

BIRD DROPPINGS;

HOODED CROWS FORAGING ON PERSIAN WALNUTS

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MASTER THESIS 60 CREDITS 2013





# **BIRD DROPPINGS: HOODED CROWS FORAGING ON PERSIAN WALNUTS**

## **Preface**

This project grew out of an observation made by John Marzluff from the University of Washington when visiting Norway some years back, but would not have been realized had my supervisor Geir A. Sonerud not remembered it and helped develop it further. I am also grateful for all the help I have recieved with the statistics, particularly from Ronny Steen and Johannes Breidenbach. Lastly, I want to thank Jared for patiently hanging in there with me, never giving up hope that I would emerge from this as a sane person.

Thank you all.

## Abstract

I conducted a study on hooded crows (*Corvus corone cornix*) foraging on walnuts (*Juglans regia*), often in the presence of magpies (*Pica pica*). The fieldwork was conducted around three mature walnut trees in a residential neighborhood in Oslo, Norway. The crows would drop walnuts to break them, and were found to use a drop height and -surface that would optimize energy output. Drop height decreased with subsequent trials and increased with wind speed. In contrast to what other studies have found, the crows did not seem to adjust drop height to the number of conspecifics nearby. Instead, I found a positive effect of the number of magpies nearby. The rate of kleptoparasitism was comparable to similar studies, and the crows may try to avoid being parasitized by means such as flying away from the drop site more often at increased risk of kleptoparasitism. Both crows and magpies were observed kleptoparasitizing, although crows accounted for more such events than magpies. Magpies and crows were both more likely to approach a nut owner after a successful drop where the nut cracked, and nuts were more likely to be stolen after having cracked. On the other hand, crows were more likely to fly away after a drop when approached by other corvids and with increasing wind, but also after successful drops. The crows in my study thereby seem to exhibit strategies to avoid kleptoparasitism that differs from those found in other studies of nut dropping. This discrepancy could stem from differences in group size and composition, and facilitates for an interesting further study.

## Sammendrag

Kråker (*Corvus corone cornix*) ble observert mens de samlet, bearbeidet og spiste valnøtter (*Juglans regia*) i et nabolag i Oslo, Norge, ofte med skjærer (*Pica pica*) i nærheten. Kråkene var nødt til å fly opp og droppe valnøttene fra en viss høyde for å knuse skallet rundt nøtten. De så ut til å velge både dropphøyde og -underlag med tanke på optimalt utbytte.

Dropphøyden sank med nye droppforsøk, og ble positivt påvirket av vindstyrken. I motsetning til tidligere studier ble ikke dropphøyden påvirket av antallet andre kråker i nærheten, derimot fant jeg en positiv effekt av nærhet til skjærer. Raten av kleptoparasitisme var sammenliknbar med lignende tidligere studier, og kråkende forsøker muligens å unngå parasitisme ved å fly avgårde ved økt risiko for kleptoparasitisme. Jeg observerte både kråker og skjærer som klarte å stjele nøtter, men kråker stjal sammenlagt flest nøtter.

Både andre kråker og skjærer nærmet seg kråker med nøtter oftere etter at nøtten var knust, og nøtter ble oftere stjålet etter at de var knust. Det var en høyere sannsynlighet for at kråker med nøtt ville fly avgårde dersom en annen kråkefulg nærmet seg, men sannsynligheten økte også med vindstyrke og dersom nøtten knuste eller var nær ved å knuse. Kråkene i denne studien utviste dermed andre strategier for å unngå kleptoparasitisme sammenlignet med andre studier på kråker som dropper nøtter. Muligens stammer disse forskjellene fra ulike gruppestørrelser og –sammensetninger, og utgjør i alle fall et spennende utgangspunkt for videre studier.

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## 1. Introduction

Urban habitats are a relatively new phenomenon and represent an environment that few species have adapted to living in. Most bird species found in urban areas today are characterized by a broadness of environmental tolerance, a diversified diet (generalist) and the ability to nest in urban areas (Hu and Cardoso 2009). These characteristics fit well with the highly omnivorous and opportunistic hooded crow (*Corvus corone cornix*). The hooded crow population has increased rapidly in Scandinavia and other parts of the world since the 1960s, and Vuorisalo et al (2003) speculates that the recent tolerance of crows in urban areas is what lead to this rapid and large population growth. In the United States the American Crow (*C. brachyrhynchos*) is still considered a nuisance in agricultural districts, but tolerated in cities and suburbs where they are also more abundant (Marzluff and Angell 2005a). The increase in suburban areas, which seems better suited as nesting habitat for crows while also providing ample food sources, could also be a determining factor in the rapid crow population growth in urban areas (Marzluff and Angell 2005b).

Social learning and behavioral flexibility are traits that may be selected for in animals living in constantly variable environments (Emery 2006). According to the optimal foraging theory (OFT), animals should be selected to forage in a way that will maximize their net energetic output (Pyke 1984). One of the main assumptions in the OFT is therefore that the foraging behavior or the capacity to learn it has a heritable component (Pyke 1984).

Corvids have the largest brain to body ratios of any group of birds, and are nicknamed “the feathered apes” because of their cognitive capacities (Clayton and Emery 2005). This seems to enable crows to solve novel problems and get access to food in the most creative ways. Crows’ ability to use their inventiveness rather than preprogrammed behavior is often mentioned as one of the main reasons for their ability to thrive in urban environments. Another similarity between corvids and apes is that their young have a long developmental period, which allows for an extended period of learning (Clayton, Dally et al. 2007). This also allows for more complex social structures (Chiarati et al 2010) and social behavior (Ha et al 2003).



A recent change in land use in Poland had a surprising consequence in that rooks (*C. frugilegus*), jackdaws (*C. monedula*) and hooded crows facilitated a dispersal of persian walnut trees (*Juglans regia*) from residential areas to abandoned fields, leading the trees to being classified as an invasive species (Lenda et al. 2012). This example illustrates how readily the corvids exploit available resources and new opportunities.

In Sendai, Japan, local carrion crows (*C. corone corone*) use a unique method for cracking walnuts; they place them on roads and wait for cars to drive over them (Nihei 1995). This phenomenon seems to be spreading culturally, i.e. horizontally by learning, among the Japanese crows, and is reinforced by local residents who strive to hit the nuts on the road (J. Marzluff, pers. com.). Similar behavior has been observed in Israel, but there are no published studies on the phenomenon from this area yet (H. Mienis, pers. com.). In Seattle, USA, American crows that had been trapped or watched a trapping by an experimenter wearing a mask would later react by scolding people wearing this mask (Marzluff et al 2010). Five years after the initial experiments, the crows in the area reacted even stronger to the mask, and the response was even seen in young birds that had not been born at the time of the first experiment (Cornell et al 2012).

Before the 1980s the hooded crows at Netzer Sereni in Israel were only observed opening pecan nuts (*Carya illinoensis*) using one method, namely transporting the nuts to a hard surface where they would peck at it until the shell cracked. However, in 1984 it was noticed that some of the crows were dropping the nuts onto hard surfaces. At that time, 10% of the crows used this method, and the numbers increased to almost 80% in 1986. The strategy used to open nuts now seems to depend on the energy saved by dropping (dependent on the thickness of the shell) and the risk of kleptoparasitism. (Mienis 1993) This illustrates how rapid a behavior can be culturally transmitted among the gregarious crows, and also their behavioral plasticity.

In order to optimize their output from a nut, crows also need to be aware of potential kleptoparasites while they are dropping and handling the nut. Kleptoparasitism is relatively common in corvids compared to other passerines (Baglione and Canestrari 2009). Crows have been found to be dominant to magpies (Rolando and Giachello 1992), and should therefore be kleptoparasitized less by magpies than the other way around. Studying four sympatric corvids in a refuse dump in Italy, Baglione and Canestrari (2009) found that the european magpies

(*Pica pica*), jackdaws and rooks at the site seemed to kleptoparasitize opportunistically whereas the carrion crows seemed to use it as a strategy and kleptoparasitized significantly more.

It may seem intuitive that larger birds should be more successful as kleptoparasites, but (Morand-Ferron et al. 2007) did a comparative analysis finding that kleptoparasitism was more likely to evolve in taxa with large relative brain size, a preference for open habitat and a diet which included vertebrate prey, and that this probability was not related to body mass. This stresses the importance of intelligence, and makes for an interesting comparison when crows and magpies compete for walnuts.

To my knowledge, there have not been any published studies on hooded crows foraging on walnuts, but several relevant studies have been conducted in Davis, California (USA), on American crows (Cristol, Switzer et al. 1997; Cristol and Switzer 1999; Cristol 2005). Large walnut trees are abundant in and around Davis, CA, whereas they are rare in Norway (pers. obs.). I was interested to see if the hooded crows in Norway behaved in a similar manner as crows in other parts of the world when foraging for walnuts. I wanted to find out if the Norwegian crows were able to maximize the energetic output when foraging for walnuts. One way they could do this is by minimizing the time spent in the air, as flying is energetically costly. Ascending flight should be much more costly than horizontal or descending flight, and so the crows should especially minimize the amount of ascending flight. To do this, the crow cannot simply drop the nut from a lower height, because the nut is then less likely to break. The crows should strive to minimize the number of drops times the height of the drops if they are to minimize energy expenditure and maximize energy gained.

