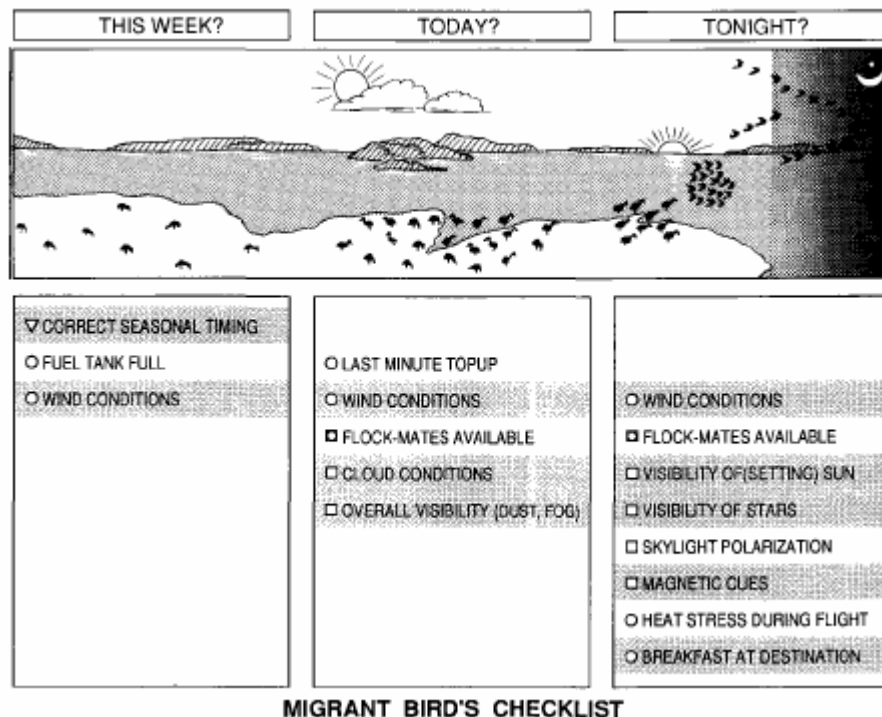


Figure 2: Checklist for a migrant bird, before departing on a long distance flight. Points indicated with an open circle refer to energetic considerations, those with squares to orientational considerations. A correct seasonal timing of departures (triangle) is a prerequisite for a successful migration to the area of reproduction. When all conditions are met, a bird is ready to leave (Piersma et al. 1990b).

### §1.3.2 Behavioural aspects of the departure

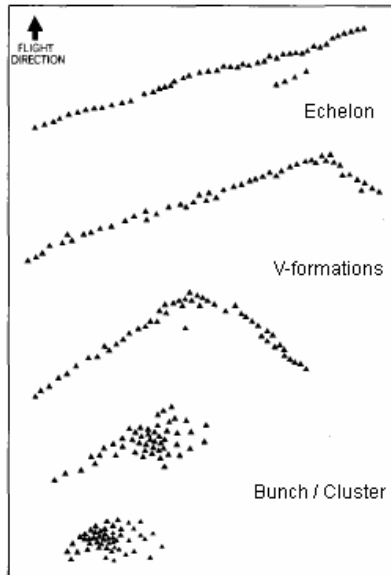
The actual departure is quite a happening to experience. Hours before the actual departure, the birds are already nervous and start flying around. When departing, small groups of birds tumble through the air noisily before joining together in a large group. First they are still flying in a cluster, like they also do outside the migrating periods, but quickly the cluster changes in a formation like a V-formation or an echelon. Sometimes the formation disintegrates again and the birds go to the mudflats. For them time is not ready yet. But if the formation remains intact, the noise declines and a fixed direction is chosen. They gain height quickly and fly out of sight to their destinations far away.

Departure starts in small noisy flocks (Piersma et al. 1990b, Barter and Tonkinson 1997). Although there is little research on descriptive studies of the vocalisations, it has become clear that it consists of repeated series of call notes (Cramp and Simmons 1983, Dierschke

1989). These calls may help recruiting for the departure and also sharing knowledge about departure direction. It is also possible that these vocalizations may be used to decide which bird will lead the formation (Piersma et al. 1990b).

Mixed flocks of different species are quite rare (Venema 1989, Piersma et al. 1990b, Barter and Tonkinson 1997). This may be because flock mates have to match in size, flight speed and flight type to benefit from group synergy (Lissaman and Schollenberger 1970, Hummel 1973).

Not every time a flock rises up, they actually depart. Sometimes they go down again on the mudflats. It has been suggested that these non-departing flocks have a recruiting purpose.



**Figure 3: Schematic view of the flock types during their departure for migration. Flocks start as a cluster and gradually form a V-formation or echelon (Piersma et al. 1990b).**

This suggestion is backed up by the fact that these non-departing flocks mostly contain fewer birds than the flocks that do depart (Piersma et al. 1990b).

The migrating birds seem to depart at various directions, where all directions are possible (Piersma et al. 1990b, Åkesson and Hedenström 2000). Flocks mostly do not adjust their departing direction for wind drifts, only when there are tail winds. If the birds adjust their direction during migration for wind drifts remains a fundamental question in research (Green and Alerstam 2002). It should also be noted that the departing direction has no correlation with the eventual migrating direction.

After departing, the birds rapidly gain height to travel their journey a few kilometres high. At this height migrating birds can gain energy savings by using wind currents (Bloch and Bruderer 1982), which might be even necessary in allowing birds to reach their destination. (Piersma and Jukema 1990). Setting course to their destination, the birds adopt either an echelon or a V-formation shape (figure 3) (Piersma et al. 1990b, Barter and Tonkinson 1997). Without mental maps, preferred flight directions and adequate orientational cues, flocks would never be able to navigate to this destination as well as they do.

