

Reaction waves in social groups



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Abstract

Biological waves occur in many social species. Bird flocks, insect colonies, fish schools and groups of mammals all seem to benefit from the formation of waves as an anti-predator response. In this paper I will discuss studies by Kastberger et al. on giant honeybees and Procaccini et al. on starlings, primarily focussing on the mechanics underlying these waves.

Through the use of the wave equation derived from physics I will explain how to justify addressing these phenomena as waves, and how to place the wave variables covered in the wave equation in a biological context. I concluded that while many papers address collective behavioural phenomena as waves, there are few amongst them who have rightly justified doing so. Using the wave equation in a biological context might be usefull to not only justify addressing these phenomena as waves but also to provide a means to research important variables and discover the mechanisms underneath.

Broad introduction

The formation of waves is a complicated and fascinating phenomenon occurring in insects, birds, fish and mammals. It is an excellent example of collective behaviour that is often induced by a predator (Kastberger et al., 2009, Procaccini et al., 2011). These collective behaviour patterns may arise through simple rules and mechanisms at the level of the individual. Figure 1 illustrates the appearance of a wave in a school of anchovies (Gerlotto et al., 2006). Through the appearance of an external stimulus, in this case a sea lion, individuals begin to produce rolling movements that result in a flash-like effect because of the illumination of the silvery underside of the fish. Each neighbour receiving this flash repeats the movement, and therefore a line of flashing is caused along the whole school, this is described as a behavioural wave. This behavioural wave has a benefit for the anchovy school in that it likely confuses or deters the predator (Gerlotto et al., 2006).

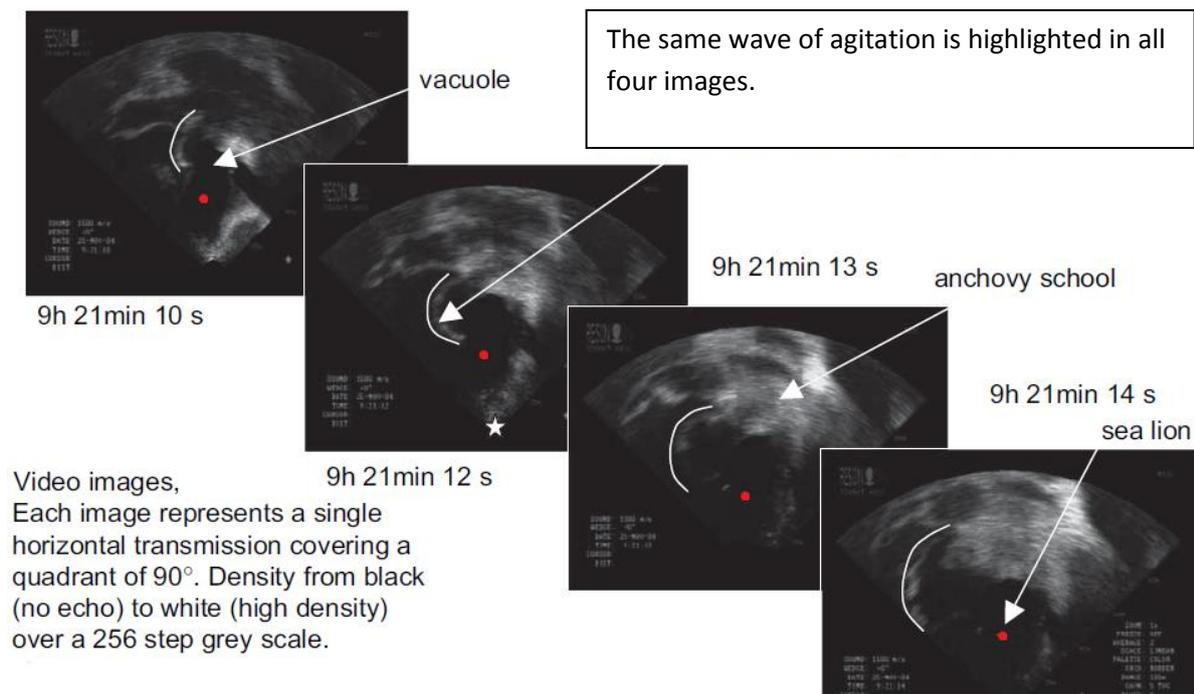


Figure 1 A wave of agitation in anchovy schools fleeing from a sea lion (Gerlotto et al., 2006)

Movement patterns like these waves can be influenced by self-organization and occur in a large variety of circumstances and species. For instance research by Beauchamp et al. suggests that rules which cause individual members of a group to adapt to their neighbours can result in a collective phenomenon, in his case the formation of 'sleep-waves' in gulls (Beauchamp et al., 2011). Waves have been observed in bird flocks, fish schools, and insect colonies and have been the subject of studies on biological processes via modeling studies (Potts et al., 1984, Procaccini et al., 2011, Gerlotto et al., 2006, Kastberger et al., 2008, Boerlijst et al., 1991). A self-organizing system, as defined by Ashby (Ashby, 1962) refers to an organized system with parts that were separate and have organized themselves by forming a connection that affects their behaviour. There is no higher power or intelligent leader dictating their movement patterns or other collective patterns for that matter, yet these creatures collectively decide on a path to take within seconds.

An example that illustrates the importance of self-organization in waves is a theoretical model by Boerlijst (Boerlijst et al., 1991). In his model Boerlijst investigates a number of species that grow from a mixed starting situation, and through providing each other with catalytic support create spiraling waves, the so called ‘hypercycle’. Figure 2 illustrates the situation wherein each species gives catalytic support to one other species, and receives the same support from another species. It also shows a parasite that receives catalytic support but does not provide any. The catalytic support these species provide one another leads to the formation of waves of species-growth that follow their catalytic supplier, showing in figure 3. Boerlijst also directly introduces us to a benefit of the

