Social Dominance and Reproduction in Jackdaws (*Corvus monedula*)

RuG

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Content

Abstract

Findings of two studies involving Jackdaws (*C. monedula)* showed contrary results of the effect of dominance on reproduction. One of these studies was done by Röell (1978), he found dominant birds to produce less fledglings, the second study done by Henderson et al (1995) found dominant birds to produce more fledglings.

This year the correlation between dominance and reproductive success in Jackdaws was looked at again, at a colony of Jackdaws in Haren, in the Netherlands. Röell's (1978) research was done at this studysite in Haren.

Dominance of the male Jackdaw was determined by means of three different methods following methods of Röell (1978), Henderson et al (1995) and Lambrechts et al (1986). Dominance was determined in two periods (5/3/1998 till 10/4/1998 and from 27/5/1998 to 18/6/1998). Reproductive parameters of the males that participated in the dominance hierarchy were collected.

Dominance of the male Jackdaw was not significantly expressed in several parameters like wing and tarsuslength, age or owning a nestbox. Dominant males produced significant fewer fledglings; their young had lower body weights and females of dominant males laid significant smaller eggs. Wing and tarsus lengths of young of dominant males were also significant shorter. So dominant male Jackdaws in our colony raised fewer and smaller young, than subdominant males raised. A significant effect of laydate was also found on the number of young, their weights and bodyparameters. If chicks came from later clutches, they fledged significant less, their weights were lower and their bodyparameters like wing and tarsus lengths were smaller. Dominance and laydate are not significantly correlated. If dominance and laydate were controlled for statistically for each other, none of both variables showed a significant result on fledged young, however trends were present.

Introduction

Dominance

Dominance can be determined by observation of aggressive interactions between individuals (Röell, 1978; Henderson et al 1995; Kikkawa 1980). The winner of two opponents is presumed to be dominant over the other and placed higher in rank. There are different functions in favour of dominance. An individual can compete for a resource and dominate another individual, whereas that same dominant individual can lose in competing for another resource. Röell (1978) observed Jackdaws (*Corvus monedula*) to be dominant at their own nestbox, whereas a linear dominance hierarchy is present in Jackdaws during foraging. Drent (1983) found location of a feeding place to determine dominance of Great Tits (*Parus major*), if a feeding place was closer to its territory, the Great tit holding that territory was more dominant than Great tits holding a territory further away from the feeding place.

A dominance hierarchy can be beneficial for all members of that hierarchy, even for the lowest ranked. It reduces fights, over resources, thus saving energy. An established hierarchy, will lead to less repeated fighting between the same individuals in the future, because the individual identifies others which can be supplanted or individuals which can supplant the individual in question. If this is known to the individuals in the hierarchy, display behaviour is sufficient enough to make the position of the individuals in he hierarchy clear (Drickamer et al 1996; Raveling 1986).

Different types of hierarchies exist. One example of such a hierarchy is the linear hierarchy. One animal dominates all. The second in rank dominates all, except number one. The third in rank dominates all, except the numbers one and two and so on. A second possibility is the dominant status of one animal dominating others, the other animals are more or less equally placed in dominance. A third hierarchy-type is a type in which coalitions can occur. In this kind of hierarchy two or more individuals might act together, to dominate another individual. Circular hierarchies are another possibility, one individual dominates a second one, the second individual dominates a third one and this third individual dominates the first individual (Drickamer et al 1996).

Which individual is dominant?

In what way differs a dominant individual from a subdominant individual? Dominance correlates with individual parameters. Lambrechts et al (1986) found song to be correlated with dominance in Great tits; birds with a high variation in song pattern were more dominant. The offspring of dominant individuals is in the case of the Red Grouse (*Lagopus lagopus scoticus*) significant more dominant than offspring of subordinates. Dominance in this specie is greatly heritable (Moss et al 1984). Weight, in Rooks (*Corvus frugilegus*) and Carrion crows (*Corvus corone corone* L.) (Røskaft 1983; Richner et al 1989), as well as tarsus length in Carrion crows and Great tits (Richner et al 1989; Garnett 1981) are body parameters, which correlate with dominance. The higher the dominance, the higher these body parameters. In Shellduck *Tadorna tadorna* L. (Patterson 1977) age determines dominance.