### §1.3.3 Orientation cues during migration

One of the greatest challenges migrating birds face is taking the correct course between their wintering grounds and their breeding grounds. The orientation of migrating birds is based on landmarks (Adler 1970), celestial cues, like the sun (Moore 1987), skylight polarization patterns (Able 1982, Moore and Philips 1988, Helbig 1991), the stars (Sauer 1957, Emlen 1975) and geomagnetic cues (Berthold 1991, Wiltschko and Wiltschko 1995).

Landmarks are specific recognition points of important sites (Terril 1990). The sun compass is the knowledge about how the path of the sun relates to compass directions (Terril 1990). At noon the sun is exactly at the south. Because birds have an internal clock (Gwinner 1996, Binkley 1997), they can pinpoint the south using the orbit of the sun. Skylight polarization patterns are used by birds to determine the position of the sun by using the e-vector as an axis of orientation when the sun is not directly visible (Terril 1990). These patterns are the most visible at sunrise and sunset (Moore 1987). The star compass is the knowledge about how the axis of the stars relate to polar directions (Terril 1990). In the northern hemisphere the Polar star is exactly at the north and in the southern hemisphere the Southern Cross is exactly at the south. Geomagnetic cues originate from the magnetic field of the earth. In contrast to the other orientation cues, the geomagnetic compass is passed on genetically (Terril 1990).



It is difficult to find out about these orientation processes by simple field observations (Piersma et al. 1990b). After three decades of intensive research, the different reference systems and how they are integrated and calibrated against each other is still a matter of wide speculation and discussion.

Moore and Phillips (1988) and Helbig (1990) found evidence for the importance of skylight polarization patterns. Moore and Phillips show clearly that birds orient on the skylight polarization patterns rather than sun or magnetic compasses. Able (1989) is sceptical about their conclusions and states that the skylight polarization patterns are not evidently the most important. Munro and Wiltschko (1995) specifically put the skylight polarization patterns below the information of geomagnetic compass. A study by Wiltschko and Wiltschko (1995) focused on magnetic cues and they assume the sun compass to be of secondary importance. In contrast to Wiltschko and Wiltschko, a study by Alerstam and Gudmundsson (1999) indicated the sun compass as most likely orientation cue. Thus, despite a lot of research on the subject, the relative importance of the various cues remains poorly understood.

In some literature a distinction has been made between the relative importance of pre-migratory cues and the relative importance of cues during migration. Wiltschko et al (1997, 1998), Wiltschko and Wiltschko (1999) and Muheim et al. (2006) state that birds in a pre-migratory phase use celestial cues to calibrate their geomagnetic compass. During migrations the geomagnetic cues become the most important compass and are used to calibrate celestial cues. There is still more research being done to the exact calibration of compasses when encountering cue-conflicts.

#### **§1.3.4 Wind drift during migration**

As mentioned earlier, another subject of discussion is the question if migrating birds compensate for wind drift. This question has been addressed in many studies (see reviews by Alerstam 1976, Richardson 1991). Birds in migratory flight can compensate for wind drift and remain on their migratory direction or can adjust their direction to the pattern of the wind (Green et al. 2004). Reasons to adapt to the wind currents can be time and energy savings (Alerstam 1979a,b). This is called adaptive drift. Difficulties of research on this subject are the existence of non-adaptive drift and pseudo-drift (Green et al. 2004). Non-adaptive drift is the case when constraints prohibit the bird to compensate and it involuntary becomes subject to drift (Alerstam and Pettersson 1976, Green 2001). Another problem occurs when within a studied sample departure and destination areas differ between populations. Difference in direction is then a result of these different areas and not the result of the wind currents (Evans 1966, Nisbet and Drury 1967). This is called pseudo-drift. Because every study has to ascertain if their results are subject to non-adaptive drift or pseudo-drift, it becomes harder to obtain clear answers.

Increasing the discussion about wind drift in migrating birds, Green and Alerstam (2002) concluded that several of the research methods used in studies on this subject do not produce robust and reliable results in all situations. They suggest a re-evaluation of these studies.

## Chapter 2: How do birds fly in a flock?

Now that it is clear when birds fly in clusters and formations, the subject of how these two types of flight are organized will be discussed. Although this subject is heavily studied, it will become clear that some aspects are still not fully understood.

### §2.1 How do birds fly in a cluster?

One of nature's most inspiring phenomena is the sight of hundreds or thousands of birds moving together in a cluster as a coordinated unit. Noisy flocks burst into flight and manoeuvre gracefully through the air. To describe how birds fly in a cluster, first of all visual aspects of cluster manoeuvres will be mentioned. The coordination of these manoeuvres is discussed next. Finally flying in a cluster will be approached through a self-organized mechanism.

#### §2.1.1 Flying in a cluster

Clusters have a three-dimensional structure. Clusters tend to be rather disorganized with frequent break offs and shifts of positions (Heppner 1974). Birds are positioned in a diamond shape (Wiens 1973). There are no birds directly to either sides and there are also no birds directly above or below each other (Breder 1976). The horizontal positioning of a cluster is shown in figure 4 and their vertical positioning in figure 5. For each bird its nearest neighbour is most likely behind and below it (Major and Dill 1978).



Figure 4: A flock of birds flying in a cluster (Heppner 1974).

When birds are transiting between feeding or roosting sites, clusters are relatively widespread and loosely organized. Clusters are not flying at maximal speed and are generally flying parallel to the ground or water in a constant direction (Major and Dill 1978). When clusters are attacked, the birds appear to increase their speed and perform rapid movements in a more compact group. They turn and swirl, ascending and descending in the air (Major and Dill 1978, Pomeroy and Heppner 1992). The reason why a cluster becomes more compact when a predator approaches may be because each member tries to obtain a central position in the cluster to make use of the physical screen (Hamilton 1971, Pulliam 1973).