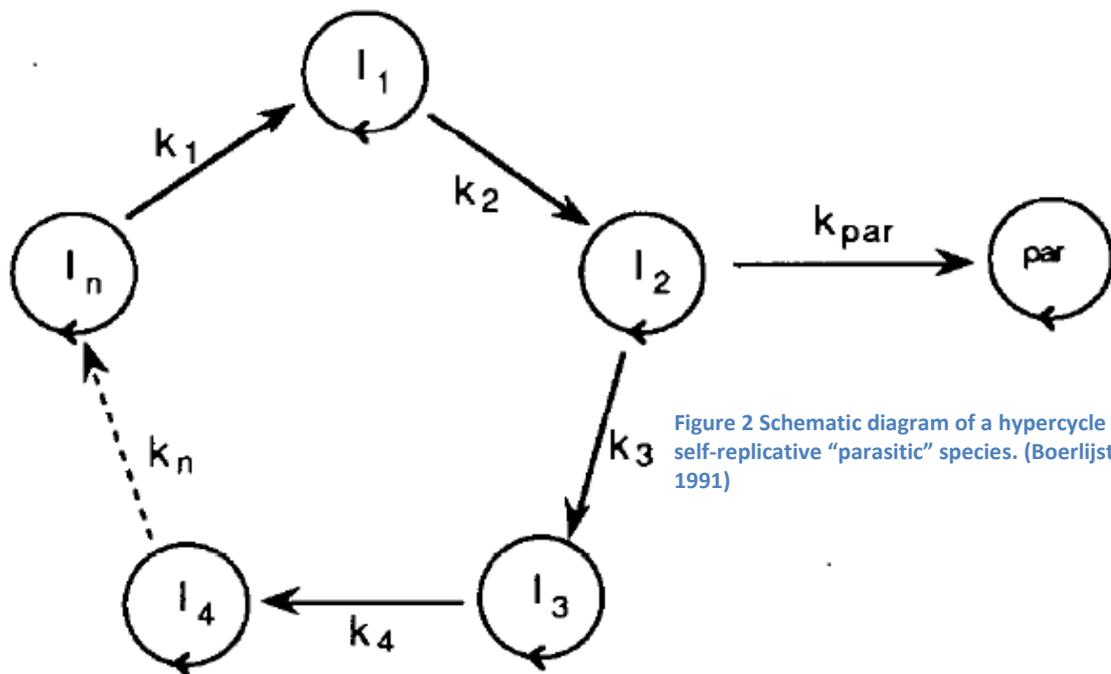


Figure 2 Schematic diagram of a hypercycle with a self-replicative “parasitic” species. (Boerlijst et al., 1991)

formation of these waves, which in this case is their stability towards parasites. In short, because the catalytic species form this spiraling formation the parasite is only able to grow on his catalytic

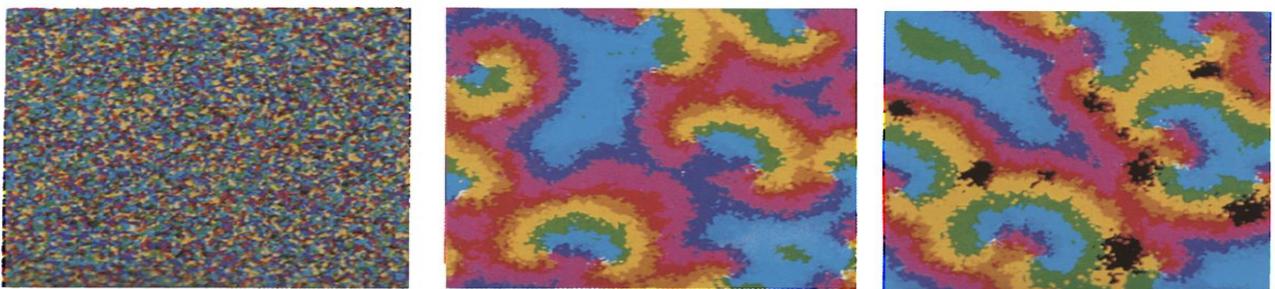


Figure 3 from a mixed starting situations hypercycles emerge. Parasites are driven towards the periphery and lose. (Boerlijst et al., 1991)

In both the cases of waves of agitation in anchovies and in Boerlijst’s hypercycle, waves are formed through mechanisms of self-organization. How animals in groups coordinate their movements to produce cohesive collective patterns has been the subject of many models but remains poorly documented empirically in the field (Couzin & Krause 2003; Sumpter et al., 2010). In this thesis I will

perform a literature study that will focus on finding out what the mechanisms behind these waves are, and how these mechanisms differ between species.

Defining waves:

When looking at and trying to understand waves, even if from a biological perspective, it's important to delve into the physical properties of waves. The wave equation covers all of the variables relevant to waves and to my study. In the simplest mathematical form a travelling wave equation is defined as $\xi = f(x - vt)$, changing for different types of waves (W.C. Lane et al., 2002). A travelling wave is a wave that consists of multiple oscillations that propagate through space in a periodic series, with a speed (defined as v) depending on the characteristics of the wave and the medium in which it travels.

Because the wave function depends on both position and time, when we wish to draw a graph of the wave we usually keep one variable fixed. Figure 4 illustrates this by showing a series of waves at a single time interval. So while we use the time as a fixed variable here, the position is spread along the x-axis. The same type of graph could also be made with position as the constant factor, and time as the variable.

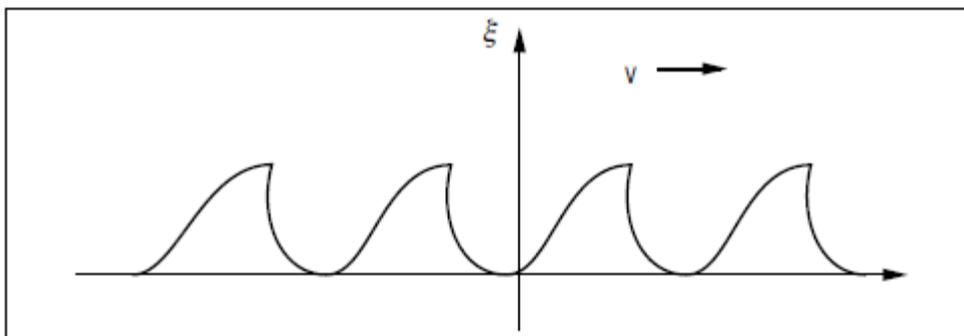


Figure 4 A graph showing a series of waves at a single time frame, the vertical axis indicates the deviation from the average water level. The horizontal axis indicates position. (W.C. Lane 2002)

The type of wave we are interested in is a so called harmonic wave. Typical for a harmonic wave are the fixed values for its wavelength, amplitude and speed. Figure 5 illustrates such a wave. λ is the wavelength, the distance the wave travels in a single oscillation. This oscillation is the movement of the wave from one maximum to the next, for instance from crest to crest as illustrated in figure 5. The amplitude is calculated by the two extremes of the harmonic wave: the absolute difference between the crest and trough in this figure, $+A - -A$. This can also be referred to as wave strength.