In a classic study, Zach (1979) found that northwestern crows (*C. caurinus*) did maximize their energy output when foraging for whelks (*Thais lamellosa*) in that they chose the largest whelks that broke more easily and minimized the amount of ascending flight. In order to maximize their output, the crows must also make sure that other animals will not steal their walnuts. Magpies seem unable to break walnuts themselves, but will readily steal one that has already been broken (G. A. Sonerud, pers. com.). Other crows may also steal the walnut, and kleptoparasitism has been found to be the main reason for prey loss in similar systems (Cristol and Switzer 1999). The crows can minimize the risk of prey loss by either flying to a less crowded site to drop or cache a walnut, or by lowering the drop height. Descending flight

takes a longer time than a falling walnut, and so the higher the drop height, the more time it leaves for potential thieves to steal the walnut. Cristol and Switzer (1999) found that crows responded to increased risk of kleptoparasitism by lowering the drop height.

Hooded crows roost communally outside the breeding season and will often follow other crows that were successful in finding food the previous day (Sonerud, Smedshaug et al. 2001). They seem very able to remember the location of food sources and will often return several days in a row to particularly rich food sources (Sonerud, Smedshaug et al. 2001). Within a few days the hooded crows in the area of my study should all have been aware that the walnuts were ripe and know where the trees were located. I therefore built on the assumption that search time and encounter rate were neglectably low in this system. Further, ripe walnuts are rather conspicuous and the crows would soon know where to find them, so I also felt confident eliminating recognition time from my model. This left a simple system where nuts are readily available, but crows would have to exert energy to get the content, and were expected to do so in a fashion that optimized the net intake.

I was interested in whether the hooded crows in Norway would exhibit similar walnut dropping behavior as the crows observed in California, where the dropping behavior seemed highly dependent on both social factors and properties of the nut (Cristol and Switzer 1999). I wanted to see if the crows were able to adjust the drop height to break the nuts in the most energy efficient way, and hypothesized that they would choose the drop heights that minimized energy expenditure while maximizing the energy output in form of the nut breaking. In order to explore this question, I conducted my own drop experiments to see how easily nuts would crack when dropped from various heights, and compared this to the nut dropping behavior of the crows. Another way of minimizing energy expenditure is by choosing a hard drop substrate, and I hypothesized that crows would do so more often than expected by chance. In addition, I wanted to explore if or how the dropping behavior was influenced by season, weather and social factors. I was curious to see how the crows reacted to the risk of kleptoparasitism, and hypothesized that there would be a negative relationship between drop height and the number of conspecifics in the area.

To my knowledge, there has not been any studies showing magpies stealing food directly from crows, but this had been observed happening at my study site earlier. I was therefore

interested to see whether the crows reacted differently or not to magpies with respect to drop height, and how often magpies would successfully kleptoparasitize the crows. Crows are thought to be dominant to magpies (Rolando and Giachello 1992), and observed kleptoparasitism between the two species are usually unidirectional in favor of the crows. However, one could speculate that magpies and crows have an equal opportunity to steal nuts that are dropped, if they do so while the nut-dropper is still in the air. I therefore hypothesized that there would be a positive correlation between drop height and the number of magpies in the area. Further, I wanted to explore what variables would influence the success of an attempted kleptoparasitism event.

To summarize, I hypothesized *a*) crows should choose drop heights that will minimize the energy expenditure needed to break a nut, *b*) crows should lower their drop height with subsequent trials, and *c*) crows should also lower drop height as a response to conspecifics, and possibly also magpies, nearby to reduce the risk of kleptoparasitism. In addition, I wanted to explore the role of climatic factors and how they might affect the drop behaviors of crows, as well as how the crows responded to a threat of kleptoparasitism from either conspecifics or magpies.

## **2. Methods**

### **2.1 Study area**

Observations were conducted in a residential neighborhood in Bygdøy, Oslo, Norway (59°53'N 10°41'E) between September 1st and October 9th 2012. In this neighborhood, there were at least three full-grown walnut trees from which the crows collected nuts. All sampled walnuts were taken from one of these (left top tree shown in figure 2.1). The majority of the houses in this neighborhood are one-story houses with flat roofs, each surrounded by a garden.

To determine the proportions of ground substrate available as a dropping surface, I created a 14 cm x 16 cm grid over a satellite photo of the study area. I then calculated the percentages of the various substrate types; asphalt, house surfaces and vegetation by determining the substrate type found under each crosshair in the grid. This produced a distribution of 20.5 % asphalt, 22.8 % house surfaces and 56.7 % vegetation. If the crows were found to use drop

substrates of a similar distribution, this would imply that they were not selective about their drop substrate. The number of crows in the area was estimated to be at least 35 individuals, as this was the count during several instances where all local crows seemed gathered in a large birch.

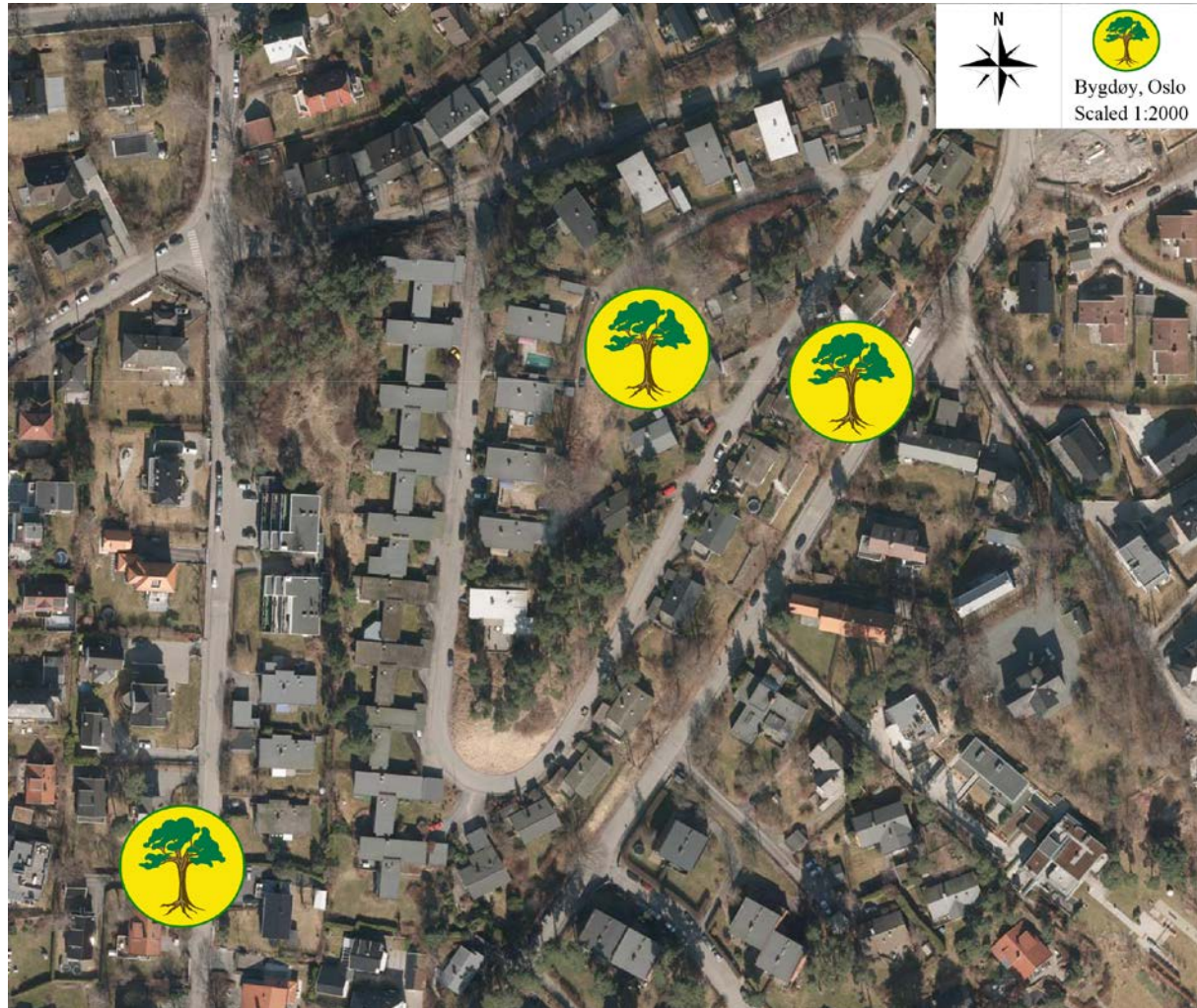


Figure 2.1: The location of the walnut trees in the study area. The two trees to the right were the oldest and largest, and the main activities of the crows were centered here. (Satellite photo from the Norwegian Public Roads Administration)

## 2.2 Observations

Initially the observations were carried out daily between 6 am and 6 pm. These observations soon showed that most walnut dropping activity seemed to occur between 9 am and early afternoon, and so the majority of the following observations were concentrated around that time period. A Vertex IV height measurer (Haglöf Inc.) was used to measure the heights of trees, buildings and lamp posts in the neighborhood, and these heights (ranging from 1.5 m to 23 m) were plotted onto sketches of the various streets and used as reference points when

estimating drop heights. Despite the fact that the crows have been known to carry nuts for great distances before cracking or caching them (Cristol 2005), nearly all observations were conducted in the streets immediately surrounding the walnut trees. This was due to the difficulty of following the crows over long distances in a quite densely populated area with a challenging topography and the lack of reference points for height outside this area. Also, initial reconnaissance trips in the surrounding areas yielded few findings of empty walnut shells and far fewer nut drop observations than in the main area.