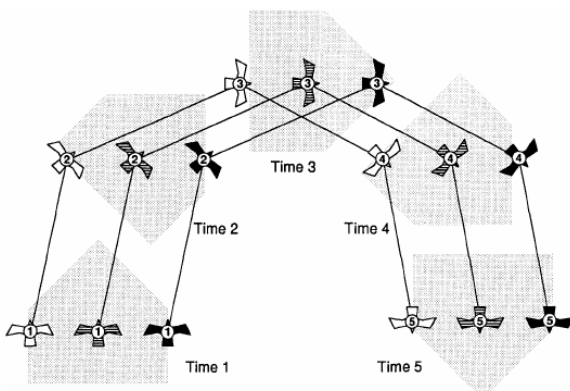


Figure 6: Flight paths of individual birds in a flock during a turn. While turning, all individuals follow arcs of similar radius at equal speed. Relative positions within the flock rotate counter-clockwise. Note that flight paths cross (Pomeroy and Heppner 1992)



Figure 5: Vertical spacings in clusters. For each bird its nearest neighbour is most likely behind and below it (birds from Heppner 1974)

Sometimes clusters of birds may start out with unpredictable manoeuvres as a whole and then break up into smaller flocks that may cross over each other, recombine, and further separate (Camazine et al. 2003). This breaking up and recombining may further confuse a predator. More about the reasons for flying in a cluster will be discussed in chapter 3.1.1.

During a turn, birds constantly reposition themselves. The empty spaces between birds make it possible to transit through the cluster structure to change their position. Pomeroy and Heppner (1992) supply a simple model of turning in a cluster of birds. The birds start to turn at approximately the same time and each bird describes an arc of similar radius (figure 6). Flight paths of different birds cross during a turn.

Birds can adjust their flight paths when almost colliding with a neighbour, but will always follow the course of the group. As shown in the figure, relative positions of birds rotate counter-clockwise. Birds at the outside of the cluster end their turn at the inside. This model shows the turn in a two-dimensional way. In three dimension reality, the turning is even more complicated.

### **§2.1.2 Coordination of manoeuvres**

A flock of birds manoeuvres gracefully, with all its members moving in the same direction. When the flock suddenly changes direction, all its members rapidly respond, moving cohesively, almost in unison, as flawlessly as if they were parts of a single organism. Many people have wondered how the birds coordinate their abrupt synchronized wheels and turns in such a great speed, without colliding with each other.

Many theories have been put forward. All theories propose that there are one or more initiators starting with the turn, although different means are suggested about how this information is transferred as rapidly through the flock that it enables the entire group to execute these swift manoeuvres. Selous (1931) speculated that telepathy could be involved. Another suggestion was the use of signals for manoeuvres (e.g. Farrar 1950, Buck and Buck 1976). Heppner and Haffner (1974) mention electromagnetic communication as a form of coordination. With the use of high speed filming a more thorough analysis of the dynamics of cluster flying could be performed. A study by Davis (1980) confirmed the possibility of one or more initiators directing the cluster. Due to the reaction time of birds, which is much smaller than the reaction time of humans, other birds in the cluster can adjust their direction very fast to that of the initiating bird based on visual information. Davis suggests that only when a certain number of birds make the same decision to adjust to the initiating bird, the whole cluster will turn. He calls this minimum number of birds the 'critical mass'.

Potts (1984) introduced the 'chorus-line' hypothesis. This theory is also based on high speed filming and showed that a single bird may initiate a manoeuvre which spreads through a flock in a wave. Just like Davis, he predicted that the adjustment of neighbours to the manoeuvre of the initiator is determined by their reaction time. However, further away in the cluster, response time should decrease as these birds have already seen the manoeuvre of birds ahead. Therefore they can react faster than the birds nearby the initiator, because they already know a manoeuvre is coming. Potts compared this to a human chorus-line where individuals observe the approaching manoeuvre wave and time their own execution to coincide with its arrival. Additionally Potts discerned that only manoeuvres banking towards the cluster were followed. When birds turn away from the cluster this does not lead to a turn.

### **§2.1.3 Self-organization in clusters**

Findings of studies like Davis (1980) and Potts (1984) assume that the movement of birds flying in cluster is the result of interaction between the behaviours of individual birds. As birds continually change positions and initiators often fall back and trade places with flock mates behind them, there appears to be no leader (Partridge 1982). The most likely explanation for this behaviour is a self-organization mechanism where each bird applies a few behavioural rules in response to local information from neighbouring birds. Individual birds use relatively simple behavioural rules to generate structures and patterns at the collective level that are relatively more complex than the components at processes from which they emerge (Camazine et al. 2003). Using this approach several scientists have developed mathematical models describing the movement of bird clusters. For example, Reynolds (1987) formulated three behavioural rules:

1. Flock Centering: attempt to stay close to nearby flock mates
2. Velocity Matching: attempt to match velocity with nearby flock mates
3. Collision Avoidance: avoid collisions with nearby flock mates

Flock Centering means that an individual bird must move closer to its neighbours in order to remain part of the flock. Collision Avoidance makes sure that the bird steers away in case of

an imminent collision. Velocity Matching serves to maintain the resulting distance between neighbouring birds ensuring a balance in attraction and repulsion. Each individual bases its behaviour on the perception of its nearest neighbours and not the knowledge of the behaviour of the whole cluster. Following these rules, birds avoid approaching each other closer than a certain minimum distance and also have a preferred distance, elevation and bearing relative to their nearest neighbour.

These three rules also show the basic components of self-organization systems: positive and negative feedback. Positive feedback brings the individual birds together as a group (*"I go where you go"*) and negative feedback triggers repulsion when one bird comes too close to another bird (*"but do not come too near to me"*) (Camazine et al. 2003).