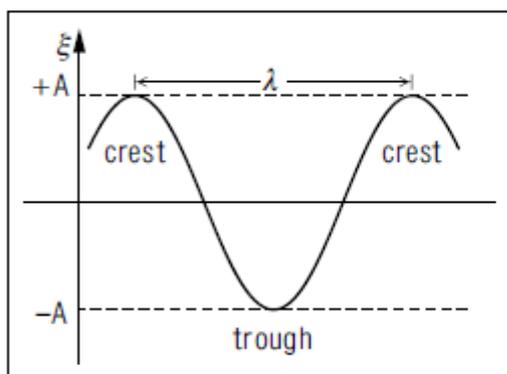


Figure 5 A harmonic wave with its amplitude ($+A - -A$) and wavelength (λ) (W.C. Lane 2002)

While in our biological situations we do encounter periodic oscillations, perfect harmonic forms of waves would be unlikely to occur in the examples I cover. Through the mechanisms of self-organisation however waves can be formed with surprising unison between the participating animals, resulting in waves with relatively stable variables. This is illustrated by comparing figure 5 and 6, where figure 5 is a theoretical example of waves and where figure 6 comes from an

experiment by Kastberger. Although we do not see a perfectly steady amplitude or wavelength in Kastberger's research, we can see it closely resembling travelling waves in a biological situation.

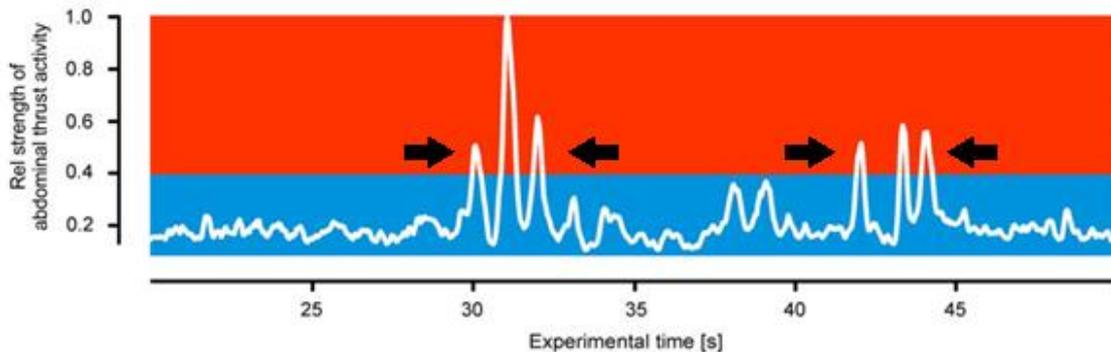


Figure 6 A graph showing the relative thrusting activity of a single giant honeybee. Black arrows indicate the formation of waves. (Kastberger et al., 2009)

Figure 6 shows us a graph coming from Kastberger's research on giant honeybees (Kastberger et al., 2009). Note that while it's a graph similar to figure 4, the x-axis now indicates a time period. This means that we look at the difference in behaviour of a single giant honeybee over a certain period of time. In this case the so-called relative thrusting activity where the giant honeybees lift their abdomens along the nest's surface to deter predators is measured. Position of the wave, in this case the bee, is the fixed variable, while time is the variable portrayed along the x-axis.

The speed of waves, defined by v , is an essential variable when considering travelling waves, also relevant to biological situations. The speed of a wave varies through difference in the medium through which the wave travels. In the biological situations where we encounter waves the medium will always be the organisms themselves, be they anchovy schools forming waves of agitation or gianthoneybees thrusting their abdomen along the nest surface in a shimmering wave (e.g. Gerlotto et al., 2006, Kastberger et al., 2009, Procaccini et al., 2011). The speed however differs in many cases, and is an interesting phenomenon to observe not only by means of comparing the collected data from several studies, but also comparing how different researchers have collected and measured this data.

In the rest of my thesis I will place studies by Kastberger on giant honeybees and Procaccini on starlings into the framework of wave variables I have just explained and try to justify why these biological phenomena can be addressed as waves. This way I hope to show how they differ from other studies where forms of collective behaviour are labelled as behavioural wafves.

Benefit of waves

Before delving deeper into the specific mechanisms of certain behavioural waves, it's important to take one more look at the broader context. So, waves have been measured or observed in species, and although they may not be harmonious waves they do display variables that closely resemble these harmonious waves, fitting in the wave equation we have discussed before. From a biological point of view the question that arises is why? Why do these waves appear, not only in for instance anchovy schools but in so many more species and systems?

From the introduction we have learned that even on a level of molecules providing each other with catalytic growth these behavioural waves spontaneously arise (Boerlijst et al., 1991). We have also directly seen that this is not only a purely coincidentally occurring mechanism, it actually provides these species with a benefit; protection from parasitization in this case. The same can be said, at least partially, for the appearance of the waves of agitation in anchovy schools. While the appearance of the wave can partially be explained through the copying of the behaviour of their neighbours, there is also an evolutionary benefit to the occurrence of these waves. The waves of agitation not only have a visual effect that is thought to deter predators but it also speeds up the transfer of information, in this case the information that a predator is nearby, throughout the whole school allowing for a better response time by the entire school to this threat (Gerlotto et al., 2006). This seems to be the general benefit of waves occurring in many species. When looking at the appearance of waves in biological settings in the literature predator-prey relations are usually the evolutionary cause of these behavioural patterns occurring (Treherne & Foster., 1981, Kastberger et al., 2009, Procaccini et al., 2011).