Importance of dominance

To be dominant can be of great importance to an individual. The dominant individual can exploit resources more than subdominant individuals. Dominant Great tits can for example maintain a territory (Dhondt 1983). Dominant Willow Tits, (*Parus montanus*) were seen occupying the best hiding places to avoid predators, this leads to less time spend watching for predators and more time spend feeding (Ekman et al 1984). A higher winter survival, of dominant Silvereyes (*Zosterops lateralis chlorocephala*) (Kikkawa 1980) and Great tits (De

Laet 1983) is observed. Dominant Silvereyes have a higher survival (Kikkawa 1980). In some bird species reproductive parameters rise as dominance of the individual rises. Dominant males of *Cacicus cela* have a significant higher opportunity to fertilise eggs than subdominant males (Robinson 1985), thus increasing their genetic input in young. Dominant Great tits and Jackdaws produce more fledglings (Dhondt et al 1983; Henderson et al 1995) than subordinate individuals. Early lay date and better hatching success in dominant Shellducks (Patterson 1977). Producing more fledglings by territorial Great tits in comparison with great tits without a territory (Dhondt et al 1983). A higher lifetime reproductive success for dominant Great tits observed by Lambrechts et al (1986). In these experiments, dominance correlates with reproductive parameters in a way that the more dominant an individual is, the higher its reproductive success is. Apparently it can be favorable to belong to the dominant part of the colony.

However is dominance always beneficial? Male sex hormones may mediate a tradeoff between dominance and parental care (A. Qvarnström and E. Forsgren 1998). To be competitive and dominant might cause a decline in maternal or paternal care. Male dominance may not reflect overall mate quality leaving females to use other choice cues than dominance. They might prefer subordinate males in some situations (A. Qvarnström and E. Forsgren 1998). It is known for Baboons at Gombe National Park in Tanzania (*Papio cynocephalus anubis*) that there is a significant higher change on miscarriage the more dominant a female is and a proportion of high-ranked females suffer from a decline in fertility (C. Packer et al 1995). Suggesting that qualities needed to enhance or maintain female rank may carry significant reproductive costs (C. Packer et al 1995). Röell (1978) found a decline in fledged young the more dominant a male Jackdaw is.

Contradictory

Henderson et al (1995) found dominant Jackdaws to produce more fledglings. The more dominant, the more chicks fledged. These results however are in contrast of findings by Röell (1978), who observed dominant Jackdaws to raise fewer chicks. Can dominance have an advantage in one population as well as a disadvantage in another population of the same species? Apparently circumstances change the influence of dominance on fledged young in the Jackdaw? Colony-density, food resources, geographic location and location to urban areas, may possibly be these circumstances causing a change in the influence of dominance on reproductive parameters.

At the colony at the Biological Center in Haren, Netherlands, a comparable experiment like Henderson et al (1995) and Röell (1978) has been caried out, looking at dominance and reproduction in Jackdaws. Röell's (1978) experiment also took place at the colony at the Biological Center in Haren. The experiment of this year was carried out to get a better perception of the correlation between dominance and reproduction in Jackdaws; hopefully finding an answer why the outcomes of the experiments of Henderson et al (1995) and Röell (1978) differ.

The difference might lie within different periods in which dominance is scored. Röell (1978) scored dominance from December 1973 to February 1974 and Henderson in April 1991. So trying to find out whether a stable dominance hierarchy is present; dominance hierarchies were calculated in the period before egglaying started (March to April 1998) and after the breeding season (May to June 1998).

We expect, if a bird is more dominant, it will have an advantage on gaining resources for its young and thus increasing its reproductive success (Lambrechts et al 1986; Drickamer et al 1996). No changes in rank are expected comparing both periods Röell (1978).