The studies mentioned above have a limitation because the number of individuals was small. Due to an improvement of computer techniques throughout the years more recent studies are able to process empirical data on large flocks flying in clusters. Ballerini et al (2009) performed such a study on flocks up to 2700 birds. The study gives several new insights in the structure of clusters. It also confirmed the turning mechanism described by Pomeroy and Heppner (1992) as mentioned earlier (figure 6). And although it subscribes adjustment through visual information, it does not fully support simulation models like Reynolds (1987). Their work shows that individual birds do not use metric distances but topological distances (i.e. whether they are first, second, third etc neighbours) (Ballerini et al. 2008). Clearly, new techniques will deliver new results, which can be used to test current models and theories.

## §2.2 How do birds fly in formation?

There are different variants of formations. An interesting question is when a certain variation is used by birds. It will become clear that the difference in formations and therefore the choice between variants is closely related to aerodynamic aspects. That is why first the aerodynamic principles will be addressed.

It should be noted that not all birds can use formation flight for aerodynamics. As aerodynamics is also important for these birds, they adopt different flight patterns. These will also be briefly discussed.

### §2.2.1 Aerodynamic aspects of formations

The aerodynamics of a bird in flight concern the forces lift and drag, which are influenced by the angle of the wings of the bird. When the wing is positioned in an angle to the air current,

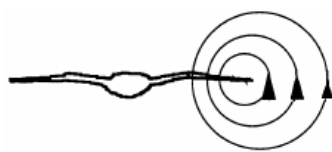


Figure 7: The wingtips generate a trailing vortex, as the air spills around the wingtip due to the difference in pressure above the wing and below it (Andersson and Wallander 2004).

air flows faster over the upper surface than it does over the lower surface. This creates a difference in pressure above the wing and below it. Because the air pressure above the wing is less, this creates a lift. The same angle also causes drag, due to the resistance of the wing to the moving air. This pushes the wing backwards (Thien et al. 2007, Linton 2007).

The difference in pressure also causes a vortex around the wingtips of the bird (figure 7). There is a flow of air from the lower surface of the wing towards the tips, around the tips and inward towards the centre of the wing. Because the bird is moving, the flow produces a vortex stream behind the bird's wing. The vortex

from the left wingtip has a clockwise direction, and the vortex from the right wingtip has a counter clockwise direction (figure 8) (Thien et al. 2007, Linton 2007).

These vortices create an area of downwash that increases the drag on a bird's wing and are therefore undesirable. However, these vortices also create a trailing area of upwash. This upwash can benefit a bird flying behind the first by getting extra

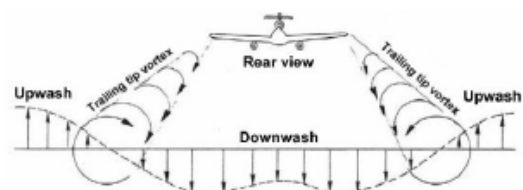


Figure 8: Regions of upwash and downwash create by trailing vortices (Thien et al. 2007).

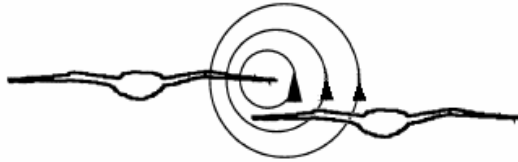


Figure 9: A trailing bird can gain energetic advantage of uplift by flying at a suitable lateral position relative to the bird ahead in such a way that there is a wingtip overlap (modified from Andersson and Wallander 2004).

lift when it puts its wingtip in the area of upwash (Lissaman and Schollenberger 1970, Higdon and Corrsin 1978, Badgerow and Hainsworth 1981, Hummel 1983). This area of upwash is located at the outboard of the wing (figure 8). Therefore the best position for the trailing bird is to be in a suitable lateral position relative to the bird ahead in such a way that there is an overlap in wingtips between the birds (figure 9) (Seiler et al. 2003, Thien et al. 2007, Linton 2007).

### §2.2.2 Different kinds of formations

Formation flight is characterized by a group of birds flying in a line or row (Heppner 1974). There are different kinds of formations. The most studied is the V-formation, which has two types: obtuse V-formation, in which the formation angle  $\alpha > 90^\circ$  and acute V-formation, in which the formation angle  $\alpha < 90^\circ$ , (figure 10). The angle is determined by the lateral and longitudinal distances between birds (Andersson and Wallander 2004).

Lateral distances between the wingtips have a strong influence on the energy savings of the group. (Lissaman and Schollenberger 1970, Hummel 1983). Theory suggests that there is an optimal lateral distance for birds in a formation (Badgerow and Hainsworth 1981). Longitudinal distances between the birds do not influence the energy savings of the whole group greatly (Lissaman and Schollenberger 1970, Hummel 1983). However, longitudinal distances influence the energy savings of individual birds within the formation. The main difference between the two types of V-formations is the longitudinal distances between the trailing birds. In an acute V-formation the longitudinal distances are greater than in an obtuse V-formation. Although the energy savings of both types are the same for the group, for individual birds the energy savings vary strongly. Although one might expect that the leading bird in an acute formation does not gain energy savings (Lissaman and Schollenberger 1970, Hummel 1995, Weimerskirch et al. 2001), a study of Sugimoto (2003) indicates that even a leading bird suffers less drag than flying alone. However, the birds following the leader gain by far the most of the energy savings. In an obtuse formation, the leader will benefit more from lift generated by the trailing birds, because they are closer to the leading bird than in a V-formation. The disadvantage of leading is reduced in obtuse formations. However, now these trailing birds gain less energy savings. Thus, although the total energy saving is the same for both types, it differs for individual birds in the group (Andersson and Wallander 2004).

