

EFFECTS OF PREDATOR CHARACTERISTICS ON HUNTING SUCCESS ON FLOCKS OF BIRDS

Bachelor project for Artificial Intelligence, University of Groningen

Author: E.J. Brilman, s2067781, e.j.brilman@student.rug.nl

Supervisors: C.K. Hemelrijk and H. Hildenbrandt

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Abstract: Starlings (*Sturnus vulgaris*) can gather in enormous flocks composed of up to millions of birds. Avian predators such as the peregrine falcon (*Falco peregrinus*) are known to attack these flocks, employing a variety of hunting strategies. Because empirical data are difficult to gather on flocks of starlings and their interactions with falcons, models are used to gain further insight into the underlying mechanics.

StarDisplay is a 3D model that uses a simplified version of fixed wing aerodynamics to simulate the flying and flocking behaviour of birds. In this bachelor project, StarDisplay was used to investigate several hunting strategies with different avian predator characteristics to determine what their effect is on predation in terms of success and efficiency per attack against both flocks of avian prey and solitary prey. Success was measured by recording how close the predator approached its prey during an attack, and efficiency was measured by the predator's path length during the attack.

Within the setting and limitations of the model, increasing the predator's speed was shown to have a mostly detrimental effect on the success rate of attacks. Increasing the predator's maximum roll rate did improve the predator's performance against prey in many cases.

The most successful hunting strategy was the repeated attacks sequence, in which the predator makes multiple attacks in rapid succession. However, this particular strategy was rather intensive in terms of energy expenditure. The posterior attack, in which the predator sneaks up behind a flock and makes a gradual approach to its target, was shown to provide a good trade-off between success rate and efficiency.

1. Introduction

Avian predators are known to attack large flocks of prey. The specific hunting strategies predators use differ per species and also depend on the type of prey. Predators seek to maximize hunting success, while prey animals seek to minimize it. In the course of the evolutionary process there is a constant pressure to search the optimal strategy to counter that of the opponent (Zoratto, Santucci & Alleva 2009).

This bachelor project will investigate several hunting strategies with different predator characteristics, to determine what their effect is on predation in terms of average success rate and efficiency per attack. The predator and prey bird that will be examined are respectively the peregrine falcon (*Falco peregrinus*) and the starling (*Sturnus vulgaris*).

1.1. Models of self-organization

Starlings gather in enormous flocks composed of up to millions of birds (Videler 2006). These flocks frequently make complex manoeuvres in the air. Amazingly, all of the individual birds involved seem to do this without much difficulty, as they all participate simultaneously in unison with each other. Empirical data on behaviour of large flocks is presently scarce, and does not sufficiently explain the underlying causes of this behaviour (Ballerini et al. 2008b, Hildenbrandt, Carere & Hemelrijk 2010). These kind of data are very difficult to acquire because of the often enormous number of birds involved and large distance between flock and observer (Major, Dill 1978).

Models are used to gain further insight into the behavioural rules of individuals. Typically, at

the individual level only a few simple behavioural rules are employed. These rules describe the physical reaction of an individual bird to other birds in its neighbourhood. Birds are attracted to other birds, align their orientation with them and avoid collisions (Reuter, Breckling 1994). At the group level, these rules result in the complex flocking behaviour that has been shown to be similar to empirical data (Hildenbrandt, Carere & Hemelrijk 2010). This process, where organized behaviour at the group level emerges from local interactions between autonomous individuals, is referred to as self-organization (Camazine et al. 2003).

Grouping behaviour of fish, also known as schooling, has been widely studied in models (Hemelrijk, Hildenbrandt 2008, Hemelrijk et al. 2010, Inada, Kawachi 2002). However, it is different from grouping behaviour of birds in multiple ways (Hildenbrandt, Carere & Hemelrijk 2010, Hemelrijk, Hildenbrandt 2012). Densities of bird flocks are independent of flock size, and do not differ between front and back, in contrast to fish schools (Ballerini et al. 2008b, Hemelrijk, Hildenbrandt 2008). Also, the shape of fish schools is oblong, while that of moving bird flocks can take many forms (Hemelrijk et al. 2010). Most importantly, in their movements fish schools stay mostly at the same depth, while bird flocks constantly move upward or downward during manoeuvres. An example is when birds change their direction in the horizontal plane. They roll alongside their longitudinal axis into the direction of the new destination and typically lose some altitude in the process because their vertical lift decreases (Pennycuik 2008). This is known as a banked turn, and the angle to the horizontal plane is called the banking angle (Videler 2006). In contrast, fish stay at the same depth when turning horizontally (Inada, Kawachi 2002).

This important distinction between fish and birds must be taken into account when attempting to model flocks. It follows that two-dimensional models do not realistically represent the movement dynamics of starling flocks as they lack vertical movement. Currently StarDisplay is the only model available that simulates flying behaviour of bird flocks in three

dimensions, and for this reason it will be used in this bachelor project.

1.2. Predation on flocks and solitary birds

Large flocks of starlings will naturally attract predators such as the peregrine falcon. The peregrine falcon often captures its prey using high-speed stoops which start as a straight, nearly vertical dive (Tucker 1998, Rudebeck 1950). This raptor has been measured to reach speeds of up to 39 m/s (140 km/h) during such dives, making it the fastest moving animal known (Alerstam 1987, Palleroni et al. 2005).

The interactions between flocks of prey and predators are even less well-studied than the flocking behaviour of prey itself. Still, from the limited empirical data several hunting strategies can be distinguished (Dekker 1988, Dekker 2003, Zoratto et al. 2010). The most common strategy used by the peregrine falcon against a flock of starlings is the dive attack (Rudebeck 1950, Zoratto et al. 2010). The peregrine falcon starts his attack from a distance above the starling flock, originating from such an angle that the flock does not display any reaction before the attack has ended. In other words, the predator uses the surprise effect to avoid evasive behaviour and thereby increase its odds of success.

Other commonly observed attack strategies are the flock pursuit, in which the falcon flies along with the flock for some time before attacking, and the repeated attack sequence, in which the predator make several attacks in rapid succession. It is important to note that there are great many amount of different possible hunting strategies, and the classification of an observed attack to a specifically predefined hunting strategy is to some extent arbitrary as the definitions of many strategies are overlapping with each other (Dekker 1988, Zoratto et al. 2010, Rudebeck 1951, Dekker 1980, Cresswell 1996).

Avian predators typically don't perform well against prey in so-called dog fight scenarios. In these circumstances the predator and prey are positioned close together and involved in a turning gambit, in which the prey can usually evade capture by outmanoeuvring the predator. This is due to a larger relative wing area resulting in a smaller turning radius (Hedenström, Rosén 2001).

Attacks on solitary prey have been reported to more often result in a successful catch than most types of attacks on a flock, in one study respectively 60.9% success against solitary prey versus an average success of 23.1% over all hunting strategies (see table 2.1 in Zoratto et al. 2010). The reason why peregrine falcons appear to mainly attack flocks of starlings as opposed to solitary starlings is not immediately obvious. Possibly, flocks are easier to visually locate (Zoratto et al. 2010).