I closely observed the foraging methods utilized by hooded crows when foraging for walnuts, as well as looking for potential kleptoparasitic interactions from magpies to crows. All data was recorded using a tape recorder, and I used a pair of 8x42 binoculars to observe events from a distance. When a crow dropped a nut within my visual range, I estimated the drop height and whether or not the nut cracked (“drop result”) and the initial state of the nut. Because I wanted to see how efficient the crows were at cracking nuts, it was important that I got to observe a whole sequence from the first to the last drop before the nut cracked. If I had observed the crow flying out of a walnut tree before dropping the nut or had visually inspected the nut properly before it was dropped, I could be reasonably sure that the nut had not been dropped before. I then noted down whether or not a drop sequence started with a nut that had not been dropped before. I also recorded the trial number in drop sequences where the same nut was dropped repeatedly, and I distinguished between the observed trial number and the cases where I knew the actual trial number. After the final drop, I would observe the crow for up to ten minutes, or until it abandoned its nut, flew away or had its nut stolen.

I also counted the number of crows and magpies nearby for every drop in the sequence, both before and after the drop, as well as estimating the distance from the “nut owner” to the nearest crow or magpie. Only individuals that were assumed to be within the visual range of the crow with the nut were included. When no magpies or crows were observed in the area, I would set the distance to the nearest crow or magpie to 101 m. This distance was longer than any recorded distance, and thought to be realistic as the area had a varied topography where the crows would rarely have a clear overview spanning more than 101 m.

After each drop I noted whether the nut owner was approached by other birds and whether it took flight. An approach was defined as getting within 0.5 m distance of the crow with the nut. Several crows flew away with their nut before it had cracked, or would fly short distances

with their nut without dropping it, and I recorded both responses as "flight". If this happened in concurrence with a car or human approaching, I noted this down to distinguish between times when the crows flew away after an approach or for no clear reason.

Kleptoparasitism is described by Brockmann and Barnard (1979) as food theft between individuals of different species, in which the food items stolen has already been procured by the producer. However, they also state that this phenomenon can be hard to separate from food theft within a species, and synonyms for kleptoparasitism rarely distinguish between inter- and intraspecific events. For the sake of simplicity, I chose to use the term kleptoparasitism for all events where a walnut was taken from the individual who first procured it, also when the nut had not yet been cracked open.

### **2.3 Drop experiments**

In order to establish whether the crows dropped nuts from an optimal height, I wanted to estimate at what drop height a nut would crack fastest and with the least energy exertion. I used methods for testing breakability comparable to those of Cristol and Switzer (1999). Firstly, I wanted to know how easily a nut would crack when dropped from certain heights. A set of nuts ( $n=20$ ) were dropped from various drop heights; 1.5 m, 3.8 m, 6.0 m, 8.0 m and 12.0 m. Each nut was dropped repeatedly from the same height until it cracked. A nut was considered to have cracked once there was a  $1\text{cm}^2$  opening in the shell or more. This test was conducted both at the beginning and towards the end of the study. All walnuts were collected from the same tree, and dropped onto asphalted ground from a staircase. Because optimal drop height may change as the nuts ripen, I also dropped five nuts from the same height (3.8 m) two times per week throughout the study and recorded how many drops they needed to break.

### **2.4 Climatic data**

I used readings on temperature from the local weather station at Bygdøy (59°90'N 10°68'E) and readings on wind speed and precipitation from the weather station at Blindern PLU (59°94'N 10°72'E), both sets of data was collected at the website [eklima.met.no](http://eklima.met.no) (06.11.2012). These weather stations were situated approximately 1 km and 5 km from my study area, respectively. All weather data had been collected on an hourly basis, and I manually interpolated these data to fit each drop event according to their date and time. Because I wanted to know if the crows would forage for whelks instead of walnuts when the tidal water

was low, I also collected data on the hourly sea level values from the Norwegian Mapping Authority, Hydrographic service (vannstand.no, 02.05.2013).

## **2.5 Statistical methods**

All data was first analyzed using JMP pro 10 (SAS Institute Inc. 2012). In addition, the statistical software R version 2.14.1 (R Development Core Team 2010) was used to create linear mixed effects models. Figures were created using both JMP pro 10 and R. Averages are reported with one standard error ( $\pm$ SE).

### **Observations of nut dropping**

Drop height was  $\log_{10}$  transformed to obtain approximately normal distributions. Using the nlme package in R, I created two global models with drop height as a response variable, with “nut ID” as a random effect and using two slightly different sets of explanatory variables. Both sets included date, trial, distance to nearest crow (DNC), distance to nearest magpie (DNM), the number of crows nearby (CIA), the number of magpies nearby (MIA), precipitation and air temperature, but differed in that one set contained the variable wind speed, and the other the variable maximum wind gust. A list describing all variables used in this study can be found in appendix 1. Wind speed and maximum wind gust were treated separately because they were found to be highly correlated (see appendix 3 for a table of correlations). Nut was used as a random effect because the same nut was generally dropped repeatedly, and by the same individual.

Both global models created 511 candidate general linear mixed models (GLMM). These models were then ranked by AIC value, and I selected the models by looking at the overall lowest AIC value, as well as the  $\Delta$  AIC value. I aimed to select the model with the lowest number of predictor variables within a range of two AIC scores from the overall lowest AIC value (Burnham & Anderson 2002). If two or more models were within this range and included equally few variables, they were considered to be equally good (see appendix 4 for a table of the top five models selected for each response variable). I then used the lme4 package in R to get the summary statistics for the top models selected.



For nut cracking (whether or not a dropped nut broke) as a response variable, a GLMM was created in the same way as for drop height, with nut ID set as a random effect, creating a global model using the explanatory variables date, drop height, trial, trial\*drop height, precipitation, air temperature and either wind speed or maximum wind gust. As I wanted to investigate whether crows timed their foraging for walnuts to match the high tide when walnuts were less attainable, I also ran a simple linear regression with number of observed drops per hour as a response and tidal level as a predictor variable.

For all nuts where I had observed the whole drop sequence from the first drop until the nut cracked, I summarized all drop heights in a sequence to get both an estimate of the cumulative drop height, and also to calculate the average drop height. I then fit a regression with cumulative height as the response variable and average drop height as the predictor variable, and tested whether a linear or non-linear regression gave the best fit.

### **Observations of social interactions**

Much in the same way as for drop height, I created multiple GLMM for the events of approaches and kleptoparasitism. Nut was set as a random effect, and the variables tested included date, time, trial, height, drop result, DNC, DNM, CIA, MIA, precipitation, air temperature, wind speed and maximum wind gust. Again, two different sets of variables were created, containing either wind speed or maximum wind gust. After creating a global model, I would rank all candidate models by AIC values and chose models based on the difference in AIC values and the number of variables as described earlier.

The same procedure was followed with flight response as a response variable, but in this case the global model also included approaches. A correlation between MIA and CIA was tested using Spearman's rank correlation.

### **Drop experiments**

For all nuts in the drop experiment, I calculated the cumulative height based on number of drops needed to crack the nut, multiplied by drop height. I then fit a regression with cumulative height as a response variable and drop height as predictor variable, and tested whether a linear or non-linear regression gave the best fit. When a quadratic regression turned out to give the best fit, I calculated its lowest point by solving for the second degree equation of the line, as this represented the drop height where nuts would crack with the least amount

of exertion. I also created a GLMM for nut cracking, including the variables drop height, trial and date, and the interactions height\*trial, height\*date and date\*trial. I used the same methods for model selection as described above, with nut ID as a random effect.

### 3. Results

#### 3.1 Observations of nut dropping

Only crows were seen dropping nuts, but magpies were observed carrying or caching husk-less walnuts on a total of four occasions. There was no correlation between tide level and the number of drops observed. I observed a total of 943 drops, on 445 different walnuts. Of the observed drops, 921 occurred on asphalted ground, 12 on roof surfaces, 8 drops were on soft substrates or were lost into thick vegetation and 2 drops did not have a registered drop substrate (fig 3.1). This is a significantly different distribution than would be expected had the crows selected drop surface at random ( $\chi^2=3449.55$ , d.f. = 2,  $p < 0.0001$ ). A list of descriptive statistics for all variables used in this study can be found in appendix 2.

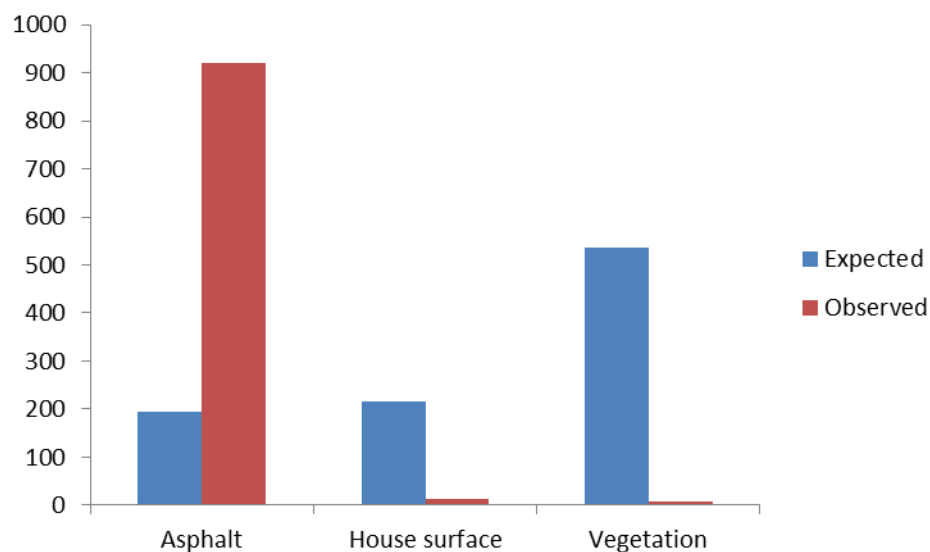


Figure 3.1: The expected and observed number of drops on the various ground covers.