A point Potts' research on dunlins raised in 1984 already (Potts et al., 1984) explains to a large extent

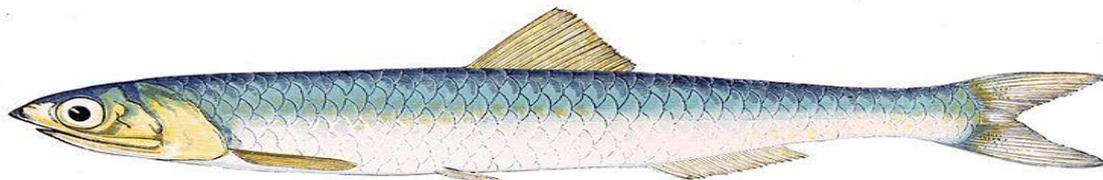


Figure 7 Anchovies show their silvery underside in a wave of agitation.

the presence and occurrence of waves in many flocking birds. For the propagation of waves individuals have to anticipate the arrival of the wave at their position, for when they would simply respond to the behaviour of the nearest neighbour the speed of information transfer and therefore the forming of the wave would be significantly lower (Potts et al., 1984). This shows us that, similar to waves in anchovy schools, this phenomenon increases the speed of information transfer, partially through anticipation, which is a massive advantage when dealing with potentially lethal predatory attacks. I will go into slightly deeper detail of Potts' experiment on dunlins to illustrate the effects of waves on the speed of information transfer.

In his experiment Potts observed the movement of dunlin flocks in response to predators, either in a natural situation or artificially induced by shooting an arrow close to the flock, simulating a predator (Potts et al., 1984). He differentiated between coordinated- and non-coordinated manoeuvres that were always initiated by a number of individuals, where coordination was defined by the reaction times of their neighbours (Potts et al., 1984). One of the first observations was that all the

coordinated manoeuvres were initiated by birds banking towards the flock. When birds banked away from the flock the number of followers was either non-existent or significantly lower, and at speeds too low to qualify as a coordinated move (Potts et al., 1984). This shows us the benefit of coordination in these flocks: by having certain movement patterns that classify as coordinated, these movement patterns benefit from the faster information transfer through the propagation of waves in the flock. In this case the coordinated manoeuvres were the ones causing the flock to form a tight formation which has been interpreted as an anti-predator response (Buchanan et al.1988; Zoratto et al. 2010).

During such a coordinated manoeuvre the propagation speeds of these waves eventually exceed the



Figure 8 Dunlins form tight airborne flocks when under risk of predation.

speeds by which individuals could react to their immediate neighbours, indicating a beneficial effect on the speed of information transfer through the occurrence of waves, providing the flock with an increased survival chance through the rapid formation of a tight-airborne flock (Potts et al., 1984, Beauchamp et al., 2012).

Giant Honeybees

Giant honeybees are a species of bees that build their nests straight out in the open. For this reason, they are susceptible to a variety of predators, most commonly birds and wasps. A mechanism that honeybees use especially to deter wasps but has been thought to also deter large herbivores is known as shimmering(Kastberger et al., 2009). Shimmering is the appearance of a wave over the surface of the nest, consisting of thousands of bees participating in it. Shimmering has the added benefit over other defence mechanisms like flying guards that it doesn't put the participating individuals in harm's way. This added benefit is caused by the release of Nasonov pheromones during the shimmering behaviour, a social pheromone that promotes grouping behaviour and reduces the amount of bees leaving the nest as flying guards. The wave is formed by bees actively raising and moving their abdomen, causing a wave to appear that shows distinct similarities with the Mexican wave observed in humans (Farkas et al., 2002) showing an intriguing capacity for very rapid communication in the nest (Kastberger et al., 2008).

Shimmering is a very complex behavioural phenomenon, and there are various mechanisms that play a role in its occurrence. Firstly, the wave has to start somewhere, and for some reason. Typically these waves are thought to form in response to hornets, and shimmering mostly occurs when a hornet comes too close to the nest. At about 50 centimetres of distance a hornet will induce shimmering waves on the nest-surface. The types of waves that these hornets induce will differ depending on certain variables. The Hornet's distance to the nest as well as the velocity of the hornet both affect shimmering behaviour. The large shimmering waves occurring over the nest, wherein thousands of bees participate, serve the main purpose of scaring off fast-moving hornets at a distance of around 50 centimetres, a rather common hovering distance for predating hornets (Kastberger et al., 2008). This causes these shimmering waves to serve as a deterring mechanism, keeping the wasps away from the nest.



Figure 9 Shimmering wave (red) spreading across nest surface (Kastberger et al., 2008).

Typically there are two explanations why these large waves would be successful in deterring the wasps from the immediate surroundings of the hive. They may reinforce innate fixed action patterns of avoidance in these wasps, something wasps have evolved to avoid collisions and possible risks from larger animals. Secondly, when the wave progresses along the nest after being triggered by the hornet, the wave front stays behind the wasp because the wave moves at speeds comparable to the wasp's speed, or slightly lower speeds (Kastberger et al., 2008). This causes the wasp to 'flee' from the place it originally wanted to predate on. The wasp will fly away from the movement of the wave, which moves him away from the nest, resulting in a predator-free zone around the nest.

However, sometimes hornets end up closer to the nest, especially those moving at lower velocities. There is a second shimmering pattern that occurs to specifically deter wasps who are in closer proximity to the nest. In this case much smaller shimmering waves are created on a local scale in the nest which causes the wasps to continuously shift his focus and his turning angle. This is interpreted as a mechanism that causes confusion in the wasps and makes it harder for them to focus on single bees, thus making predation very difficult.

While we now know what external factors trigger the formation of shimmering waves, we also need to understand the mechanisms playing a role at the nest surface. Let's start at the beginning of the wave. Research shows that while, through the self-organisational mechanisms that we suspect to play a role, we expect the waves to start from a few random individuals in the wasp's proximity and then to progress through the colony Kastberger et al. actually find that there are so called 'special agent' bees spread over the nest, specialised by for instance age or other criteria, who will always be the ones to initiate a shimmering wave. This also means that shimmering does not necessarily start close to the threatening source(Kastberger et al., 2009). Similar research also suggests that bees with different workloads play different roles in shimmering, these workloads being linked to the areas on the nest where the bees reside. For instance the initiation of a wave never occurs in the so called 'mouth' zone, the zone where most of the incoming foraging material is processed and where the workload is expected to be highest (Kastberger et al., 2001).