1.3. Reasons for avian grouping behaviour

There are several benefits for an individual prey bird to be part of a flock, in aspects such as partner selection, foraging and movement efficiency (Hummel 1983, Bajec, Heppner 2009). For starlings, protection against predatory birds such as falcons appears to be the primary reason of flocking (Zoratto, Santucci & Alleva 2009, Carere et al. 2009, Wood 2010).

There are multiple ways in which flocking behaviour proves beneficial in this respect. A selection will be discussed.

The selfish-herd theory explains how individual birds in a flock can use their fellow flock members located at the edges of the flock as living shield against predators (Hamilton 1971).

Additionally, a densely concentrated flock makes it difficult for a predator to spot, follow and catch a specific prey within such a flock, because there are a large number of similar targets moving through the predator's visual field creating a disorientating effect. This causes the predator to lose focus on its target and is known as the confusion effect (Zoratto, Santucci & Alleva 2009).

Another advantage of being in a flock is the avoidance and dilution effect, which consists of two components (Turner, Pitcher 1986). Firstly, a single concentrated flock of prey is harder to find than the combined chance of finding any single one of those prey when they are all flying solitary (Vine 1973). Secondly, when finally locating a flock, a predator is not likely to eat all members, because of constraints in time, energy and satiation. As a result of this, members of a large flock under attack have a smaller chance of being singled out and killed.

Finally, the many-eyes theory should be mentioned. A group of individuals has a greater probability of detecting an attacking predator than a single solitary bird (Siegfried, Underhill 1975). While feeding, this means that individual birds can divert more time to locating and consuming food, and less time to looking around for predators. After all, it is likely that other group members will detect incoming predators and sound the alarm by engaging in evasive manoeuvres.

On the other hand, there are also disadvantages for a bird to be in a flock. Most notably, flying in flocks lead to higher competition over feeding grounds close to the flock, especially when there is a limited availability of food. This cost must be weighed against the benefits, which consist mainly of anti-predatory advantages. Of course, it follows that the extents of food availability and predatory pressure play a decisive role. If there are no or barely any predators, it makes little sense to sacrifice food consumption for protection against predatory attacks that might never occur. Thus, the decision of whether or not to form groups involves a balancing act between costs and benefits, based on local conditions (Zoratto, Santucci & Alleva 2009). Evolutionary pressure ensures that behaviour that leads to greater odds of survival is selected for. In the case of starlings, empirical evidence has shown that flocking apparently presents a net benefit in most situations.

2. Methods

As stated before, the goal of this bachelor project is to investigate several hunting strategies with different predator characteristics in order to determine what their effects are on predation in terms of success rate and efficiency per type of attack. Success is measured by recording the smallest distance the predator was to a prey during an attack: the minimal predator-prey distance. Efficiency is defined as the distance travelled by the predator per attack. To get a more complete overview of what movement the predator has to carry out, both the total distance travelled and the climbed distance travelled are measured.

A total of 55 experiments of different hunting strategies and predator parameter settings were

carried out. Each experiment was repeated 30 times. Per experiment, the average minimal predator-prey distance and predator's path length was measured. Also the standard deviation of these measured variables between repetitions was calculated to provide an indication of the variance between iterations.

2.1. Statistical analysis

The minimal predator-prey distances and path lengths cannot be assumed to be approximately bivariate normally distributed (based on preliminary analysis of the data), so non-parametric statistical tests were used.

To test if a given predator parameter has a statistically significant effect on the minimal predator-prey distance, the Kendall rank correlation coefficient test was used. The correlation coefficient τ is a measurement of the proportion of concordant pairs minus the proportion of discordant pairs. The null hypothesis is that the predator-prey distance and tested parameter are statistically independent of each other.

For statistical tests between the individual attacks of the repeated attacks sequence and between different hunting strategies, the Kruskal-Wallis rank sum test was used. The null hypothesis of the Kruskal-Wallis rank sum test is that the samples of all groups come from identical populations.

For both tests, the critical significance level is chosen to be at $\alpha = 0.05$.

2.2. StarDisplay

To simulate the starling flocks and predatory falcons the computer model StarDisplay¹ was used. This three-dimensional model employs a simplified version of fixed wing aerodynamics, with each individual bird experiencing lift, drag and gravity. The characteristics of the predator are roughly based on the peregrine falcon, and those of the prey are based on starlings. For a more extensive explanation of this model the reader is referred to the original article describing the model (Hildenbrandt, Carere & Hemelrijk 2010). The values of several

parameters will be described in the text below; the complete description of used parameters within StarDisplay and their values can be found in Appendix A.

Realistically, the midpoint of the predator should approach the midpoint of the prey within 20 cm apart during an attack for it to be considered a successful catch. However, the final phase of the attack in which the predator breaks to reduce its speed (thereby decreasing its turning radius and improving manoeuvrability), then strikes and catches its prey, is currently not explicitly modelled within StarDisplay. Because of this, the predator is almost always well beyond 20 cm of its prey during the attack with all predator settings and hunting strategies, so almost no catches can be recorded. To still have some kind of quantitative measurement for how well the predator is performing at a given parameter setting and hunting strategy, the minimal predator-prey distance was recorded as a measurement how good the predator was at catching prey, instead of recording catches in the model by setting a (somewhat arbitrary) predator-prey threshold value catches.

2.3. Prey

Flocking behaviour of the simulated starlings was created by the three classic rules of attraction, alignment and collision avoiding (Hildenbrandt, Carere & Hemelrijk 2010, Hemelrijk, Hildenbrandt 2012). The input was based on neighbours within the topological range, which was set to 6.5 neighbours as this aligns best with empirical data (Ballerini et al. 2008a, Camperi et al. 2012). The cruise speed of the starlings was set to 10 m/s or 36 km/h (Ward et al. 2001). When the predator was within 20 meters of the starlings, they started to react to it. At this point, they spread their state of alarm to other birds within their topological range and their reaction time was cut in half, reflecting their increased sensitivity to outside stimuli when alarmed. The starlings began using the turn-inward defensive strategy, in which they try to move into the densely populated sections of the flock. This corresponds with video footage of manoeuvres of starling flocks in which the flock seems to compress when under attack. To ensure that the flock has a realistic emergent shape, the simulation is allowed to run for 30 seconds at

¹ Made by Hanno Hildenbrandt, Behavioural Ecology & Self-organization Group, University of Groningen (h.hildenbrandt@rug.nl)

Predator maximum speed (m/s)	Predator cruise speed (m/s)	Predator roll rate (deg/s)
20	7.5	500
30	11.25	750
40 (default)	15 (default)	1000 (default)
50	18.75	1250
60	22.5	1500

Table 2-1: Tested predator parameters

Hunting strategy	Flock size(s)
Dive attack	1 and 5000
Posterior attack	1 and 5000
Repeated attacks	5000

Table 2-2: Tested hunting strategies and flock sizes

each iteration before the predator attack is initiated.

2.4. Predator

The predator's cruise speed is the approximate speed at which the predator flies during horizontal movement, driven by its simulated muscles and its maximum speed is the maximum downward free-fall speed that drag allows. The default cruise speed of the predator was set to 15 m/s (54 km/h) and the default maximum speed was set at 40 m/s (144 km/h), based on empirical data of peregrine falcons (Videler 2006, Alerstam 1987, Dekker 1980).