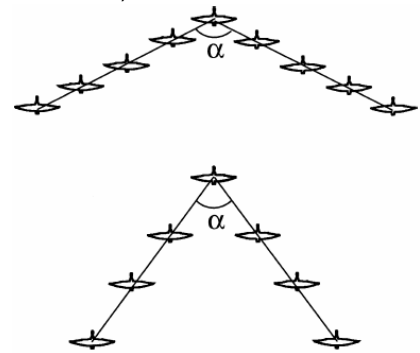


Figure 10: There are two types of V-formation: the upper one is an obtuse formation ( $\alpha > 90^\circ$ ) and the lower one is an acute formation ( $\alpha < 90^\circ$ ). The angle is determined by the lateral and longitudinal distances between birds (Andersson and Wallander 2004).

Birds are also frequently seen in formations like J or echelon (figure 11). These are variants of the V formation. In a J-formation the sizes of the legs are different and in an echelon one leg is missing entirely (Heppner 1974, Seiler et al. 2003).

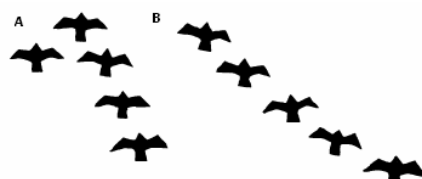


Figure 11: A) J-formation B) Echelon (Heppner 1974).

Although J-formations and echelons are more often observed than true V-formations (Gould and Heppner 1974, Williams et al. 1976, Heppner et al. 1985), the V-formation is the most studied. This is because the symmetry attracts notion (Heppner et al. 1985). A J-formation or echelon also may give more evenly spread energy savings between the birds (Lissaman and Schollenberger 1970). This could mean that the leading

bird may not need birds on either side of it for favourable upwash conditions (Gould and Heppner 1974).

Another kind of formation is the U-formation, also known as the bow-formation. In this formation the birds do not fly in a straight line, but in a bow where the leading bird is only a little ahead of its nearest neighbours and the longitudinal distance between neighbours increases along the arms of the formation (figure 12). Just like an obtuse V-formation spreads the energy savings more than in an acute V-formation, the energy savings in a U-formation are even more egalitarian spread. Flying within the U-formation, every bird has the same amount of drag reduction (Lissaman and Schollenberger 1970, Filippone 1996, Sugimoto 2003).

### §2.2.3 Kinship and reciprocity

If there are different formations, one might ask when a certain variant is used by birds. Andersson and Wallander (2004) suggest that the variation is related to flock kinship structure and to reciprocity that depends on group size. They predict that small groups which include relatives will often use acute V-formation. Although being the leader confers a disadvantage because it is energetically more expensive than trailing positions, the leading bird gains inclusive fitness if the followers are relatives like offspring or siblings. These acute formations are seen in small flocks of geese, swans, cranes and other large birds that migrate in family flocks of parents and young (Prevett and MacInness, 1980, Scott 1980, Alonso and Alonso 1993, Ely 1993, Speakman and Banks 1998). The behaviour of the leading bird may then be a form of aerial parental care (Andersson and Wallander 2004). The advantage for the young is large, because they are smaller and lighter than their adults. Therefore their energy saving will be particularly high (Hummel 1995). Kin selection may also occur in flocks of multiple families migrating together (Andersson and Wallander 2004), where related females breed near each other and mothers, daughters and sisters can recognize each other as adults (Andersson and Ahlund, 2000; van der Jeugd et al. 2002). Migrating flocks of swans or geese may consist of several related females and their mates, plus offspring from several years (Warren et al. 1993).

Reciprocity can also be the reason for acute V-formations. Individuals take turns as leader. When the leading bird is getting tired, it retreats into the formation and another bird flies to the leading position. In this way they share the energetic costs of this unprofitable position (Andersson and Wallander 2004). Reciprocity is mainly expected in small stable flocks in which individuals recognize each other, because they have interacted repeatedly over long time (Trivers 1971, Axelrod and Hamilton 1981, Boyd and Richerson 1988, Dugatkin 1997). In a large group birds may try to avoid the costly behaviour of flying at the leading position. Recognition, which is easier in a small group, facilitates punishment of a cheater, for example by mobbing it in the air or, perhaps more likely, at a stopover site (Andersson and Wallander 2004).

Obtuse V-formations or U-formations are predicted in large groups with unrelated individuals that are not able to recognize each other, because these formations are energetically more egalitarian. Andersson and Wallander (2004) predict that acute formations will not be stable in large flocks. When a leading bird is saving less energy than the others it can easily reduce flight speed so far below the optimum that its trailing neighbour will close on him resulting in



**Figure 12: Energy savings in an acute V-formation are unequally distributed as the leader expends more energy than the others (top). Energy savings in an obtuse U-formation is more egalitarian as frontal birds gain uplift from their neighbours (bottom). The average energy gain is similar for both formations, because the number of birds and the distance between wingtips are similar (Andersson and Wallander 2004).**

a more obtuse formation. Large groups may also contain related or familiar individuals. Kin selection and reciprocity within these smaller subgroups may add to the dynamic nature of the formation of large groups. In this case a formation could have several leading positions, as seen in flocks of Branta geese (Andersson and Wallander 2004).

Although the concepts of kin selection and reciprocity offer an explanation for the occurrence of different kinds of formations, this theory of Andersson and Wallander (2004) has not been tested yet.

#### §2.2.4 Migration without formation flight

Not all flock migrants fly in formations. Sparrows, warblers, blackbirds or other small birds that travel in large groups do not fly in V's or echelons (Heppner 1974). Small birds will probably save relatively less energy in formation than large birds do, in which flight formations are more common (Alerstam 1990, Cuts and Speakman 1994). In general large birds have large wing spans and low wing beat frequencies, which enables them to get the aerodynamic advantage. Small birds have short relative wing length, and their rapid, large amplitude wing strokes create complex wake patterns that may prevent energy saving by formation flight (Hummel 1995). These small birds however have a different way to gain energy savings which is known as intermittent flight.