#### Drop height

Mean drop height was 4.8 m ( $\pm 0.14$  SE). Mean drop height for the first drop was 7.8 m ( $\pm 0.76$ ), and decreased with subsequent trials (fig 3.2).

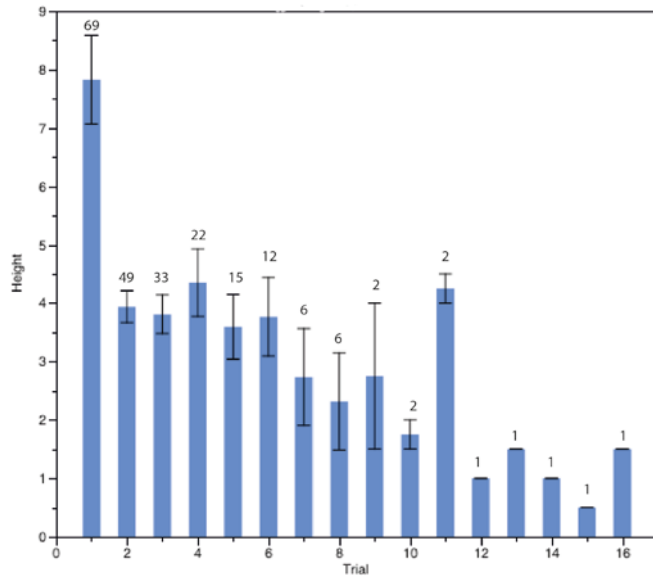


Figure 3.2: Average drop height (error bars showing SE, numbers = n observations) with increasing trials. The first drop tended to be markedly higher than subsequent drops.

When running a GLMM with nut as random effect, two models came out as equally good for explaining the variation in drop height. The first included trial, number of magpies in the area (MIA) and maximum wind gust (table 3.1), whilst the second model included trial, MIA and air temperature (table 3.2). Drop height increased with MIA, and temperature or wind, and decreased with trial (fig 3.3).

Table 3.1: Summary of the first model for drop height, AIC = 267.3

Variable	Estimate	SE	T	p
(Intercept)	0.614	0.032	19.079	<0.001
Trial	-0.032	0.005	-5.871	<0.001
MIA	0.040	0.208	2.186	0.029
Maximum gust	0.011	0.004	2.658	0.008

Table 3.2: Summary of the second model for drop height, AIC = 267.6

Variable	Estimate	SE	T	p
(Intercept)	0.521	0.067	7.737	<0.001
Trial	-0.033	0.005	-5.973	<0.001

MIA	0.040	0.017	2.323	0.021
Air temperature	0.014	0.006	2.506	0.013

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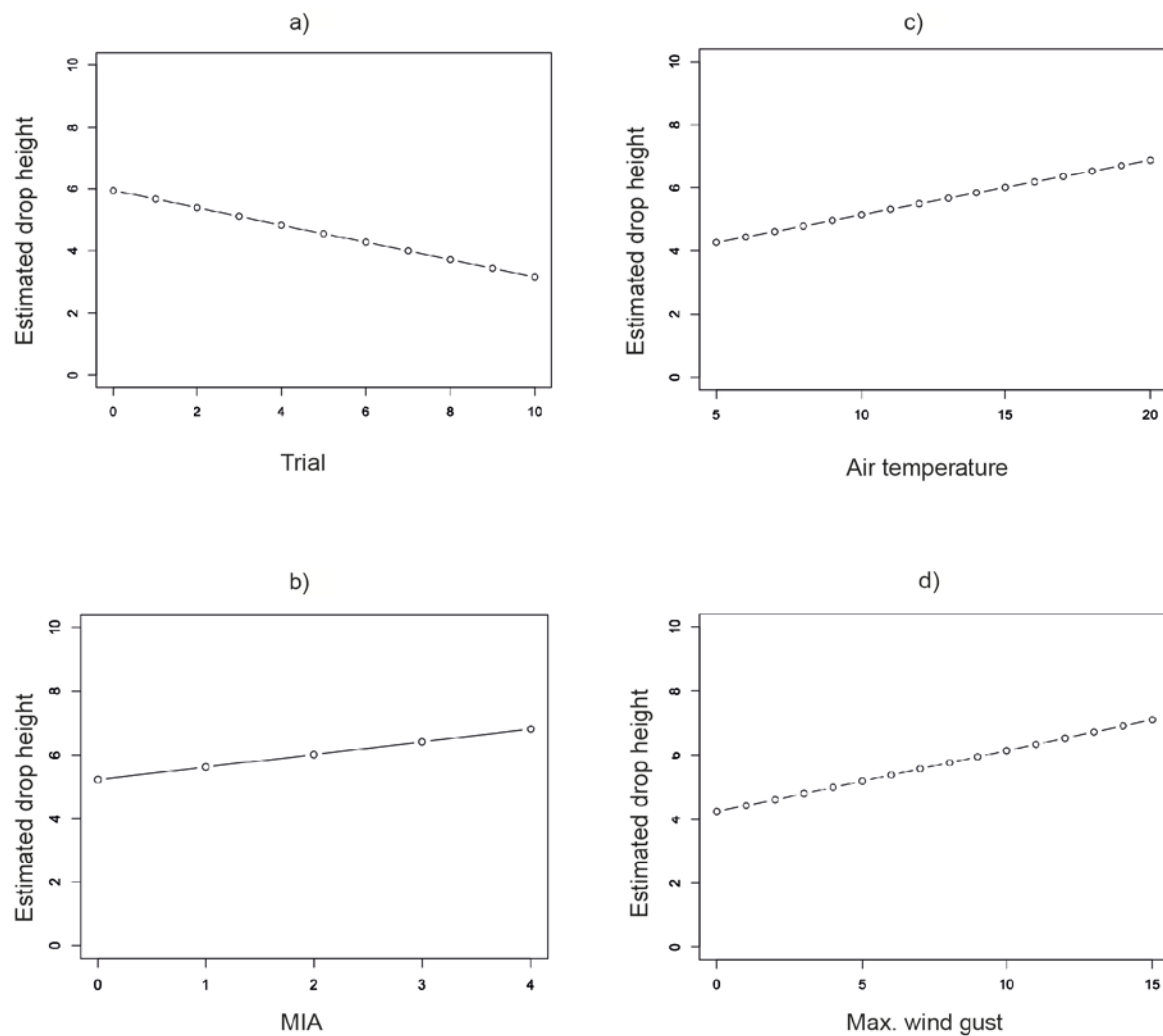


Figure 3.3: The predicted influence on drop height from *a)* trial, *b)* the number of magpies in the area (MIA) and *d)* maximum wind gust, based on the first model for drop height, and the predicted influence of *c)* air temperature based on the second model for drop height.

## Nut cracking

A nut was more likely to crack with increasing drop height and trial, but there was also an interaction between drop height and trial (table 3.3, fig 3.4). In addition, there was a positive effect of temperature on the likelihood of a nut cracking. Height and trial were found to be highly correlated (a correlation of 0.64, see appendix), but these variables were still included in the same model because I was interested in the effect of their interaction (fig 3.3).

Table 3.3: Summary of the chosen model for drop result (nut cracking)

Variable	Estimate	SE	Z	p
(Intercept)	-0.902	0.496	-1.818	0.069
Height	0.094	0.039	2.385	0.017
Trial	-0.006	0.082	-0.073	0.942
Air temperature	-0.114	0.040	-2.863	0.004
Height*Trial	0.056	0.021	2.674	0.008

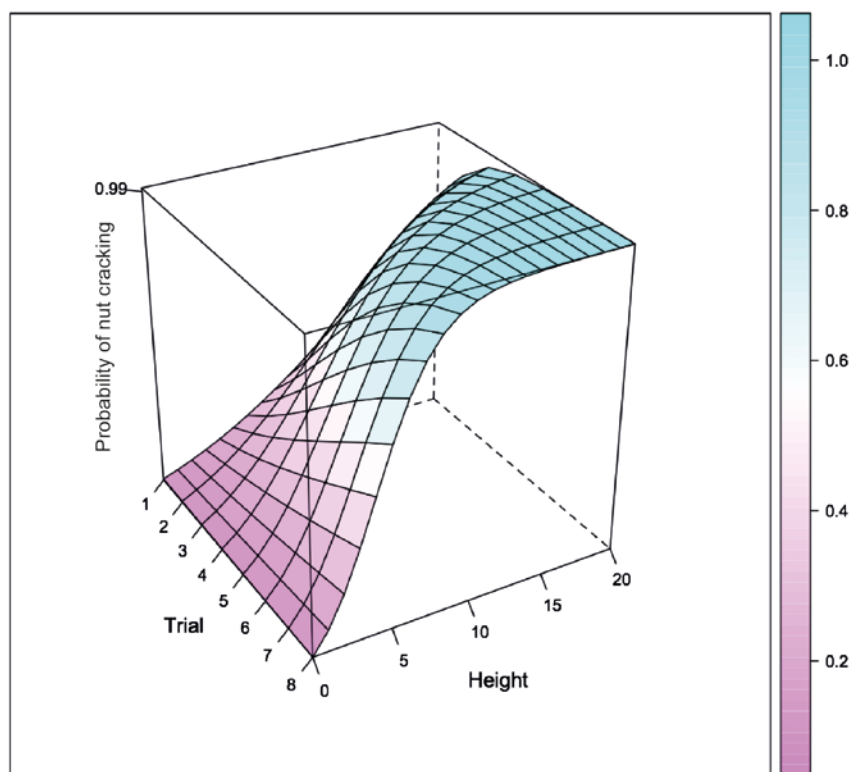


Figure 3.4: The predicted probability of a nut cracking as a function of the interaction between drop height and trial, showing that lower heights have greater effect after multiple trials.