About the maximum roll rate of a peregrine falcon is currently little to no empirical data available. Unlike the cruise speed and the maximum speed, it does not have an explicit value within the model but is controlled indirectly through attraction vectors. These attraction values were evolved to give an approximate maximum rolling rate of 1000 degrees per second at the default setting.

To see what the effect is of different values for predator characteristics, values lower and higher than the default parameter values were tested. For each parameter five different settings have been investigated as shown in Table 2-1.

While testing different settings of one parameter, the other predator parameters were always set to their default value.

2.5. Hunting strategies

For the peregrine falcon, the most effective hunting strategies found in literature will be used. These are the dive attack, flock pursuit,

attack on solitary prey and repeated attacks (Zoratto et al. 2010, Cresswell 1996).

The dive attack consists of the predator moving to a position 50 meters above and slightly behind the starling flock, followed by a dive attack aimed at prey at the highest point in the flock. Attacking a prey further inside the flock involves a high risk of colliding with a non-targeted prey, which is likely the reason that avian predators rarely have been observed to do this (Rudebeck 1950, Rudebeck 1951).

During flock pursuit, the predator attacks the flock from a starting position behind the flock at the same altitude. This attack strategy will be referred to as a posterior attack.

Finally, during repeated attacks, the predator performs multiple attacks in rapid succession which results in breaking the flock up into several smaller and therefore more vulnerable flocks. In reality, the number of attacks can differ, and up to 11 subsequent attacks have been observed (Cresswell 1996). To limit the amount of collected data in this project, it is chosen to execute four attacks during an attack sequence. The first attack is a dive attack from an elevated position (similar to the single dive attack), followed by three attacks in rapid succession. Each of the follow-up attacks is aimed at the smallest flock visible to the predator.

For attacks on a flock the size of the flock size was set at 5000 birds. Table 2-2 summarizes the hunting strategies tested and the flock sizes each strategy will be tested with. During the experiments with attacks on a singleton, the predator performs its attack on a single isolated prey instead of on a flock.

For the free-fall dive attack the cruise speed of the predator has no limiting effect on the predator's actual speed. The same is true for the maximum speed during posterior attacks, as the maximum speed is never even approached during horizontal flight. Therefore different settings for the cruise speed during dive attacks and different settings for the maximum speed during posterior attacks were not tested.

3. Results

Table 3-1 shows the results of the Kendall rank correlation test applied on the combinations of

the hunting strategies with different predator parameters. A negative correlation coefficient means increasing a given parameter decreases the minimal predator-prey distance, and therefore improves the performance of the predator in terms of getting closer to prey. The opposite is true for a positive correlation coefficient. In the following pages, graphs of the results can be found including a short analysis. In the graphs, both the means (displayed as symbols) and the standard deviations (bars) are shown.

Type of attack	Trait of predator (parameter)	Flock size	Kendall rank correlation test between traits of the predator and the minimal predator-prey distance		
			correlation coefficient τ	p-value	significant (p < 0.05)
Dive attack	Maximum speed	1	0.42757	< 0.001	yes
		5000	0.08575	0.153	no
	Roll rate	1	-0.25367	< 0.001	yes
		5000	0.00438	0.9418	no
Posterior attack	Cruise speed	1	0.44452	< 0.001	yes
		5000	-0.13202	0.027	yes
	Roll rate	1	-0.32227	< 0.001	yes
		5000	0.07997	0.183	no
Repeated attacks	Maximum speed	5000	0.06700	0.264	no
	Cruise speed	5000	-0.08994	0.134	no
	Roll rate	5000	-0.20620	< 0.001	yes

Table 3-1: Results of the Kendall rank correlation test on the experimental results: the correlation between a given trait of the predator and the minimal predator-prey distance