When looking at the propagation and specifics of the wave itself, a surprisingly high level of complexity can be seen. It is believed that every individual bee is free to decide on joining the wave or not, and if so can join the wave with a flipping abdomen varying in angles anywhere from 0° to 120°(Kastberger et al., 2012). This participation varies so strongly from agent to agent because of agent-specific factors: for instance the location in the nest, the participation of their neighbours and their age. This leads to a wave with a high level of complexity and unpredictability. This means that generally there are a lot of variables that influence the mechanism of wave forming in these

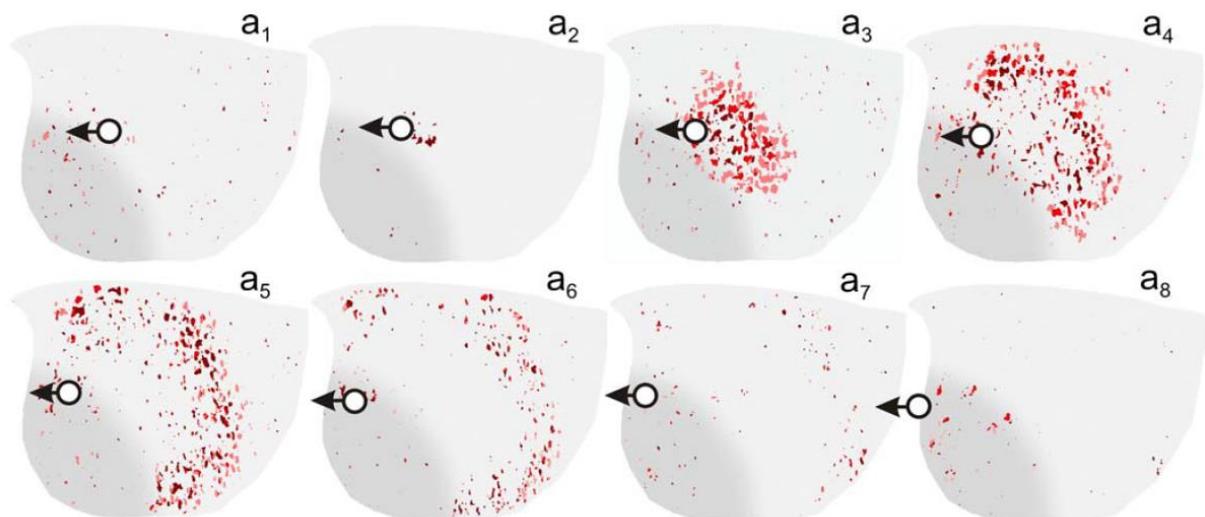


Figure 10 A shimmerign wave occuring after introducing a hornet (black circle with arrow). A2 shows us the 'special agents' instigating the wave (dark red) (Kastberger et al., 2009).

honeybees. Three variables that Kastberger mentions and measures are the linearity, continuity and graduality of the wave. When a perfect neighbour-copying situation would cause the wave to propagate throughout the nest, one would expect this wave to propagate in a linear route, in a continuous fashion and the wave would be relatively gradual in its strength.

If the wave would progress linearly, this would mean the information transfer that causes the wave occurs in a straight line. So if the shimmering wave starts in the left-most part of the nest, all the cues that stimulate bees to participate will be given by neighbours to the left of them, causing the wave to linearly move towards the right side of the nest. Continuity would mean that the wave would

progress in a continuous fashion. No bees are skipped, the wave is not delayed or stopped before it reaches the end of the nest. Finally, a gradual wave means that the strength of the wave, in this case the relative thrusting activity of the participating honeybees, is similar or differs gradually between a bee and his neighbours. If all three of these conditions are met, we can speak of a bucket-transfer mechanism, which allows all the neighbours to transfer the signal to join the wave in a linear line, in a continuous and gradual fashion (Kastberger et al., 2012).

However, Kastberger showed that the individual bees are free in their choice to participate, already causing a loss of continuity. The intensity they respond with could vary, and Kastberger shows that at the start of the wave, newly participating bees are more likely to respond to their neighbour's cues with a higher activity, while later on in the shimmering wave the activity slowly decreases causing the wave to eventually die out. This leads to the formation of a wave wherein continuity and linearity are lacking in many phases of the shimmering wave because there are many bees not participating in the wave, but there can be parts of the wave where the intensity remains at stable levels, resulting in a partially gradual wave as illustrated in Figure 11.