In intermittent flight birds do not flap their wings continuously (Tobalske and Dial). They alternate phases of flapping with phases of wing motionlessness.

There are two styles of intermittent flight: flap-gliding (also known as undulating) and flap-bounding (Rayner 1977, 1985, Tobalske and Dial 1994). In flap-gliding flapping phases are alternated with glide phases where the bird has extended its wings. In flap-bounding birds alternates flapping phases with phases where the bird has folded its wings against its body (Tobalske and Dial 1994). Both flight patterns are illustrated in figure 13. Although

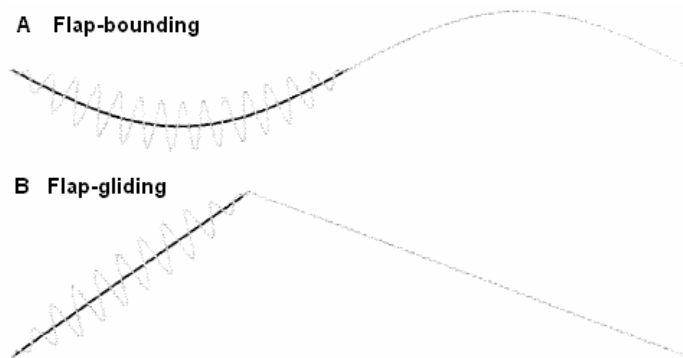


Figure 13: Intermittent flight patterns. A) Flap-bounding B) Flap-gliding (Rayner et al. 2001).

flapping generally is associated with ascending and non-flapping with descending in height, this may not always synchronize (Rayner et al. 2001).

Birds tend to flap-glide at lower speeds and flap-bound at higher speeds (Rayner 2001). Also as body size increases the usage of flap-bounding decreases and birds above a certain weight do not use flap-bounding at all (Tobalske 2001). Larger birds tend to use flap-gliding.

Small birds with rounded, low aspect ratio wings tend to use flap-bounding, while birds with pointed high aspect ratio wings use both flap-gliding and flap-bounding (Tobalske 2001). A bird's body and tail also have a small effect, but insufficient to influence the usage of flap-bounding (Rayner et al 2001).

Although at first, all birds that use intermittent flight have been categorized as either flap-gliders or flap-bonders, more and more studies show that several species can use both (Rayner 1985, Tobalske and Dial 1994, Tobalske 1995, 2001).

## Chapter 3: Why do birds fly in a flock?

After discussing the organization of clusters and formations, the reasons for flying in flocks still need to be addressed. This subject has the focus of the final chapter.

### §3.1 Why do birds fly in a cluster?

Birds often form groups as a response to predation threat (Krause and Ruxton 2002). There are more advantages to living in a flock than predation prevention, like efficient exploitation of food (see e.g. Murton 1968, Krebs 1973, Krebs and Davies 1981). But because predation prevention is specifically related to the manoeuvres of a cluster, also known as predation-flight, this advantage will have the focus.

#### §3.1.1 Predation prevention

A flock of birds has several benefits in comparison to an individual bird when it comes to predation. First of all, a flock consisting of multiple individuals has a greater probability of detecting an approaching predator (Pulliam 1973, Elgar 1989), because many eyes see more than one pair of eyes and many ears hear more than one pair of ears. This increased vigilance also occurs even when some individual birds are less alert (Pulliam 1973, Elgar 1989). The less alert individual benefits from the vigilance of others. However, predation risk is lower for the vigilant individual, because it can respond more efficiently than birds that get only the indirect information (Lima 1995a,b, Lima and Zollner 1996, Hilton et al 1999). Vigilance is most often a relevant issue when a group of birds is foraging because a bird is less alert while foraging.

Also, the probability of an individual being the victim of a predator will decrease as flock sizes increases. This is called the dilution effect (Hamilton 1971, Foster and Treherne 1981). It is a simple matter of mathematics, where the average chance of being the victim of the predator for one specific bird decreases with every other member joining the flock.

Members of a flock may additionally gain protection from the neighbours' bodies between themselves and the predator. Other individuals function as a physical screen, so being in the middle of a cluster may be safer than being at the edge (Hamilton 1971, Pulliam 1973), because birds in the center have the maximum number of individuals between themselves and the predator. However, for a bird it is still better to be at the edge than separate from the cluster. If they leave the flock, they become the odd prey item, exposing themselves to increased danger from predators (Mueller 1971).

Because it is harder for predators to deal with multiple targets, there is also a confusion benefit for flying in a flock (Vine 1971, Packer and Abrams 1990). There is evidence that predators suffer from confusion when attacking a group of prey (Neill and Cullen 1974). This confusion can be illustrated by the old trick of throwing three tennis balls to somebody at the same time. It is difficult to track one rapidly moving object when there are multiple rapidly moving objects in the visual field. The confusion effect may explain why attacks should be directed at the edge of a group (Krebs and Davies, 1981).

If a large group is compact and wheels and turns unexpectedly, this may prevent the predator from attacking as it risks injury from a collision. That is why a cluster of birds makes manoeuvres when a predator approaches (Driver and Humphries 1988).

### §3.2 Why do birds fly in formations?

A group of birds flying in a formation which sometimes reflects the letter V perfectly has always attracted attention from its viewers. But the question rises why the birds adopt this specific formation or even why the birds do not fly solitary. There are two major supported hypotheses that may explain formations: the *aerodynamic advantage* hypothesis and the *orientation communication* hypothesis.