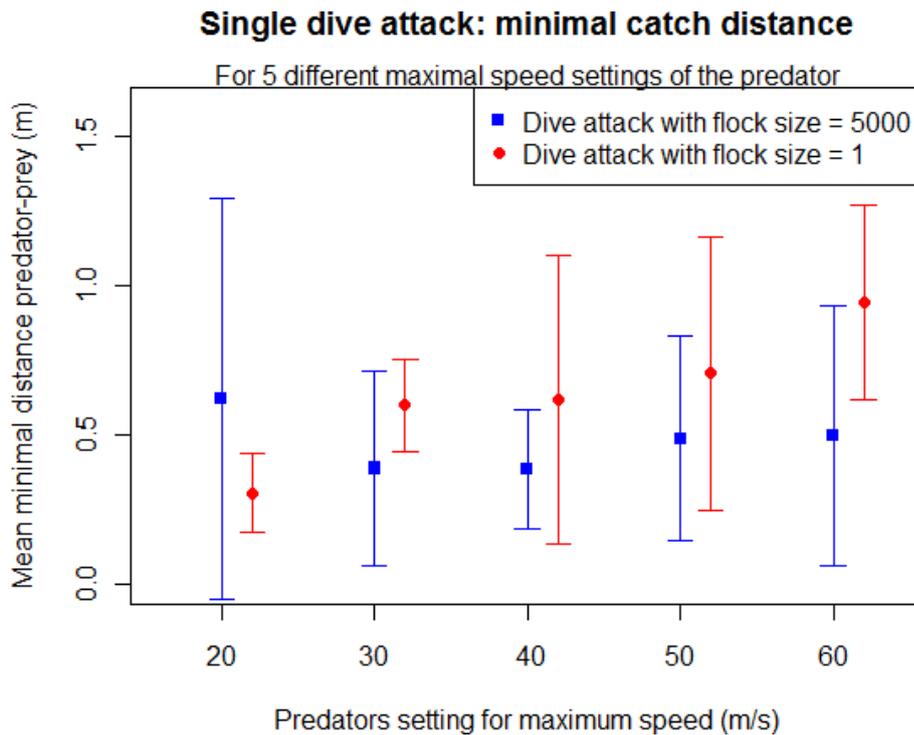


Figure 3-1: Effect of maximum speed on dive attacks

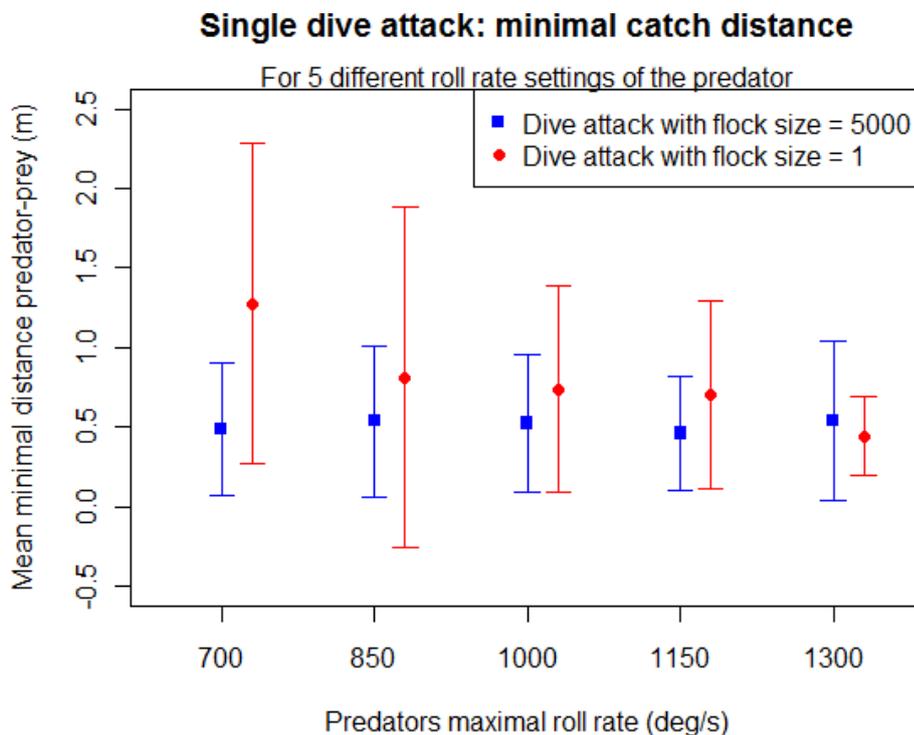


Figure 3-2: Effect of maximum roll rate on dive attacks

3.1. Dive attacks

With dive attacks against solitary prey increasing the predator's maximum speed has a positive effect, perhaps counter intuitively. Against flocks no significant effect is shown.

Against solitary prey, changing the maximum roll rate has no effect. Against a flock, increasing the maximum roll rate leads to decreased minimal predator-prey distances.

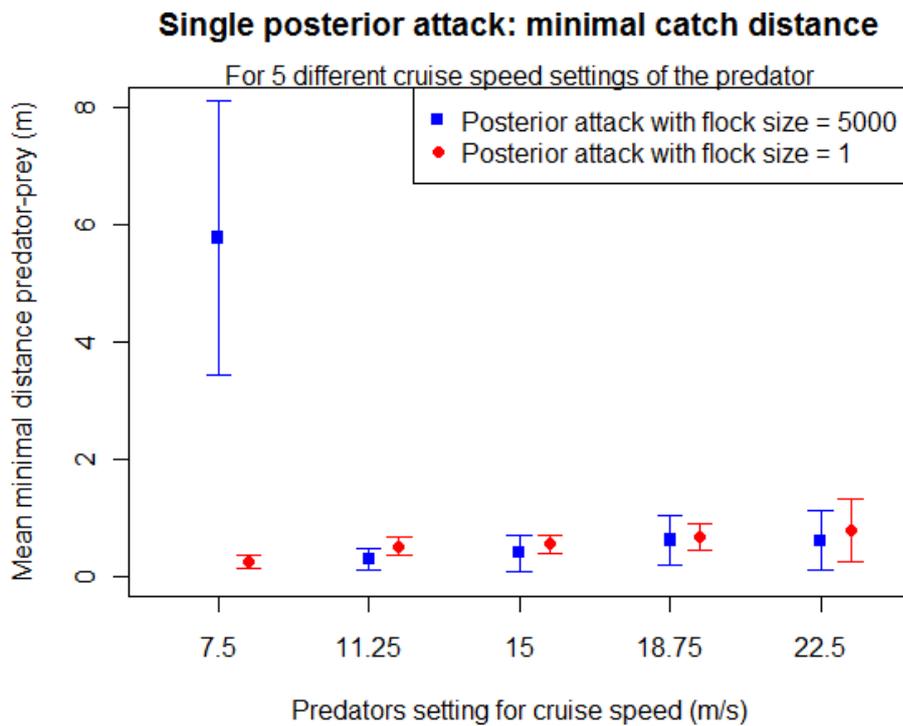


Figure 3-3: Effect of cruise speed on posterior attacks

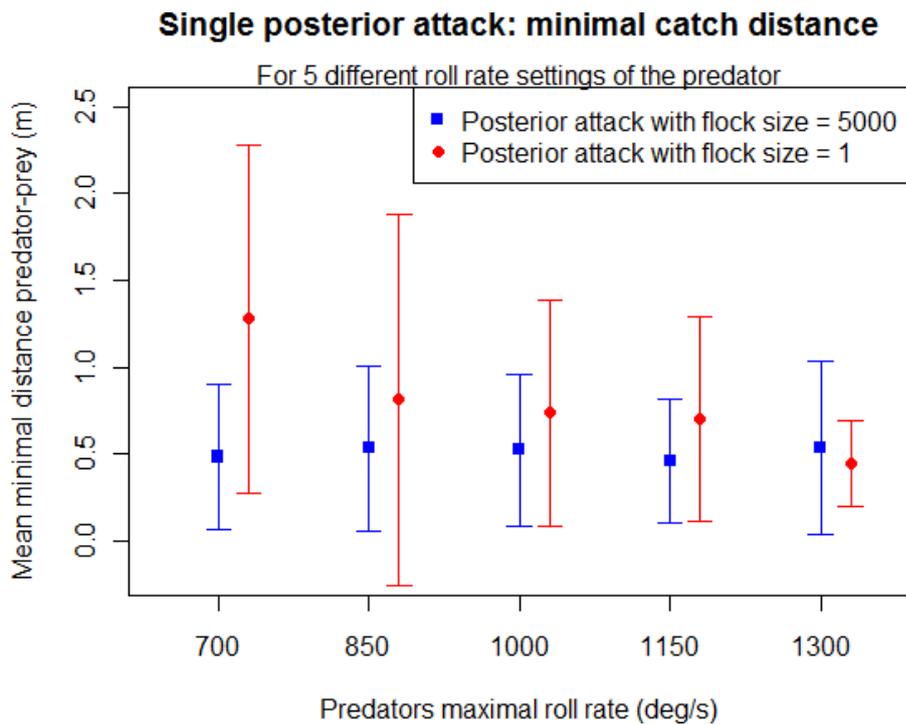


Figure 3-4: Effect of maximum roll rate on posterior attacks

3.2. Posterior attacks

With posterior attacks, against both solitary prey and flocks, increasing the predator's cruise speed leads to higher predator-prey distances. The only outlier is at a cruise speed of 7.5 m/s against a solitary prey, where increasing the cruise speed

one step up does decrease this distance quite dramatically. This is probably caused by the fact that at this cruise speed, the prey is actually faster than the predator.

Increasing the roll rate decreases the distance against solitary prey. Against a flock, there is no effect.