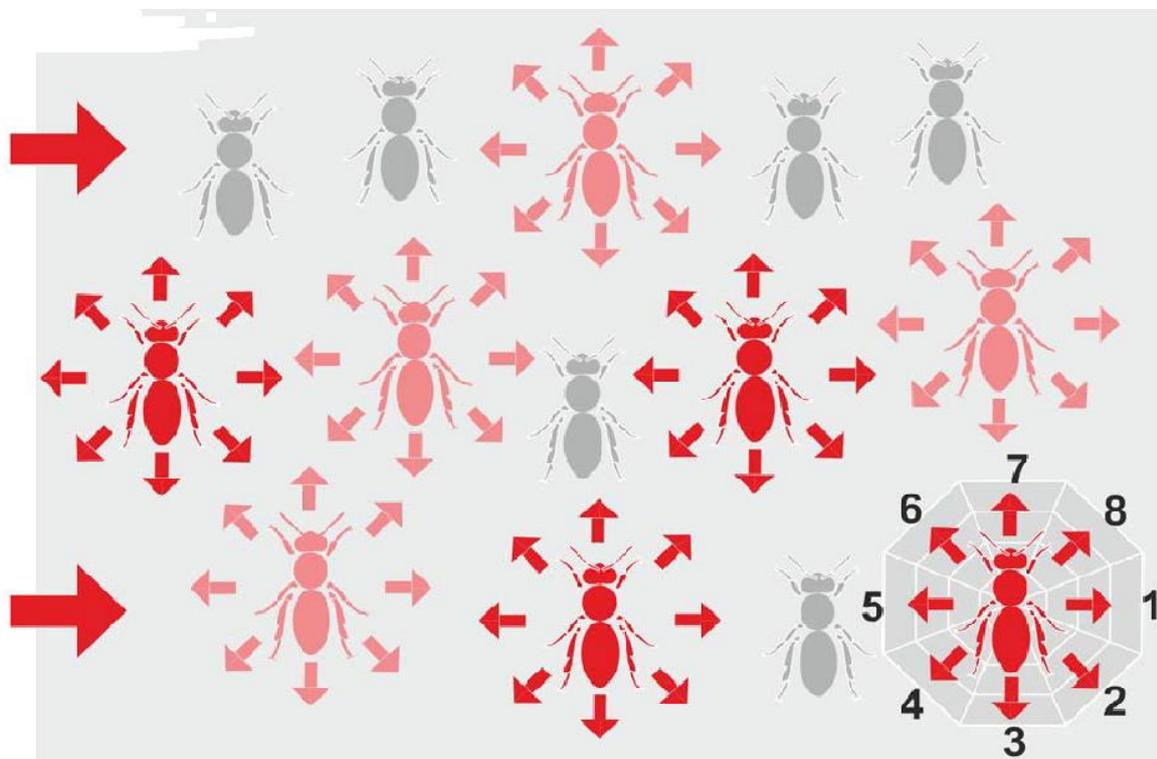


Figure 11 A wave propagating through the nest. Because of the individual choice some bees are left out of the wave, causing discontinuity. Signals from bees to all sides causes previously-inactive bees to respond to signals from other directions, resulting in in-linearity. Varying waving strengths between individuals lead to partial in-graduality (Red -> Light Red). (Kastberger 2011)

Finally, on the wave specific variables in shimmering behaviour: Shimmering waves are an excellent example of a travelling type of wave occurring in biological situations, resembling the harmonious wave previously shown. Figure 12 illustrates the shape of the shimmering wave. Along the entire nest's surface, usually one or a few waves propagate at the same time. Because in a wave there are usual several oscillations, it has a wavelength and speed. Figure 13 shows us the propagation of a wave along the nest.

This wave lasts only for about 700 to 800 milliseconds, with wavelengths differing between waves. Typically, shimmering waves occur in less than a second (Kastberger et al., 2009). The amplitude in the case of shimmering waves refers to the maximum number of bees participating at a given time; differences could be found depending on the size of the wave and the nest and in different circumstances. The only specific circumstance Kastberger looked at was how the maximum shimmering activity, or amplitude, differed for the hornets' distance to the nest and its velocity. He found that with decreased distance and increased velocity the amplitude increases in both cases. In

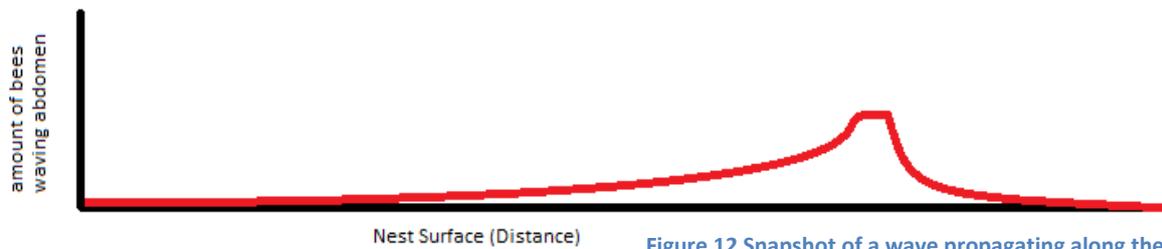
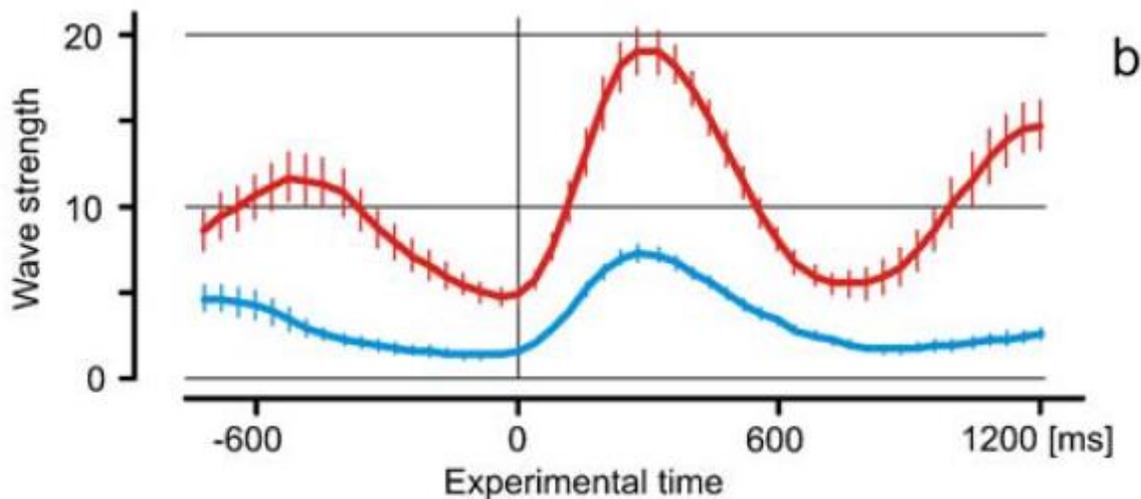


Figure 12 Snapshot of a wave propagating along the nest surface.

figure 13 twenty individuals are participating per frame, thus over the course of a bigger wave hundreds or thousands of bees will participate, likely giving us amplitudes of a higher value.

How exactly these wavelengths and amplitudes differ between nests has not yet been studied. Kastberger has already performed a tremendous amount of research with the use of 3D cameras to give some insight in the decision making process of honeybees forming shimmering waves, and the mechanisms behind them. To further investigate the specific variables of these waves new studies would have to be undertaken.