Methods

The Jackdaw colony at the study-site

The Jackdaw population has been present at the Zoölogical Laboratory at least since 1964 (Röell 1978). Jackdaws are usually monogamous birds, so unless one of them dies, the pair stays together for life (Röell 1978; 1979). The Jackdaw breeds in holes, not made by the Jackdaw itself. 36 Nestboxes are available at the study site. The nest boxes are almost all occupied. Some Jackdaw pairs occupy two nestboxes.. The pair breeds in the same box every year, or a box close to the old one. The pair defends their box fierce and fights over the boxes are regularly observed. Sometimes they are driven away by another pair, or they leave the box due to the death of their mate, it's impossible to defend a box alone (Röell 1978). Jackdaws were seen foraging on fields surrounding the study-site and sometimes they ate geese-food (artificial), which was available at the study-site.

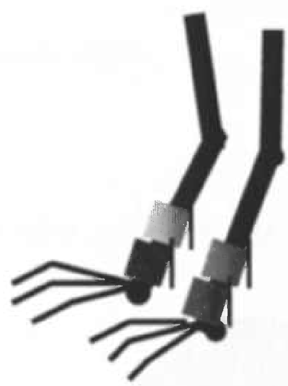
Clutch size varies between 3 to 6 eggs. Jackdaws fed their young from the crop. Insects like caterpillars, sometimes even bread, was found in the crops of captured Jackdaws.

Identification of a Jackdaw

The Jackdaws were individually recognizable. This was possible by checking their colourcodes; most of the individuals had three colourrings and an aluminium ring in different combinations.

The rings which were used:

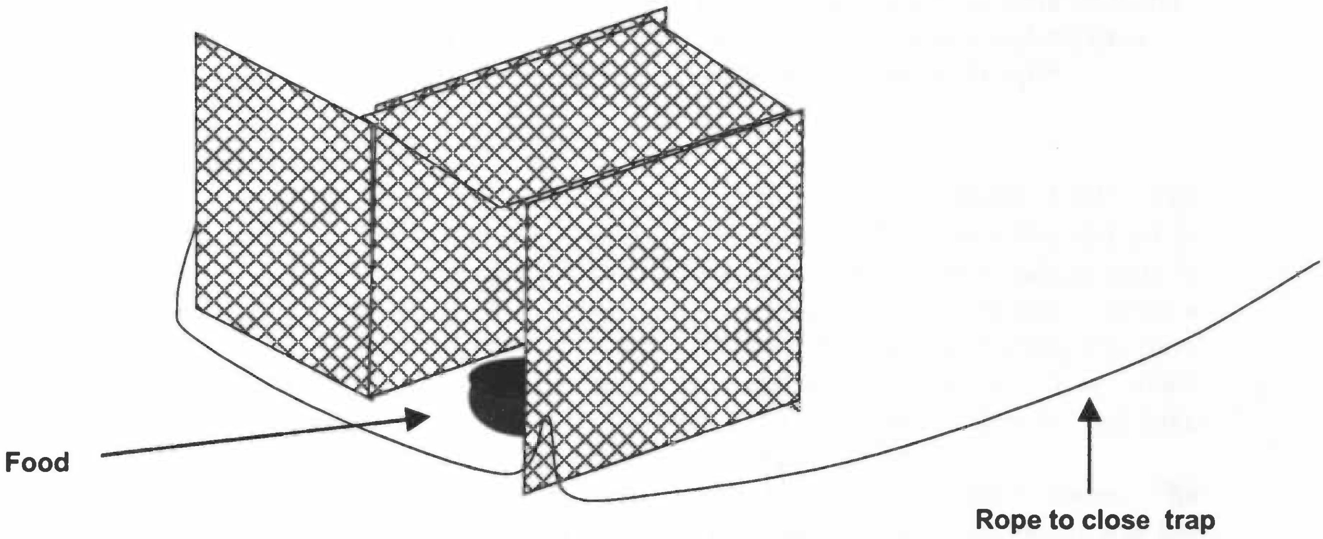
Aluminium	(A)
Red	(R)
Yellow	(Y)
Dark Green	(G^{+})
Light Blue	(B^{-})
Dark Blue	(B^{+})
Mint	(M)
Orange	(O)