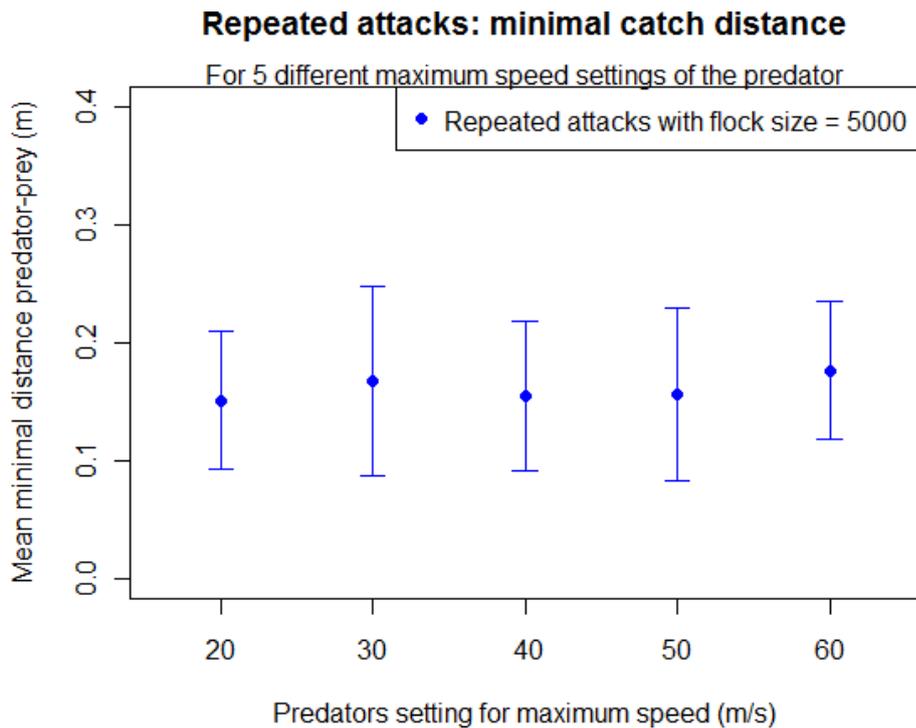


Figure 3-5: Effect of maximum speed on repeated attacks

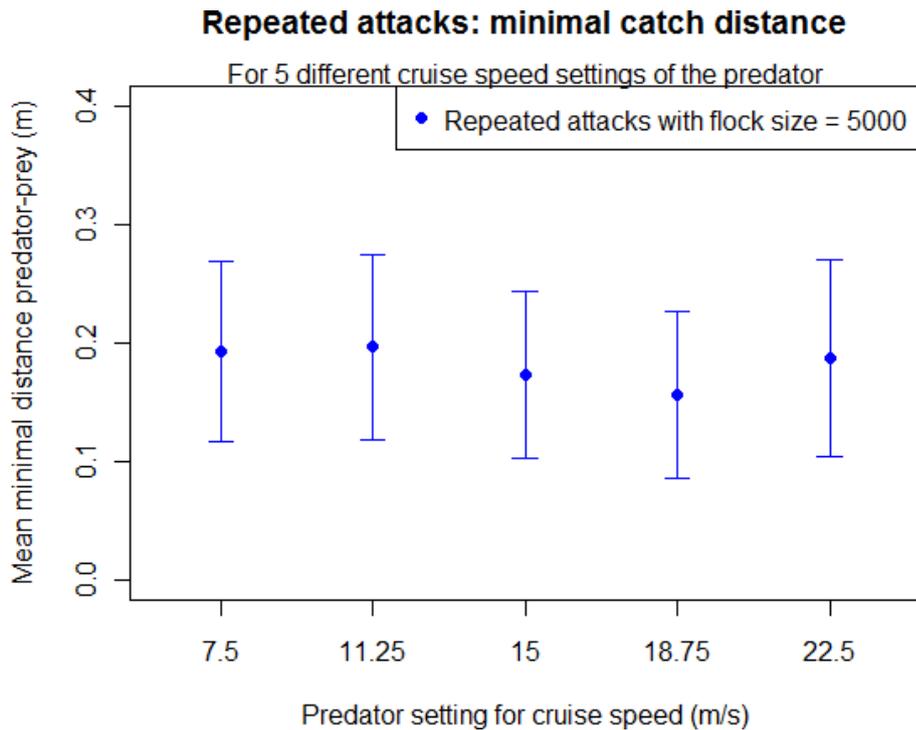


Figure 3-6: Effect of cruise speed on repeated attacks

3.3. Repeated attacks

Increasing the predator's maximum speed shows no significant improvement or deterioration in performance.

Changing the cruise speed also does not show a difference in the predator's performance regarding the minimal predator-prey distance.

Figure 3-7 (page 7) shows that increasing the maximum roll rate shows a minor but consistent decrease in the minimal predator-prey distance against the flock when attacking repeatedly.