Figure 13 Graph showing the wave strength (number of individuals participating per frame) over time. (Kastberger 2009)



Starlings

A different wave occurs in starlings, but shows surprising similarity. Through video recordings Procaccini et al. attempted to generate empirical data on this phenomenon involving thousands of individuals (Procaccini et al., 2011). Their attempts to shed some light on the quantitative

characterization of this phenomenon have resulted in interesting findings about these waves and their relation to predation.

European starlings, an extremely gregarious bird species, come together in flocks of thousands of individuals during the autumn and winter (Feare et al., 1984). Procaccini found that under threat by hunting activities of peregrine falcons these flocks of starlings form waves, thought to have an effect on anti-predator defences. The wave is observed as a local increase in optical density of the flock, moving along the flock in a matter of seconds. Figure 14 illustrates the appearance of these waves in



Figure 14 A wave of density propagating in a starling flock, indicated by the darker areas. (Procaccini et al., 2011.)

two flocks in Italy. These so called wave events were defined as a train consisting of several pulses of optical intensity propagating along the flock. They needed to be separated from other 'trains' by at least 10 seconds (Procaccini et al., 2011).

One of the important points Procaccini's research focusses on is the relation to predation, which can be seen as a large evolutionary benefit. In agreement with several other similar studies, in species of insects and fish for instance (Webb et al., 1980, Treherne & Foster, 1981, Gerlotto et al., 2006, Kastberger et al., 2008), he found that these wave events occur almost exclusively under predator threat. This suggests that they can be classified as anti-predator behaviour (Procaccini et al., 2011). Importantly, wave events were more frequent and more likely to occur during unsuccessful hunting sequences. This leads us to believe that they serve a purpose in deterring these predator through inciting confusion. Confusion, as opposed to other deterring behaviour like for instance mobbing where the predator is harassed by a collective swarm of individuals (Krause & Ruxton 2002), occurs by changing or breaking the spatial order of the group, reducing the predator's chance of success.

So, while these waves are triggered by hunting activities of peregrine falcons, what are the mechanisms on the individual level that cause these waves to occur? That density is a key quantity in determining these dynamics appears is suggested by nearly all the issues addressed in the study (Procaccini et al., 2011). Before the falcon appears, the starlings are in a so called resting state, where they are airborne and flocking but do not display escape behaviour. The appearance of the falcon causes a disturbance of this resting state, at least in a specific part (or a few parts) on the surface of the flock. The appearance of this falcon causes these starlings to initiate their escape from the predator, they fly away. If they would be free to move, they would fly away and no wave would

occur. However, since they are flying in a flock this causes the starlings on the surface to fly into the flock of their conspecifics. So, after a very short distance they meet with their neighbours, tightening the flock. Their escape triggers the same behaviour in their conspecifics causing a wave of fleeing behaviour to roll through the flock. Because the flock relies on mechanisms that cause the birds to keep a certain distance from each other, the initially fleeing birds constrain their fleeing behaviour to avoid collisions, and fall back to a set inter-individual distance according to flock mechanisms. This causes a deformation of the wave following the initial wave appearance. This wave behaviour is illustrated in figure 15, where we can see a rapid increase in optical density followed by the

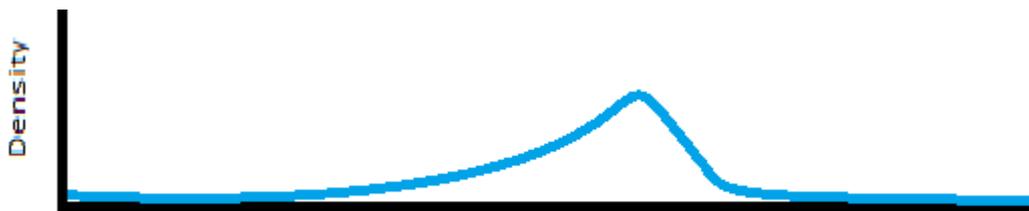


Figure 15 Wave in starlings as a function of position in the flock

deformation throughout the flock. One such sequence is called a pulse, with multiple pulses often following after another in a single wave-event (Procaccini et al., 2011)

Wave variables were also studied. Wave velocity was often greater than the absolute velocity of either the predator or the flock. This property seems to be a reoccurring phenomenon in waves and applies to similar phenomena in other species (Radakov et al., 1973, Potts et al., 1984, Axelsen et al., 2001, Gerlotto et al., 2006). A table with variables differing between different series of wave events was published by Procaccini:

Important to note is that many wave events consist of a series of pulses, the number of pulses differing between these wave events. Between 2 and 20 pulses were observed in this experiments, with values between 3 and 6 being most common. The average frequency of pulses differed between 0.5 and 3 pulses per second, with values between 1 and 1.5 being most common. Although these values still differ quite a lot between wave events, this gives us some idea as to the values of some of the variables.

Wave event	Total frames	Duration (s)	Velocity (m/s)	Error (m/s)
Series 1a	10	0.33	15.56	1.52
Series 1b	27	0.90	6.89	0.49
Series 4	12	0.40	25.24	4.21
Series 8a	31	1.033	17.47	1.35
Series 8b	11	0.37	25.10	2.06
Series 8c	17	0.57	13.73	1.10
Series 8d	37	1.23	7.79	0.62
Series 9	22	0.73	18.26	3.04
Series 10	57	1.90	7.63	0.54
Series 12	15	0.50	9.44	0.67
Series 13	26	0.87	3.66	0.61
Series 15a	18	0.60	14.48	1.24
Series 15b	14	0.47	11.76	0.84
Series 18	10	0.33	8.21	0.70
Series 19	16	0.53	10.44	1.74
Mean	21.5	0.72	13.04	1.66

Figure 16 Variables of different wave events in starlings (Procaccini et al., 2011)

Discussion:

So far in my thesis I have discussed waves in a few select cases: in giant honeybees and in starlings. Both are excellent examples of wave formations in social groups. To put this in perspective however, it's important to look at other wave-forming mechanisms. Throughout biological literature waves have been mentioned, but haven't always been addressed properly. For instance Beauchamp mentions the appearance of waves in sandpipers and gulls (Beauchamp et al., 2011, Beauchamp et al., 2012), but has put little research into the specifics and variables of these waves. It is therefore hard to even label these phenomena as waves, because there are certain criteria a wave has to fit.