### Observed whole sequences

Due to the difficulties of distinguishing whether a nut had been dropped previously and the fact that crows would often fly away before successfully cracking a nut, I was only able to select 24 whole sequences that had been observed from first drop until the nut cracked.

Among these sequences, the mean number of drops per nut was  $4.72 (\pm 0.65)$  and the mean total drop height (added heights of all drops per nut) was  $21.50 (\pm 1.86)$ . Based on the total

drop height for a whole sequence, I calculated the mean drop height per nut by dividing the total drop height by the number of drops in the sequence. A linear and a quadratic fit was tested to see what would best fit the data, and only the quadratic fit turned out to be significant ( $F=3.50$ ,  $p = 0.049$ ,  $N = 24$ ,  $R^2 = 0.25$ ).

### 3.2 Drop experiment

The cumulative height varied between the various drop heights, and the number of drops needed to break a nut decreased with increasing drop height (table 3.4). However, the total drop height (number of drops multiplied by drop height) did not decrease linearly with increased drop height, but was at it's lowest at a drop height of 8.41 m (fig 3.5). This is not significantly different from the average drop height of the first trial in the observed drops.

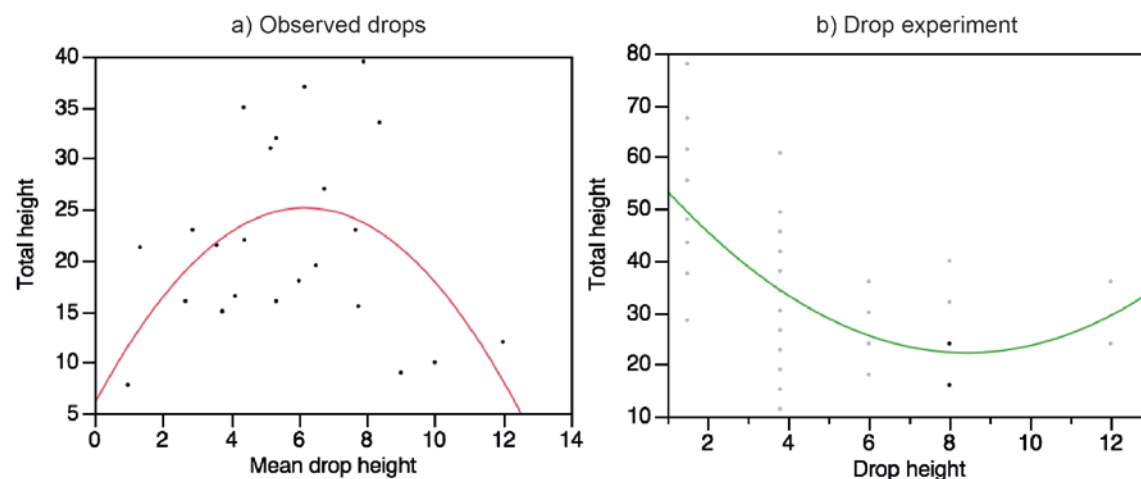


Figure 3.5: a) The relationship between the total drop height (all observed drop heights in a sequence summarized) and mean drop heights used by crows in the whole sequence observations, and b) the total drop height (drop height multiplied by the number of drops needed to crack the nut) by drosen drop height in the drop experiment. The line shows a quadratic fit to the data in both cases, but with oposite curvature.

Table 3.4: average number of drops and cumulative drop height (m) from various heights

Height	N observations	Mean drop number ( $\pm$ SE)	Cumulative height ( $\pm$ SE)
1.5	10	33.80 ( $\pm$ 3.14)	50.70 ( $\pm$ 4.71)
3.8	65	8.92 ( $\pm$ 0.32)	33.91 ( $\pm$ 1.23)
6.0	10	4.30 ( $\pm$ 0.26)	25.80 ( $\pm$ 1.56)
8.0	10	3.00 ( $\pm$ 0.33)	24.00 ( $\pm$ 2.67)
12.0	10	2.40 ( $\pm$ 0.16)	28.80 ( $\pm$ 1.96)

When looking at the relationship between total height and mean drop height, a quadratic line gave the best fit to the data ( $F=24.77$ ,  $p < 0.0001$ ,  $N = 105$ ), albeit with a relatively low  $R^2$  ( $=0.33$ ). This compares to the observed drops, with the exception that the lines curve in opposition to each other. The best model to explain whether a nut would crack or not included date, trial, drop height and an interaction between drop height and trial (table 3.5).

Table 3.5: The model for drop results from drop experiments

	Estimate	SE	Z	p
(Intercept)	-11.628	1.002	-11.600	<0.001
Trial	-0.298	0.045	4.347	<0.001
Height	0.270	0.102	2.657	0.008
Date	0.087	0.020	-6.693	0.001
Height*Trial	0.333	0.028	11.742	<0.001

### 3.3 Observations of social interactions

The number of magpies present after a drop was found to be negatively correlated with the number of crows present before the drop ( $r_s = -0.14$ ,  $N = 897$ ,  $p < 0.0001$ , fig 3.6).

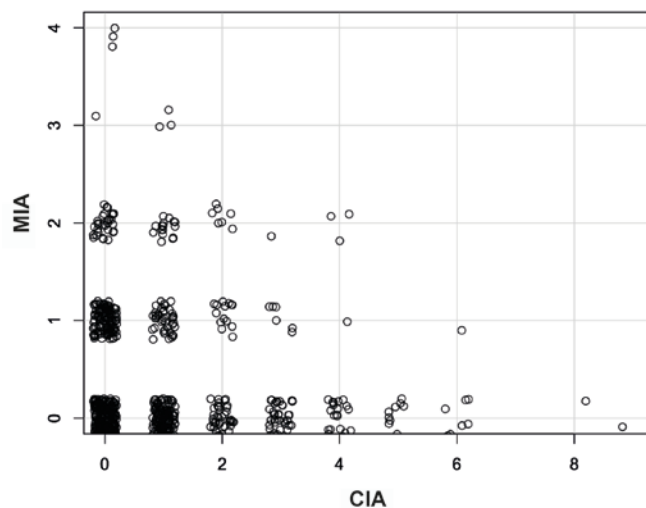


Figure 3.6: The observed densities of magpies plotted against various densities of crows illustrates the negative correlation between the two variables. The data points are slightly spread out to give a better illustration of the values.

In 91 out of 375 events where at least one crow was registered in the nearby area of a nut owner did it lead to an approach, and of these 91 events, 41 resulted in the nut owner flying away, 43 in kleptoparasitism and in 7 events the nut owner did neither (fig 3.7). Similarly, in

46 out of 259 events where at least one magpie was in the area of a nut owner did the magpie approach, and of these 46 events, 17 resulted in the nut owner flying away, 23 in kleptoparasitism and in 6 events the nut owner did neither (fig 3.7).

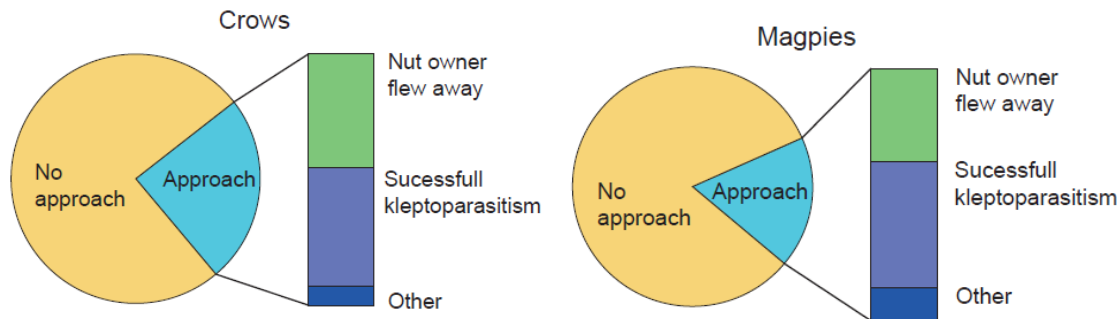


Figure 3.7: The proportion of approaches relative to the number of events were either crows or magpies respectively were registered in the area, and the registered responses by the nut owner. The nut owner would most often either be kleptoparasitized or fly away after an approach, and would only in a few instances defend the nut successfully against the approacher.

## Approach

A nut owner was more likely to be approached after cracking the nut, and with decreasing distances to the nearest crow or magpie (table 3.6, fig 3.8).