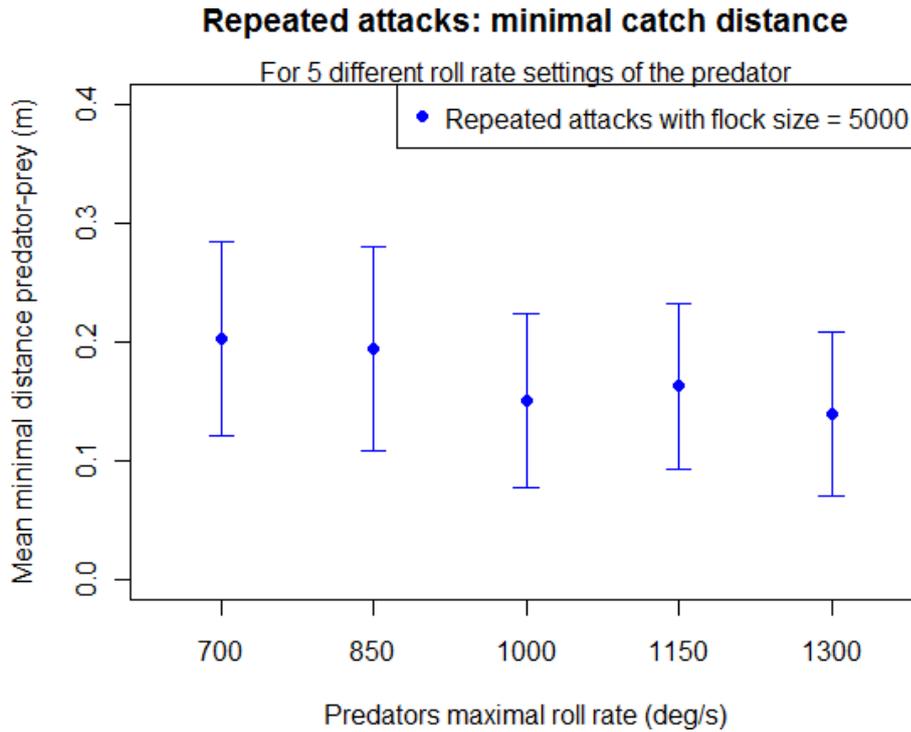


Figure 3-7: Effect of maximum roll rate on repeated attacks

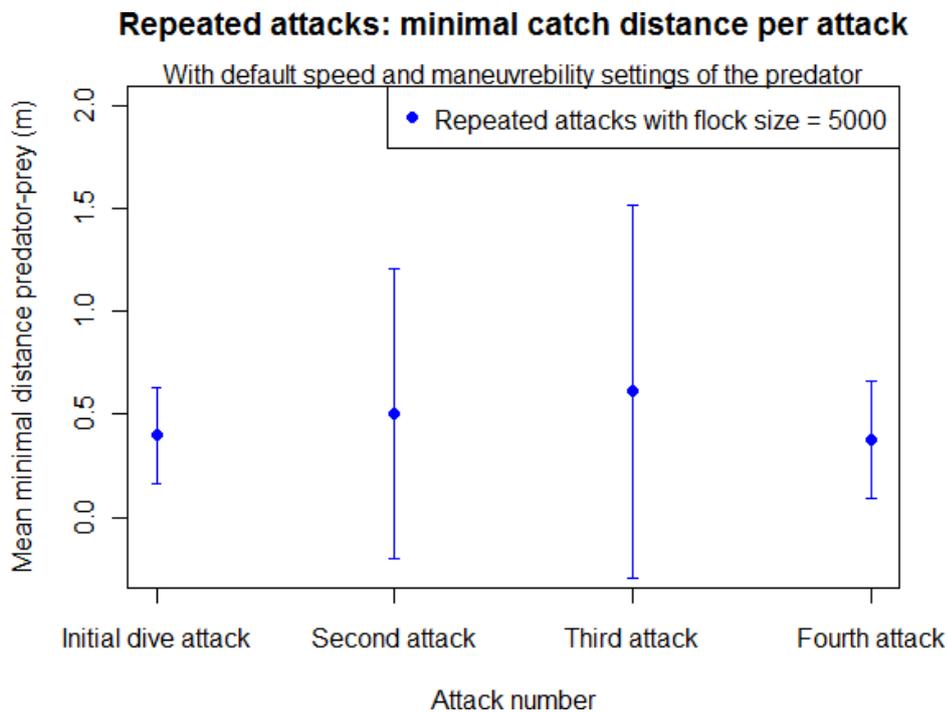


Figure 3-8: Performance of the four individual attacks during the repeated attacks sequence

In Figure 3-8, the individual mean minimal predator-prey distance of the four discrete attacks that combined form the repeated attacks sequence is shown. Casual visual inspection may suggest that both the initial dive attack and the

final fourth attack perform somewhat better than the second and third attack. However, a Kruskal-Wallis rank sum test shows no statistically significant difference between the four attacks ($H(3) = 1.53, p = 0.67$).

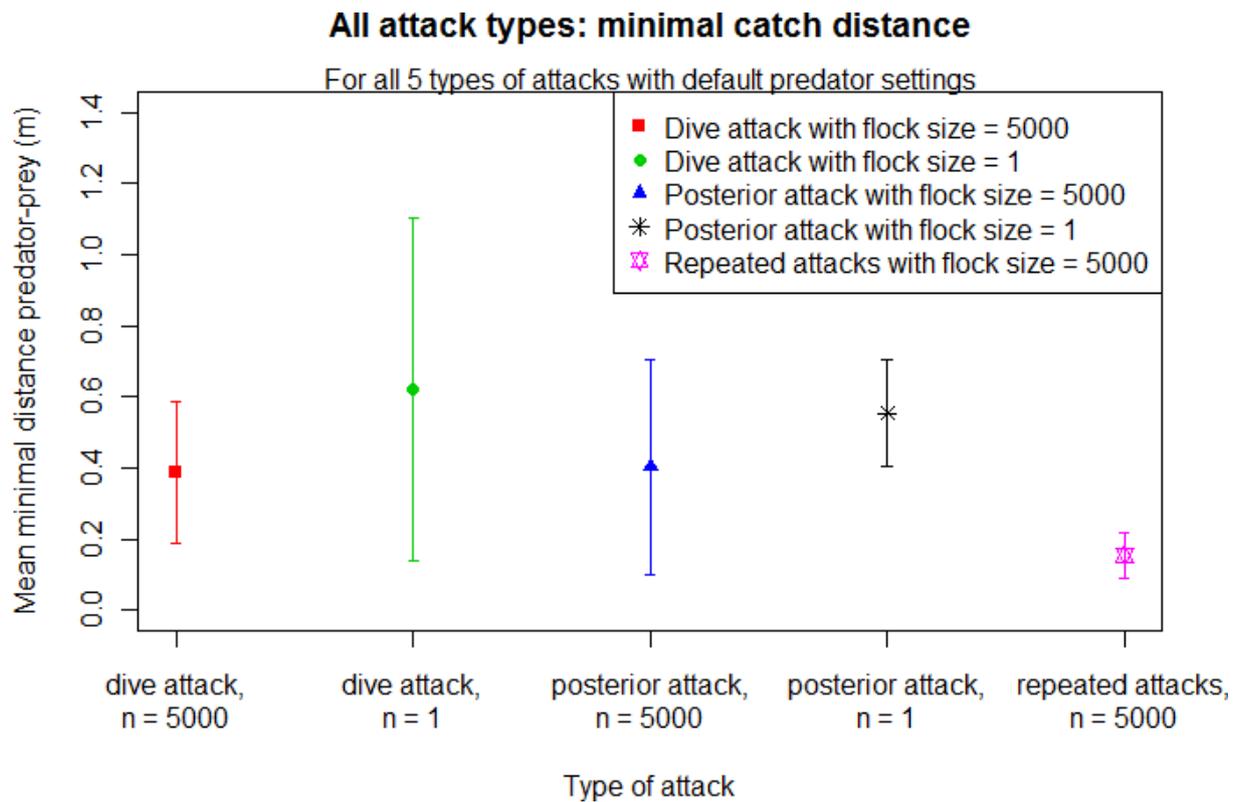


Figure 3-9: The hunting strategies compared to each other, at default predator parameter settings

3.4. Hunting strategies compared to each other

When comparing the five previously tested hunting strategies to each other as shown in Figure 3-9, it becomes clear that certain strategies are more effective than others in the model. This is confirmed by a Kruskal-Wallis rank sum test ($H(4) = 67.22, p < 0.001$). Post-hoc pairwise Wilcoxon-Mann-Whitney rank sum tests on the samples of the five hunting attacks show that the repeated attacks strategy is statistically significantly better by having a lower mean minimal predator-prey distance. Other than this, there are no statistically significant differences between pairs ($p > 0.05$). This is probably caused by the relatively large standard deviations of the minimal predator-prey distances of the attacks.

Figure 3-10 (page 12) shows the total travelled distance by the predator, per attack. For repeated attacks, the total distance travel is divided by four since there are four attacks, so the value above shows the average distance per attack for repeated attacks. According to a Kruskal-Wallis rank sum test, there are significant differences in the total travelled

distances between the hunting strategies ($H(4) = 126.34, p < 0.001$). It seems there are roughly three groups in terms of total distance travelled: the dive attacks, the posterior attacks, and repeated attacks. This observation is confirmed by post-hoc pairwise Wilcoxon-Mann-Whitney rank sum tests between the samples of the five hunting attacks.

In Figure 3-11 (page 12) the mean climbed distance travelled per attack by the predator is shown. In the case of the dive attack and repeated attacks, the predator will first have to climb up 50 meters before it can start its dive attack. Because of this, there were significant differences in climb distance between the five hunting strategies according to a Kruskal-Wallis rank sum test ($H(4) = 128.75, p < 0.001$). Post-hoc pairwise Wilcoxon-Mann-Whitney rank sum tests between the samples of the five hunting attacks show that again there are three different groups again: the dive attacks, the posterior attacks, and the repeated attacks. The difference with the total distances is that this time repeated attacks has a lower average distance than dive attacks and the relative differences in distances between the hunting strategies are far greater.