### §3.2.1 Aerodynamic advantage hypothesis

The aerodynamics principles of birds flying in formation have already been discussed (chapter 2.2.1). When flying in the upwash of preceding birds, followers gain aerodynamic advantages which lead to energy savings. The amount of energy savings for a trailing bird depend on certain variables, like for example bird size and lateral and longitudinal distances between the wingtips of the birds (Lissaman and Schollenberger 1970, Hummel 1983, Speakman and Banks 1998, Chicka et al. 1999, Andersson and Wallander 2004).

Analysis has shown that the amount of energy savings can be very high. Schollenberger and Lissaman (1970) showed that a bird in formation could reach a 45% drag reduction compared with flying solo. Weimerskirch et al. (2001) measured a maximum of a 45% reduction in wing beat when using well-trained Great white pelicans (*Pelecanus onocrotalus*) and also the heart rate was 11.4%-14.5% lower than birds flying alone. Additionally, the pelicans beat their wings less frequently and glide longer periods of time, saving 1.7%-3.4% energy. Their results provide empirical evidence that compared with solo flight, formation flight leads to a significant aerodynamic advantage which allows birds reduce their energy expenditure. Reducing energy expenditure is a relevant advantage, because the energy reserves of birds are finite, and energy can at times be critical to reproduction or survival (Higdon and Corrsin 1978, Badgerow 1988).

### §3.2.2 Orientation and communication hypothesis

Flight formation may also lead to better communication and orientation. The advantage of a group for better communication and orientation has already been determined for other animal species, like fiddler crabs, *Uca* spp. (Herrnkind 1972), schooling fish (Pitcher et al. 1982), thick-billed Murre, *Uria lomvia* (Gaston 1987) and also already in bird flocks on the ground (Krebs et al. 1972).

A skewed position relative to the bird in front of it enhances the orientation of a trailing bird. Vision might be essential in coordinated, close-order movements (Potts 1984). To be able to adjust their direction and velocity to the other birds in the group, they have to be in visual range (Gould and Heppner 1974, Heppner 1974, Heppner et al. 1985, Badgerow 1988). First of all, unhindered visual communication and orientation helps avoid collisions (Gould and Heppner 1974, Williams et al. 1976). But optimal visual orientation also leads to the most direct migratory route, which saves time and energy for the group (Badgerow 1988).

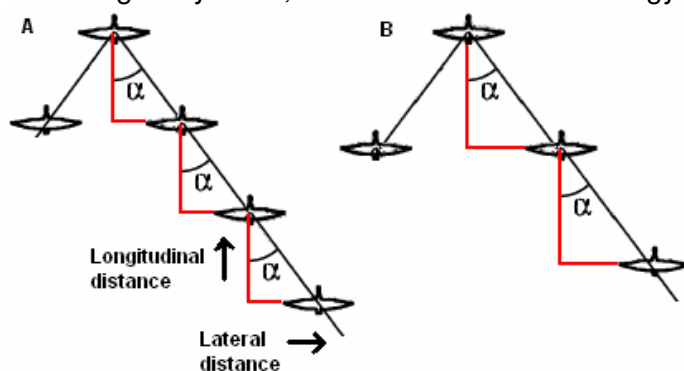


Figure 14: To maintain a fixed angle, when a bird increases its lateral distance, it also has to increase its longitudinal distance. Angle  $\alpha$  is the same in figure A and B (birds from Andersson and Wallander 2004).

The visual angle of a bird is determined by its retinal features and the location of the eye on the head (Gould and Heppner 1974, Heppner 1974, Heppner et al. 1985, Badgerow 1988). Research has shown that the optimal angle is somewhere in front and to the right/left of the bird (Hamilton 1967). This could mean that the V-formation is a result of birds trying to maintain an optimal resolution visual image of its adjacent neighbours (Heppner 1974). To maintain the optimal visual angle a fixed correlation between the lateral and longitudinal distances between

the birds should be maintained (Badgerow 1988). Thus, when a bird increases its longitudinal distance to the bird in front of it, to maintain the optimal angle the bird should increase its lateral distance also, as shown in figure 14.

Another advantage in formation flight is to enable younger birds in the flock to learn migration paths and traditional feeding sites (Speakman and Banks 1998). In this way, less experienced birds benefit from the experience of older birds.

### §3.2.3 Aerodynamics versus Orientation and Communication

So, in the literature, two explanations have been postulated for why birds fly in formation. One is the aerodynamic advantage hypothesis, the other is the communication and orientation hypothesis. These explanations are not mutually exclusive, and various studies have given support to both of them. As early as 1912, Forbush suggested that birds may gain an energetic advantage by flying in formation. This hypothesis was supported by Weiselsberger in 1914 and after that by many more scientists. Forbush (1912) also put forward the communication and orientation hypothesis. This hypothesis has also been the focus of studies by many other scientists. It has been a topic for studies for almost a century and even after all this time no clear answer has been given yet as no conclusive evidence for either hypothesis has been found.

An example of the debate that has been going on through the years can be illustrated by the paper by Gould and Heppner (1974) about energy savings. They collected data of bird formations and analysed them. They concluded that the energetic advantage was trivial. In 1981, Badgerow and Hainsworth re-analysed the data of Gould and Heppner (1974) and concluded that the energy savings of flying in formation were up to 51% over solo flight. Concerning the debate on the communication and orientation hypothesis, Cutts and Speakman analysed the data of Pink-footed geese formations in 1994 and found support for this hypothesis. However, in 1998, a similar research by Speakman and Banks contradicted the support for the communication and orientation hypothesis. In the same paper it became clear that even a mistranslation of articles written in German had led to misunderstandings about the exact optimal wingtip distance by Hummel (1973). At first Speakman and Banks believed Hummel had calculated a different optimal distance of wingtips than they did. But later they discovered that this was not the case and that both researches had calculated the same optimal wingtip distance, increasing their confidence in the aerodynamic advantage hypothesis.