Table 3.6: Summary of the chosen model for approaches

Variable	Estimate	SE	Z	p
(Intercept)	-0.682	0.332	-2.048	0.041
DNC	-0.024	0.003	-6.923	<0.0001
DNM	-0.007	0.003	-2.291	0.022
Drop result (=1)	1.701	0.263	6.467	<0.0001



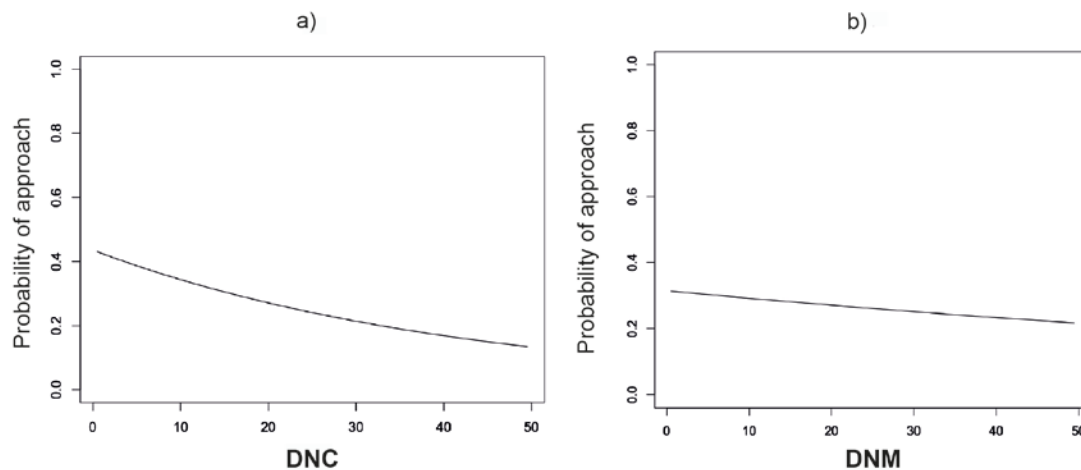


Figure 3.8: The predicted probability of an approach given various distances to a) nearest crow and b) nearest magpie. The probability of an approach was higher at short distances for both species.

With the exception of one incidence, there was little display of violent aggression. Any approaches to the nut owner generally resulted in either successful kleptoparasitism or the nut owner flying away.

### Flying away

In 47.0 % of all the observed events ( $N = 445$ ), the nut owner would fly away with the nut, either to a nearby location or out of sight. In 58.9 % of the observed cases where the crow flew, the nut had not yet cracked, whereas in 15.3 % of the cases it had cracked and in the remaining events (25.8 %) the state of the nut was uncertain (fig 3.9). In 48 of the observed cases, the crow was most likely scared off by a passing car or pedestrian.

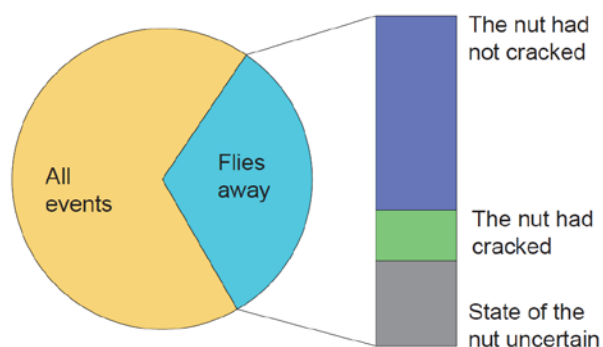


Figure 3.9: The proportion of events ending in the nut owner flying away and all other events. In the majority of the cases where the nut owner took flight, the nut had not yet cracked.

Two different models for flying away fit the data equally good, both containing wind speed and approaches, but differing in containing either trial or drop result (table 3.8 and 3.9, fig 10).

Table 3.7: Summary of the first model for flying away. AIC = 698.2

Variable	Estimate	SE	Z	p
(Intercept)	-1.690	0.231	-7.322	<0.0001
Approach	-0.704	0.127	-5.531	<0.0001
Drop result	0.231	0.131	1.765	0.078
Wind speed	0.189	0.061	3.085	0.002

Table 3.8: Summary of the second model for flying away. AIC = 698.4

Variable	Estimate	SE	Z	p
(Intercept)	-1.292	0.234	-5.511	<0.0001**
Approach	-0.601	0.115	-5.229	<0.0001**
Trial	-0.120	0.058	-2.080	0.038
Wind Speed	0.178	0.055	3.241	0.001

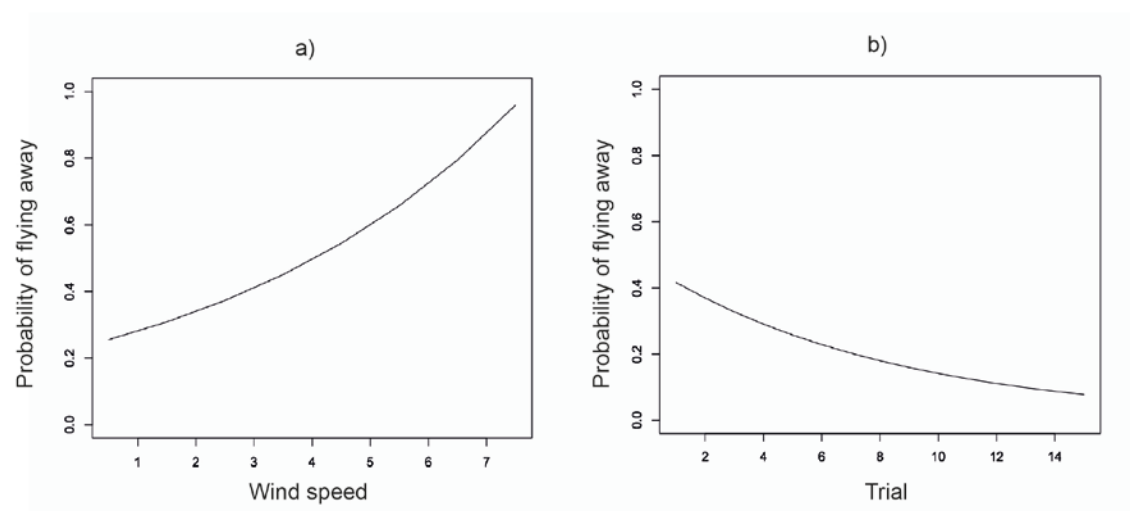


Figure 3.10: Probability of flying away as a function of a) wind speed, as predicted in the first model, and b) trial number, as predicted in the second model

## Kleptoparasitism

14.4 % (N = 445) of the dropped nuts were kleptoparasitized, out of which 67.2% were stolen by crows and 32.8% by magpies (N = 64). With only one exception, all events of kleptoparasitism seemed to occur through displacement rather than physical aggression. The model that best fit the data for kleptoparasitism included drop result only (table 3.9).

Table 3.9: Summary of the chosen model for kleptoparasitism. AIC = 218.4

Variable	Estimate	SE	Z	p
(Intercept)	-15.061	3.788	-3.976	<0.0001
Drop result	-5.495	2.301	-2.388	0.017

#### 4. Discussion

The crows showed a clear preference for dropping nuts onto hard, flat surfaces, thereby maximizing the probability of a nut cracking from any given height. Other studies have found that crows will use hard drop substrates when available, but may sometimes drop on less optimal substrates as a trade-off against travel costs or risk of kleptoparasitism (Whiteley et al. 1990, Cristol & Switzer 1999). Lowering drop height in subsequent drops is economical, as the drop experiments showed that the walnuts were more likely to break with each drop and that the effect of height was positively influenced by trial. The crows did not seem to lower their drop height as a response to potential kleptoparasites in the surroundings, but they did seem to take some precautions against food theft by flying away when approached or when their nut was close to breaking.

##### Drop height

Drop height should be held constant if the probability of a prey breaking is independent of previous drops, unless the likelihood of loss increases with drop number (Switzer & Cristol 1999). The probability of a walnut breaking was influenced both by drop height and the number of previous drops. By lowering drop height with trial number, the hooded crows in Norway exhibit similar prey dropping strategies as do American crows in California. In prey dropping systems where prey breakability does not increase with trial, crows have not been found to lower drop height with increasing trial (Northwestern crows dropping whelks in

Canada; Zach 1978 and carrion crows dropping mussels (*Mytilus edulis*) in Scotland: Whiteley et al. 1990). Crows therefore seem to be capable of developing either strategy, depending on what is most profitable.

The crows in this study might have had ample opportunities practicing prey dropping on mussels, and may therefore not be as inexperienced as first assumed. Several of the crows may also have been foraging for walnuts in this area for multiple years. The neighborhood was situated less than 1 km away from a fjord where the crows had easy access to mussels (*M. edulis*). Crows in the area have been observed to drop mussels by the beach (G. A. Sonerud, pers. com.), and this was even observed on one occasion in the study area. Mussel dropping has not been studied in this population of crows, so little is known about how often it occurs and what strategies the crows employ. It would be interesting to see whether the crows use decreasing drop height on mussels as well, or if they have different drop strategies for walnuts and mussels.

Compared to the studies on American crows dropping walnuts in California, the average drop heights used by the crows in my system was somewhat higher. Cristol and Switzer (1999) reported an average drop height for walnuts of 3.4 m based on the first drop in a sequence only, whereas in my study the average height for the first drop was 7.8 m. The crows in California dropped nuts that had lost their husk and could therefore be considered fully mature (Vander Wall 2001), whereas the crows in this system dropped nuts with the husk still intact. The husk sits outside the hull and acts as a cushion to the walnut inside, making the nut harder to break than had it been removed. The thickness of the hull (the outer shell of the nut) also varies considerably both within and between various cultivars of persian walnuts, making direct comparisons of breakability difficult (Vander Wall 2001).