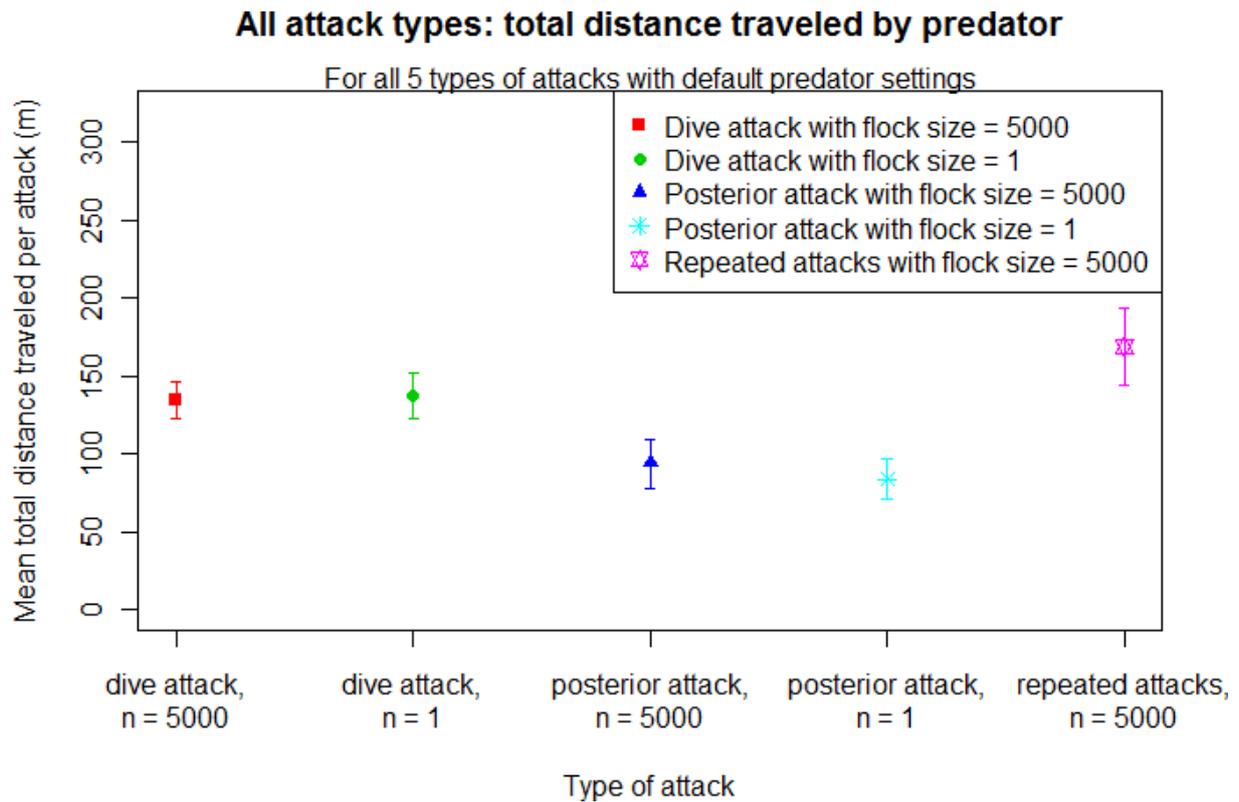


Figure 3-10: Total distance travelled by predator, per hunting strategy

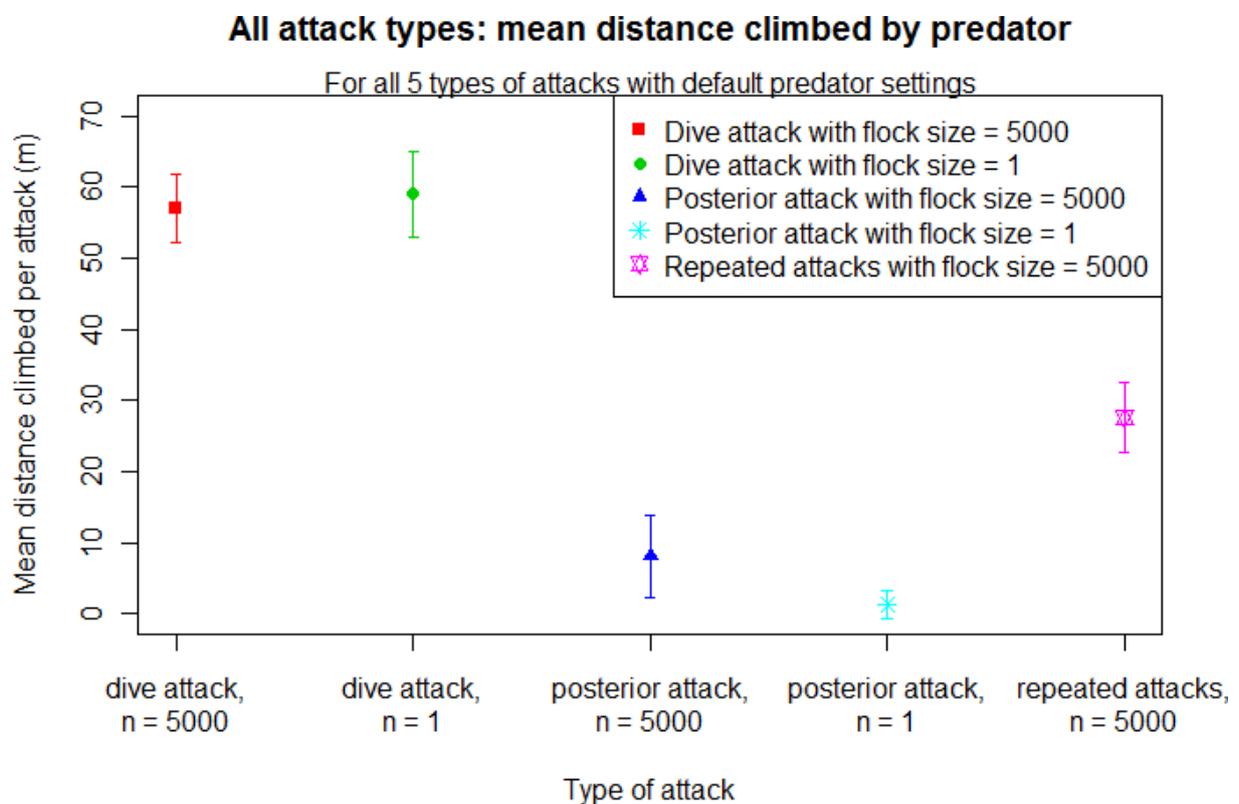


Figure 3-11: Distance climbed by predator, per hunting strategy

4. Discussion

The experiments as conducted in StarDisplay have yielded some interesting results. When compared to empirical data (Zoratto et al. 2010, Rudebeck 1951), it becomes obvious that the model results show significant differences. Most notably, predator attacks within the model in general are much less effective than as recorded in empirical data. In literature, values between around 10% and 25% success rates in terms of catching prey per executed attack are reported (Dekker 1988, Zoratto et al. 2010, Rudebeck 1951, Dekker 1980, Cresswell 1996). With the catch threshold distance set to 20 cm in the model the average success rate in the model was 0-4%, depending on the hunting strategy. A likely cause of the poor results in the model was the way predator targeting behaviour is implemented in the model: the predator was just not very good at planning its intercepting course to its targeted prey. Additionally, as mentioned in the Methods section, the final phase of the attack was currently not explicitly modelled within StarDisplay.

During the time the experiments were carried out, other implementations of predator targeting were in development that aimed to improve the predator's performance in closing in with its prey. However, testing those implementations fell outside the time frame and scope of this bachelor project.