Focus points in all studies is the angle of the formation in which the birds fly. This angle is determined by the lateral and longitudinal distances between wingtips. With the use of aerodynamic theory an optimal wingtip distance can be determined. This spacing has been calculated to be negative (Badgerow 1988, Speakman and Banks 1998), meaning that there is an overlap between wingtips. In aerodynamic theory the longitudinal distance is of less importance (Hummel 1995, Speakman and Banks 1998, Chichka et al. 1999). So, energy saving can be obtained at multiple angles. Communication and orientation hypothesis focuses on the angle between birds when the bird ahead is seen at its highest resolution image (Badgerow 1988). To maintain this angle, there has to be a correlation between the lateral and the longitudinal distance of wingtips between birds. If a bird increases its lateral distance, it also has to increase its longitudinal distance to retain its high resolution image (see chapter 3.2.2). So, communication and orientation must be obtained at a fixed angle. This fixed angle is different for every bird specie. Although both hypotheses are not mutually exclusive, they are mutually restrictive in their demands on positioning (Badgerow 1988). The optimal angle for energy saving is not the same as the optimal angle for communication.

Through the years, many scientists have performed many studies in which formations of certain species were photographed to determine the angle of the formation. Notable is that often within one study examples of both optimal angles of flight were found. Statistical calculations were then used to support or reject a hypothesis. Williams et al. (1976) performed research on Canada Geese and their data led them to the conclusion that V-formation flight was probably not the result of energy saving. They suggested that it might have a social behavioural component as well. O'Malley and Evans (1982) analyzed formation flight functions in American White Pelicans, and found support for both hypotheses. Heppner et al. (1985) concluded that V-formation in Canada Geese flight seems so rare and variable that it probably does not have any functional advantage of significance. The formations they examined never flew in any of the two optimal angles. Cutts and Speakman (1994) observed Pink-footed Geese, a smaller bird relatively, and found a significant correlation between distances of wingtips and depth which indicates support for the communication and orientation hypothesis. They did not find support for the aerodynamic advantage hypothesis.

Speakman and Banks (1998) as mentioned before did not find this significant correlation when examining Greylag Geese. They then stated that both hypotheses could be correct but appropriate for different sized species. They suggested that communication and orientation is more important to relatively smaller birds, while energy saving is more important to larger birds. Larger birds have a higher energy demand to make their flights, so saving energy is of more importance. Also Weimerskirch et al. (2001) found in their study of the Great white pelican that aerodynamics and social benefits can coevolve.

In 2003, Seiler et al introduced control theory in the debate. Control theory had already shown that small disturbances in a chain of vehicle were amplified throughout the chain in such a way that the rear vehicles could not track the preceding vehicle. They showed that this is also the case in formation flying birds. When the leading bird adjusts its direction or velocity, the trailing birds make the same adjustments enlarged. They suggest that birds do not fly in any of the two optimal angles, because it is difficult for the birds to fly in formation. This difficulty of flying in formation is supported by other research. Theoretically the benefits of travelling in a group increase with group size, so a maximally large group is expected. The size of departing groups of birds varies between 1 and 400 birds (Piersma et al. 1990b), although hundreds or thousands of birds are present at departure sites (Piersma 1982, Rappoldt et al. 1985). Also researches indicate that birds arrive at stopover sites in smaller groups than they departed (Dick et al. 1987, Blomert et al. 1990). These two outcomes could mean that it is difficult to maintain formation during long flights.

Andersson and Wallander (2004) acknowledged that V-formation is more common in large birds. They also imply that this is because large birds have a greater need for energy saving. As small birds gain little or no energy savings, they rarely use formation flight even though they could gain a communication and orientation benefit. Andersson and Wallander therefore suggest that the importance of communication and orientation is less than the importance of energy saving.

Thus, although the research of the past few decades has given rise to a number of interesting explanations for the reasons to fly in formation and has tried to give insight to why different species use different angles of formation, no conclusive evidence has been found for any of the two hypotheses. The debate remains unsolved. Both the 'aerodynamic' and the 'behavioural' camps have strong support and strong criticism. A major reason for this is that the advantages of both hypotheses have never been fully quantified (Rayner 2001). Even the results of most recent studies have still to be verified and further research is necessary.

## Summary

This thesis entailed a literature review on the subject of bird flight in groups. It discussed the major questions of 'When', 'How' and 'Why' birds fly in flocks.

Flying flocks are roughly dividable in two types: clusters and formations. Research has given a clear view of the use ('the When') of both clusters and formations. Cluster flight is generally used by birds that live in groups as a default. Formation flight is generally used for migration during migrating season. However, in migration flight there is still much unclear about the behaviour of the birds.

Research has also given a clear view of the organization (the 'How') of both clusters and formations. Although clusters seem disorganized, movement is directed by various initiators whose manoeuvre is followed by the rest of the cluster by visual perception. In formations birds organize themselves in fixed positions with a certain longitudinal distance and wingtip spacing. However, the behavioural rules behind the self-organization in clusters are not yet fully understood. Also, the behavioural choices for acute or a more obtuse formation are yet to be determined.

While research has given a clear view of the reasons (the 'Why') for cluster flight, the reasons for formation flight are still highly discussed. Cluster flight grants several benefits in predation prevention, like increased predator detection, a dilution effect, physical protection of neighbours and a confusion effect, in addition to the other benefits of living in a group. Formation flight theoretically has aerodynamic advantages and orientation and communication advantages, although results of research concerning these advantages vary. This thesis has shown that despite a good understanding of the basics of flock flying, there is still much discussion about the more complex behavioural aspects.

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