According to my drop experiments, the optimal drop height to maximize probability of a nut breaking while minimizing ascending flight would be around 8.4 m. The observed first-drop height fits well with this, suggesting that the crows do aim to optimize their energy expenditure when choosing drop heights. This is consistent with other literature on prey dropping in corvids (Zach 1979, Whiteley et al. 1990, Cristol & Switzer 1999), and fits with my initial hypothesis.

### **Observed compared to experimental drops**

The drop experiment showed that the walnuts in my study would break more easily as the season progressed, but during the same period the crows did not change their drop height significantly. This does not support the hypothesis that crows optimize their energy output, but it could also indicate an element of learning, assuming the increase lead to a more optimal drop height. Maron (1982) found a difference between adults and juveniles of Western gulls (*Larus occidentalis*) dropping clams where the adults adjusted the drop height according to substrate, whereas juveniles did not and also consistently chose lower drop heights. Corvids are characterized by having an especially long period of development, involving social learning (Clayton & Emory 2005). It is not unlikely that some of the crows foraging in my study area were young birds trying to learn the “tricks of the trade” by mimicking their conspecifics.

Another explanation could be that the crows were used to dropping clams, which are heavier than walnuts and do not need such great drop heights to break, and that it took the crows some time to adjust to dropping the walnuts. The crows were perhaps also more selective when choosing which walnuts to drop, whilst for my experiment I only had access to the nuts that were either on the lower branches of the tree or that had just fallen down. While the crows should select nuts that would give the highest yield, my aim was to select nuts that seemed representative and that grew on different sides of the tree. Because the walnuts were easier to break as they matured, the crows might have selected the most mature nuts available at any time, and this would obscure the effect of season on the observed drops. Zach (1978) found that northwestern crows exclusively chose the largest whelks when given the option to select small, medium or large whelks for dropping. Large whelks would not only yield the largest profit to the crows, but is likely to be easier to handle and to relocate after a drop. The crows would usually reject several whelks before picking one for dropping, suggesting that they are highly selective in their prey selection (Zach 1978).

The fact that the cumulative drop height on average was lower for the observed drops than for the experimental drops I conducted myself, suggests that the crows optimized the energy output when dropping walnuts. The discrepancy between the experimental and the observed values are likely to stem from several factors. An observer bias could have lead to lower estimates for drop heights in the field, whereas the heights used in the experimental drops

were strictly controlled. However, the crows did two things that should lower their cumulative drop height significantly. Firstly, they would often peck at the nut to remove the outer husk and sometimes in attempt to further break a nut. The outer husk is a thick layer of soft flesh, acting as a protective shield to the nut inside (Vander Wall 2001). Because the husk sometimes needed several drops before it was loose enough to be manually removed with ease, and not all crows seemed as diligent at removing the husk, I chose not to remove the husks before dropping nuts in my experiment. Secondly, the crows tended to lower the drop height with trial number. They could thereby adjust the total drop height more freely, and for example chose a low drop height if a nut seemed close to breaking or simply peck it open with their beak.

The tendency of lowering drop height with trial should therefore also account for parts of the discrepancy in the graph depicting optimal drop heights calculated from the drop experiment and from the observations. Drop height was held constant in the drop experiment, and yielded a nice polynomial fit between total height and drop height, dipping at 8.4 m. The line based on the observed whole sequences curves in the opposite way, but this is in large part because the crows did not hold drop height constant. A drop exceeding 15 m might break a nut on first try, but if it does not, the crow should lower the height for the next drop in order to minimize the total amount of ascending flight. When calculating an average drop height from such sequences, it would generally be much lower than the initial drop.

### **Social influences on drop height**

I found a negative correlation between drop height and the number of crows nearby during initial data explorations, but the presence of crows did not turn out to be significant in the GLMM for drop height. Instead, there was a positive effect of the number of magpies nearby. These results may seem puzzling at first, as magpies should be unlikely to represent a larger threat or significance than other crows to walnut-dropping crows. Considering the number of successful kleptoparasitism events, crows accounted for far more such events than magpies. However, since the number of magpies was found to be negatively correlated to the number of crows in the area, the positive effect of magpies on drop height could in fact represent the effect of few other crows in the area. Crows are thought to be dominant to magpies in food

competition (Rolando & Giachello 1992), and magpies have been found to avoid foraging along side other corvid species (Waite 1984).

Perhaps crows do not assess the risk of kleptoparasitism in a straight forward way based on the number of conspecifics nearby. Other factors may come into play, such as dominance relations, experience, kinship, residency status, pair bonding (Beuchamp 2000) or even personality (Kurvers et al 2010). If the crows used the number of observed magpies to infer how many crows were nearby, I should have seen an effect of the number of crows nearby on drop height, not just the number of magpies in the area. It could be that the presence of most other crows did have a negative influence on drop height, but that this was masked by a selective tolerance for low-ranking individuals or close relatives to the nut owner.

Cristol and Switzer (1999) found that the drop height used by American crows was influenced by the distance to and number of conspecifics, but that this correlation was s-shaped rather than linear. The crows seemed to respond to the risk of kleptoparasitism only when it exceeded a threshold level. Whiteley et al. (1990) found a similar pattern in carrion crows foraging for mussels in Scotland, where there was a significant difference in drop height between crows dropping mussels when being by them selves, and those surrounded by five or more conspecifics. This could explain why the number of crows nearby and their distance did not seem to influence drop height in my case. A crow might have a better chance of defending a prized food item against a single or few other corvids, but may have a hard time keeping track of all potential thieves and defending against them when they are numerous.

### **The risk of kleptoparasitism**

The observed rate of kleptoparasitism in my study (14.4 %) is similar to that of other studies (12% in both Cristol (2005) and Cristol and Switzer (1999)). However, a great portion of the kleptoparasitism events I observed occurred some time after the nut had been dropped, and not in concurrence with the drop itself. This contrasts the study by Cristol and Switzer (1999) on American crows dropping walnuts, where the birds were only observed for 30 s after a drop. Kleptoparasitism attempts in Davis, CA - where these studies were conducted - seem to occur more often midair or right after a drop (pers obs).

Cristol & Switzer (1999) reported that in California, nearly half of all first-time drops were attempted kleptoparasitized, and that drop height was the best predictor found to explain the variance in kleptoparasitism risk. This contrasts the findings of my study, where neither of the models for the social measures related to kleptoparasitism included drop height.

The percentage of approaches were also much lower, perhaps indicating a lower kleptoparasitism pressure. The lower corvid density in my study area may cause fewer occurrences of kleptoparasitism events immediately after a nut is dropped. At the same time, a low walnut availability and number of individuals to scrounge from could make other corvids in the area more persistent in their attempts to steal nuts once an opportunity presented itself and also make them more willing to focus on smaller pieces of nuts, rather than whole nuts solely. There might also be a higher degree of relatedness among the individuals foraging for walnuts in Bygdø, as the number of crows in the area was lower, and crows are known to form social groups often consisting of family members (Chiarati et al 2010). Acceptance of food stealing from family members should be tolerated more often, especially from dependent young and subadults.

Magpies stole only half as many nuts as did crows, and was also seen to approach nut owners less often. Although it was hard to quantify how much of a nut was stolen, it seems that magpies would steal smaller pieces nuts, whereas this varied more between the crows. Magpies also tended to take hiding soon after acquiring a piece of a nut more often, and were never seen displacing a crow or kleptoparasitizing using force.

My definition of kleptoparasitistic events did not distinguish between events where whole nuts or just scraps of a nut were stolen, as would perhaps have been ideal. Because the crows would often peck at nuts to open and eat them, it was difficult to determine how much of a nut had been eaten, if any. It could also be difficult to determine how much of the nut the nut thief had been able to steal. If nearby crows or magpies got hold of parts of a nut that the crow had abandoned after eating, the event was not considered as kleptoparasitism.

### **Climatic factors**

Wind had a positive influence on drop height, and it could be that crows utilized the wind to soar higher up without expending more energy. There were several windy days during the registration period, and on such days I would frequently observe crows flying much higher than usual with the nuts. I registered three drops from heights greater than 30 m, and all



happened in concurrence with strong winds. In neither of the comparable studies on prey dropping mentioned above did they test for nor find an effect of wind on dropping behavior. However, the fact that some birds use the wind to conserve energy when flying is nothing new, and is particularly well described in birds living by the sea. Paiva et al (2010) found that the flight pattern of Cory's shearwater (*Calonectris diomedea*) corresponded to the prevalence of the most beneficial winds; with flight concentrated to the morning and afternoon, and using tailwinds for traveling and cross winds for foraging. I also found an effect of air temperature both on drop height and the probability of a nut cracking, and this could be related to the maturity of the nuts, or the state of the husk.

Wind had a positive influence on whether or not a crow would fly away after dropping a nut, and this lends support to the hypothesis that stronger winds makes flight less costly. Since risk of kleptoparasitism increased with observed trial, birds could lower this risk by flying to a new location before fully cracking their nut. Flying to more than one location to drop a single nut is costly, and thus reduces the net output from a nut. The crows seem faced with a trade-off between risk of kleptoparasitism and cost of flight, choosing flight more often on windy days.