4.1. Influence of predator's parameters

Besides noting the generally poor results in terms of minimal predator-prey distance, there are other important differences with empirical data. In terms of what effect changing the predator's parameters had, part of the results seem counterintuitive. In theory, as discussed in the introduction, a higher speed could allow the predator to avoid detection by the prey and delay their defensive tactics, potentially leading to improved odds of catching prey. However, in the model increasing speed did not in any way improve the performance of the predator and in many cases actually had a large detrimental effect. Again this can partly be explained by the predator's targeting and manoeuvring in the last stage during the attack. In the model the predator aimed at a point behind the prey, and

this point moves closer to the prey as the predator closes its distance to the prey. Increasing the maximum speed during dive attacks caused the predator to overshoot, because the predator could not make quick turns towards a moving prey anymore due to the inertia caused by the high speed. This observation has also been made in empirical data, where a falcon that dived straight down (perpendicularly to the ground) had too high a speed to make the necessary movements and overshoot its targeted prey (Rudebeck 1951).

In the case of posterior attacks, increasing the cruise speed also had a negative effect. The cause of this is less clear than in the case of dive attacks. Possibly, a smaller difference in the speed of the predator and prey allowed the predator to make a more gradual and reliable approach to the prey. It should be noted that at lower cruise speeds, it does take the predator longer to catch any prey, so while improving performance it takes more time to complete an attack. An exception to the rule that less speed is better was when the predator's cruise speed was set to 7.5 m/s against a flock of prey, because this was a lower speed than the prey's cruise speed (10 m/s during all experiments). This means that at this speed the predator could not catch its prey when the prey was flying straight away from the predator. However, the prey did make turns from time to time to stay in the proximity of the centre of the 3D model (the "roosting area"), so during those times the predator had the opportunity to catch up and close the distance to some degree. The fact that even at 7.5 m/s the predator still had good results against a solitary prey was because the solitary prey failed to notice that a predator is pursuing it. After all, a solitary prey does not receive any warnings from nearby neighbours to start evasive behaviour, like it would when flying in a flock.

In contrast to the speed parameter, increasing the predator's maximum roll rate never decreased the predator's performance and in many cases improved it. This agrees with the intuitive idea that by improving the predator's manoeuvrability, the predator becomes better at pursuing and closing the distance with its prey. In the case of dive attacks and posterior attacks, increasing the roll rate significantly improved performance against solitary prey, but did little

to help against flocks of prey. This was likely because against a flock the predator can simply target another prey if it loses its lock-on on its current target. On the other hand, against a solitary prey the predator is forced to stick to pursuing the only target that is available to it. With the repeated attacks strategy, increasing the maximum roll rate had a small but statistically significant positive effect.

4.2. Success of the different hunting strategies

Figure 3-9 shows the results of all tested hunting strategies compared to each other. Only repeated attacks really stood out from the rest in a positive way, matching empirical data where the repeated attack strategies had an average success rate of 29.9% versus a total average success rate over all attacks of 23.1% (Zoratto et al. 2010).

Of course, with repeated attacks the predator makes four attack runs, so it has four opportunities of closing in with its prey. However, at least in theory, attacking repeatedly should allow the predator to break up the flock into several smaller flocks and profit from the prey's confusion by gaining better odds to catch prey (Rudebeck 1950). Although Figure 3-8 seems to suggest that the final fourth attack is somewhat more successful than the two attack previous to it, the difference was not statistically significant ($p > 0.05$).

Other than noting the relative success of the repeated attacks strategy, the other four strategies did not have statistically significant differences in terms of minimal predator-prey distance. This was likely caused by the relative high variations between the iterations of the hunting strategies, resulting in a large standard error. For what it is worth, Figure 3-9 does suggest that against a flock the predator did seem to perform a little bit better in both the dive attack and posterior attack when compared to attacks on a singleton. This was probably caused by the fact that the predator has more opportunities to get close to a prey when attacking a flock, as previously discussed. The mean values of the dive attack and posterior attack at equal flock sizes were nearly identical, so apparently either strategy was equally successful in the current model.

4.3. Travelled distances of the different hunting strategies

Finally, in Figure 3-10 and Figure 3-11 the total travelled distance and the climbed distance per type of hunting strategy are shown. This is a measurement for how much energy the predator has to spent per type of attack. This time there are significant differences between the various strategies.

The dive attacks required the largest climbed distance travelled, because to carry out such a type of attack the predator was forced to climb up first. This was also the case for repeated attacks, but because for this hunting strategy the climbing distance was divided over the four separate attacks that compose the entire repeated attacks sequence the net effect of the initial climb on the climbing distance was less severe.

Even when the combined distance was divided over the four attacks, the repeated attacks strategy required the largest amount of total distance travelled per attack. It was followed by the dive attack. The posterior attack required the least amount of total distance travelled per attack sequence. Again, this was probably because the posterior attack requires no initial climb. Apparently, during posterior attacks the predator did not spend a lot of time chasing the prey over a long distance, as one might expect from this stalking-type of strategy. This might be because the predator sneaked up from behind the prey in its blind angle, and the prey does not notice the predator. Effectively, this means that the posterior attack is a sort of surprise attack. These kinds of attacks have in literature been noticed to be relatively effective in terms of the time and distance spent per attack (Dekker 1988, Cresswell 1996), which was fortunately reproduced by the test results of this project. Why the repeated attacks sequence had the highest total distance travelled is not immediately clear. Possibly, the predator had to spend a lot of time chasing prey in the second, third and fourth attack. During these attacks, the prey is already alarmed because of the initial first dive attack and has more time to engage in evasive behaviour, thereby prolonging the pursuit during the follow-up attacks.

In any case, the posterior attack required both the least total travelled distance and climbed distance. Since the dive attack and

posterior attack were equally successful in terms of minimal predator-prey distance, the posterior attack was the superior strategy of the two according to the test results. The repeated attacks strategy did produce the best results in terms of minimal predator-prey distance, but at the cost of requiring a lot of energy on a single complete attack sequence. When the predator is high on

energy, but short on time and wants to catch prey as quickly as possible, repeated attacks might therefore be the best option. Otherwise, posterior attacks are probably the best choice as they provide a good compromise between performance (minimal predator-prey distance) and efficiency (distance traveled).

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Appendix A

StarDisplay settings

Used version: 5.1.1.0

Parameter	Value
Drag/lift-coefficient	0.303
Falcon's blind angle	20 deg
Falcon's body mass	0.9 kg
Falcon's deflection parameter (forward, up, side)	(-0.25, 0.0, 0) m
Falcon's drag/lift-coefficient	0.303
Falcon's maximum lift	2 N
Falcon's reaction time	0.01 s
Falcon's wing span	1 m
Integration time step	5 ms
Starling's blind angle	90 deg
Starling's body mass	0.08 kg
Starling's cruise speed	10 m/s
Starling's detection range of predators	20 m
Starling's maximum lift	2 N
Starling's reaction time when alerted	N(0.05, 0.005) s
Starling's reaction time when not alerted	N(0.1, 0.01) s
Starling's wing span	0.4 m
Topological range	6.5 birds

Please refer to the original article for additional information (Hildenbrandt, Carere & Hemelrijk 2010).