A key factor when researching waves is that contagious behaviour itself does not necessarily lead to the formation of collective waves of activities (Beauchamp et al., 2011). This shows us the main issue many wave-related studies run into. Although Beauchamp himself raises the issue, it's relevant in relation to his research as well. In his research on sandpipers for instance he calls the escaping behaviour of grounded flocks of these birds a wave. The rest of his paper however focusses on the speed of these waves in relation to density and group size. While an interesting question, since the wavelength and amplitude remain a large mystery and the mechanisms aren't uncovered I believe he might be wrong in addressing this phenomenon as a wave. Although the biological phenomenon is certainly interesting, and so is the research topic on density and group size that he builds around it, to address this as a wave he would have to put in some effort to take the wave equation and it's variables into consideration.

This is the case for many other researches in the area of collective or contagious behaviour, and self-organization. This is why in my thesis I have focussed on the researches by Procaccini and Kastberger. In both giant honeybees and starlings waves have been researched and their mechanisms have been speculated on, but these speculations are still far from conclusive. Both studies only raise suggestions and sometimes provide alternatives. Kastberger shows us the special agent and bucket-transfer theories, but they are not proven (Kastberger et al., 2008, Kastberger et al., 2009, Kastberger et al., 2012). Procaccini mentions density as a possible factor in these waves occurring, but also mentions the need for further research in this field to yield an answer to what the mechanism behind this phenomenon is (Procaccini et al., 2011, Hildenbrandt et al., 2010, Hemelrijk & Hildenbrandt 2011).

I would therefore like to conclude my thesis by saying that while there are many interesting biological phenomena that resemble waves or wave-like behaviour in other species, it is important to keep in mind the rules that many physicists have supplied us with. Before addressing a phenomenon as a wave, it's important to go back to the wave equation and prove these assumptions. This not only rightly describes the phenomenon as a wave, but also gives insight in the variables and can shed light on the mechanisms that play a role in the formation of these waves.

Reference List

- Ashby, W. R. (1962). "Principles of the self-organizing system," in *Principles of Self-Organization: Transactions of the University of Illinois Symposium*, H. Von Foerster and G. W. Zopf, Jr. (eds.), Pergamon Press: London, UK, pp. 255-278
- Axelsen, et al., 2001. Pretty pattern but a simple strategy: predator & prey interaction between juvenile herring and Atlantic puffins observed using multibeam sonar. *Canadian Journal of Zoology*, 79, 1586e1596.
- H. Von Foerster and G. W. Zopf, Jr. (eds.), *Transactions of the University of Illinois Symposium*, Pergamon Press: London, UK, pp. 255-278.
- Beauchamp G. 2011. Collective waves of sleep in gulls (*Larus* spp.). *Ethology*. 117:326–331.
- Beauchamp G. 2011. Consistent waves of collective vigilance in groups using public information about predation risk, *Behav Ecol* 23:368–374
- Beauchamp G. 2012. Flock size and density influence speed of escape waves in semipalmated sandpipers, *Animal Behaviour* 83:1125-1129.
- Boerlijst, M.C. and Hogeweg, P. (1991a), Spiral wave structure in pre-biotic evolution: hypercycles stable against parasites, *Physica D* 48, 17-28.
- Boerlijst, M.C. et al., (1993), Evolutionary consequences of spiral waves in a hostparasitoid system, *Proc. R. Soc. London B* 253, 15-18.
- Boerlijst, M.C. et al., (1995), Spatial gradients enhance persistence of hypercycles, *Physica D* 88:29-39
- Buchanan, J. L et al., 1988. Merlin predation on wintering dunlins: hunting success and dunlin escape tactics. *Wilson Bulletin*, 100, 108e118.
- Couzin, I. D. & Krause, J., 2003. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, 32, 1e75.
- Davis, J. M 1980. The coordinated aerobatics of dunlin flocks. *Anim. Behav.* 28, 668-673
- Gerlotto, F. et al., 2006. Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. *ICES Journal of Marine Science*, 63: 1405e1417
- Farkas I, Helbing D, Vicsek T (2002) Social behaviour: Mexican waves in an excitable medium. *Nature* 419: 131–132.
- Feare, C. J. 1984. *The Starling*. Oxford: Oxford University Press.
- Hemelrijk, C. K. & Hildenbrandt, H. 2011. Some causes of the variable shape of flocks of birds. *PLoS ONE*, e22479, doi:10.1371/journal.pone.0022479.
- Hildenbrandt, H., Carere, C. & Hemelrijk, C. K. 2010. Self organized aerial displays of thousands of starlings. *Behavioral Ecology*, 21, 1349-1359.
- Kastberger, G, et al., (2008) Social waves in giant honeybees repel hornets. *PLoS One* 3(9):e3141. doi:10.1371/ journal.pone.0003141
- Kastberger, g, et al., (2009) 'Special agents' trigger social waves in giant honeybees (*Apis dorsata*), *Naturwissenschaften*. 96:1431–1441
- Kastberger, G et al., (2012) How to join a wave: decision-making processes in shimmering behaviour of giant honeybees (*Apis dorsata*). *PLoS One* 7(5):e36736. doi:10.1371/journal.pone.0036736
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.

- Potts, W. K., 1984. The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature*, Vol. 309, No. 5967, pp, 344-345.
- Procaccini, A. et al., 2011, Propagating waves in starling, *Sturnus vulgaris*, flocks under predation. *Animal Behaviour* 82 (2011) 759-765
- Radakov, D. V. 1973. *Schooling in the Ecology of Fish*. New York: J. Wiley.
- Sumpter, D. J. T. 2010. *Collective Animal Behavior*. Princeton, New Jersey: Princeton University
- Treherne, J. E. & Foster, W. A., 1981, group transmission of predator avoidance behaviour in a marine insect: the trafilgar effect, *Anim. Behav.*, 1981, 29, 911-917
- Webb, P. W. 1980. Does schooling reduce fast-start response latencies in teleosts? *Comparative Biochemistry and Physiology*, 65, 231-234.
- Zoratto, F et al., 2010. Aerial hunting behaviour and predation success by peregrine falcons *Falco Peregrinus* on starling flocks *Sturnus vulgaris*. *Journal of Avian Biology*, 41, 427-433.