### **Limitations of my study**

The crows would often spend a great deal of time pecking at the nut, and it would have been interesting to have a measure of how much time they spent doing this. Pecking seemed to be used most commonly to remove the outer husk of the nut, as well as to open a nut that was almost or partially cracked. Therefore, time spent pecking is likely to affect how many drops or the drop height needed to crack a nut. However, it was hard to distinguish between when a crow was pecking to open a nut, and when it was actually eating the content, as the two behaviors seemed to be exhibited intermittently. Also, some crows would peck at their nut with far more energy and tempo than others, and this would be hard to take into account.

I was initially interested in observing caching behavior as well as nut cracking, and had planned to record all observed caching events in detail. However, I only observed three caching events throughout the whole study, and was thus forced to discard those data from further analysis due to the low number. I also observed a pair of jackdaws kleptoparasitize

crows in a highly cooperative manner on two occasions, but the low number of events and individuals forced me to discard these data as well.

I tried to avoid pseudoreplication by using nut ID as a random effect, but this does not fully make up for the variance among individual crows and magpies as the same individuals are likely to have been observed several times. It would have been a great benefit had the birds been sexed, banded and sorted by age-class before this study, as I am now curious about the strategies of individuals in this system. Knowing the role of relatedness in this system could provide an exciting study. It would be of great interest to know whether the same individuals tend to be represented as either scrounger/kleptoparasite or producer, the role of kinship, and if there is a difference in how efficient adults and subadults forage for walnuts. Further studies could also look into the time aspect, to see whether magpies wait longer after a nut has been cracked before they attempt to approach a crow or steal its nut.

## **Conclusions**

The crows in my study seemed to optimize the net output from their nut dropping by adjusting their drop height and by using a hard drop substrate. Weather factors also appeared to play a role in influencing the drop behavior, in that the crows tended to increase their drop height and fly away more often with strong winds. The crows did not seem to respond to the risk of kleptoparasitism by lowering their drop height, but may instead have chosen to fly away to a different drop site. A future study on the role of individual traits and kinship in influencing strategies for drop behavior, kleptoparasitism and theft avoidance could yield further insight into this fascinating system.

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## Appendix 1 – List of variables and abbreviations

Variables used in various models		
#	Variable	Description
1	Time	Hours after midnight
2	Trial	Number in drop sequence
3	DNC	Distance from nut owner to nearest crow
4	DNM	Distance from nut owner to nearest magpie
5	# CIA	Number of crows in the area
6	# MIA	Number of magpies in the area
7	*DNC	Distance to nearest crow <i>in the period after</i> a drop
8	*DNM	Distance to nearest magpie <i>in the period after</i> a drop
9	Height	Drop height
10	Precipitation	Measure of precipitation
11	Air temperature	Measure of air temperature
12	Drop result	Whether a nut cracked or not, 0 = uncracked, 1 = cracked
13	Approach	Another bird approaching nut owner within 0.5 m
14	Species of closest bird	The species in closest proximity to the nut owner
15	Wind speed	Measure of wind speed
16	*CIA	Number of crows in the area <i>in the period after</i> a drop
17	*MIA	Number of magpies in the area <i>in the period after</i> a drop
18	Date	Measured as days since start of field study

## Appendix 2 – Descriptive statistics for variables used

Abbreviation	Meaning	Mean ( $\pm$ SD)	Range
Time	Time of observation	11.05 ( $\pm$ 1.69)	7.53 - 17.48
Trial	Number in drop sequence	2.57 ( $\pm$ 2.82)	1 - 25
Height	Drop height	4.82 ( $\pm$ 4.17)	0.2 - 35 m
DNC	Distance to nearest crow	18.41 ( $\pm$ 16.82)*	0.5 - 100 m*
DNM	Distance to nearest magpie	20.48 ( $\pm$ 15.88)*	0.5 - 70 m*
CIA	Number of crows in the area	1.05 ( $\pm$ 1.47)	0 - 9
MIA	Number of magpies in the area	0.44 ( $\pm$ 0.7)	0 - 4
Precipitation	Measured as mm/hour	0.07 ( $\pm$ 0.33)	0 - 3.25
Temperature	Air temperature	11.87 ( $\pm$ 2.56)	5.16 - 19.9
Wind speed	Wind measured as m/s	2.84 ( $\pm$ 1.64)	0.59 - 7.22
Max. wind gust	The strongest wind measured/h	6.05 ( $\pm$ 3.14)	1.81 - 14.5

\*excluding instances where no birds were seen nearby and where the default was set to 101 m

Measure	Occurrences (total)	Meaning
Drop result	178 (821)	Whether a nut cracked or not
Approach	139 (932)	Whether the nut owner is approached
Flies	209 (933)	Whether the nut owner flies off
Kleptoparasitism	64 (933)	Whether the nut is stolen from nut owner

### Appendix 3 - Correlation of Fixed Effects

	(Intr)	1.	2.	3.	4.	5.	6.	7.
1. Date	0.052							
2. Time	-0.377	-0.759						
3. Height	-0.392	0.012	-0.043					
4. Trial	-0.264	-0.246	0.162	0.394				
5. DNC	-0.368	0.221	-0.130	0.366	0.100			
6. DNM	-0.054	0.483	-0.371	0.225	-0.131	0.369		
7. CIA	-0.439	-0.297	0.248	0.216	0.335	0.168	-0.456	
8. MIA	0.069	-0.057	0.072	-0.299	-0.050	-0.711	-0.180	0.099
9. Drop.result	-0.439	-0.168	0.084	0.567	0.637	0.269	-0.185	0.676
10. Air temperature	-0.154	0.675	-0.723	0.191	-0.104	0.251	0.264	0.046
11. Precipitation	-0.156	-0.726	0.588	0.011	0.385	-0.239	-0.503	0.491
12. Wind speed	-0.131	-0.124	0.073	0.156	-0.098	0.021	-0.144	0.172
13. Max. wind gust	0.175	0.212	-0.203	-0.166	0.048	-0.023	0.133	-0.204
14. Approach	0.222	0.059	-0.254	-0.295	-0.187	-0.055	-0.044	-0.081
15. Kleptoparasitism	-0.419	0.024	-0.005	-0.046	-0.089	-0.100	0.023	-0.072
16. Flying away	-0.032	-0.273	0.382	-0.303	-0.095	-0.337	-0.299	0.002

	8.	9.	10.	11.	12.	13.	14.	15.
1. Date								
2. Time								
3. Height								
4. Trial								
5. DNC								
6. DNM								
7. CIA								
8. MIA								



9. Drop result	-0.103							
10. Air temperature	-0.065	0.146						
11. Precipitation	0.191	0.425	-0.427					
12. Wind speed	-0.234	0.157	0.209	0.139				
13. Max. wind gust	0.183	-0.176	-0.134	-0.241	-0.947			
14. Approach	0.205	-0.170	0.138	-0.111	-0.292	0.281		
15. Kleptoparasitism	0.037	-0.115	-0.013	-0.052	0.042	-0.033	-0.035	
16. Flying away	0.270	-0.163	-0.351	0.132	-0.149	0.171	-0.244	0.038

#### Appendix 4 - AIC tables

Model	Variables	AIC	$\Delta$ AIC
<b>Drop height</b>			
1.	Trial + MIA + Maximum wind gust	236.6	0
2.	Trial + MIA + Air Temperature	237.4	0.8
3.	Trial + DNM + Max. wind gust	237.4	0.8
4.	Trial + DNM + Wind speed	239.2	2.6
5.	Trial + CIA + MIA + Max. wind gust	236.5	0.1
<b>Nut cracking</b>			
1.	Height + Trial + Height*Trial (H*T) + Temperature	729.8	0
2.	Height + Trial + H*T + Temperature + Wind Speed	730.5	0.7
3.	Height + Trial + H*T + Temperature + Precipitation	730.5	0.7
4.	Height + Trial + H*T + Temperature + Date	730.9	1.1
5.	Height + Trial + Temperature	735.5	5.7
<b>Approach</b>			
1.	Drop result + DNC + DNM	522.0	0
2.	Drop result + DNC + MIA	523.0	1.0
3.	Drop result + DNC + DNM + Date	522.6	0.6
4.	Drop result + DNC + DNM + Time	522.7	0.7
5.	Drop result + DNC + DNM + Trial	523.0	1.0
<b>Flies</b>			
1.	Approach + Drop result + Wind speed	698.3	1.5
2.	Approach + Trial + Wind speed	698.5	1.7
3.	Approach + Drop result + Trial + Wind speed	697.4	0.6
4.	Approach + Drop result + Temperature + Wind speed	697.5	0.7
5.	Approach + Drop result + Max. wind gust	700.5	3.7
<b>Kleptoparasitism</b>			
1.	Drop result	218.4	0
2.	Drop result + DNC + Trial	220.2	1.7
3.	Drop result + Precipitation	220.4	2.0
4.	Drop result + Height	220.4	2.0
5.	Drop result + Temperature	220.5	2.1
<b>Drop experiment, nut cracking</b>			
1.	Date + Height + Trial + H*T	458.1	0.9
2.	Date (D) + Height + Trial + D*T + H*T	458.4	1.2
3.	Date + Height + Trial + D*H + H*T	459.3	2.1

4.	Date + Height + Trial + H*T + D*T + D*H	457.2	0
5.	Height + Trial + H*T	474.3	17.1

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