Code: **RB^{+}AG^{+}**

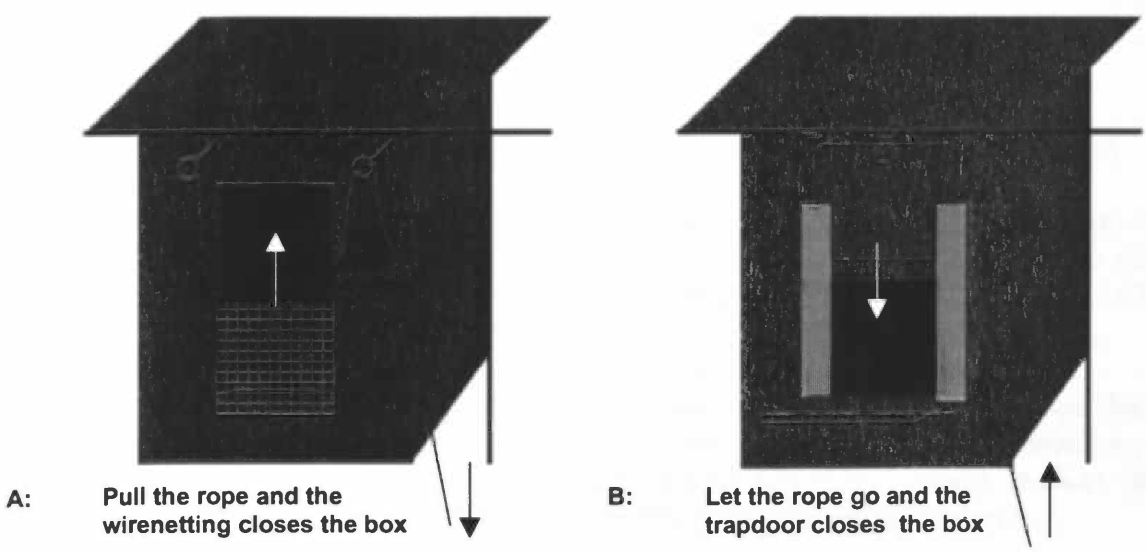
Capturing Jackdaws

Jackdaws without a code are presumed to be immigrants from other colonies, or birds from our colony, which weren't ringed in past years; also birds with incomplete or unreadable codes are present. To be able to identify these birds during observations, they must be captured and given a distinct code. To capture them, they were lured into a cage with food in it (*sketch 1*).



Sketch 1, Cage in which Jackdaws are captured during the season

Capturing them in a cage was done from 3/4/1998 to the first egg was layed 10/4/1998.



Sketch 2, Some capturing methods, at the nestboxes.

Moreover we tried to capture the birds in their nestboxes. Five days after eggs of pairs hatched we started these nestbox capturings. Birds were not captured on the nestbox if the possibility existed that they carried eggs. There are three different mechanisms to capture them on their nestbox. Inside of the Aquariumhouse (a part of the Zoölogical Laboratory) at the attic there are 8 nestboxes situated of which the box is closed with help of a trapdoor. Other boxes (*sketch 2*) have a little piece of wirenetting, if a rope is pulled the wirenetting blocks the entrance (*sketch 2a*). Thirdly there are boxes, which have a trapdoor that has to be dropped in front of the entrance to close the Jackdaws in (*sketch 2b*). These last two catching methods required a mirror to see if a Jackdaw went in. The captured Jackdaws were hold and transported in wooden boxes. Before ringing took place, the Jackdaws were weighed, their wing and tarsus length was measured and blood was taken to obtain a DNA-sample.

Dominance by interactions

A linear dominance hierarchy exists in Jackdaws (Röell 1978; Van Beek 1985). The dominance hierarchy was measured by observing the Jackdaws fighting at a feeding-pit in which universal food was put. The feeding pit had a diameter of 8-cm. At this feeding-pit only one or two (a pair) Jackdaws could eat, without getting into a fight. The Jackdaw needs a period of about a week to get familiar with the feeding regime. At first two feeding pits were used, but after some days, the Jackdaws seemed to get satisfied and did not interact much anymore. Probably because there was more than enough food available, so they did not have to fight over it. So the experiment continued with one feedingpit.

The interactions and bird identities were noted by telescope observations. The interactions were spoken into a tape recorder. A video camera was also used, but it was too difficult to determine the colours of the rings on the television screen.

The bird, which supplants another bird at the feedingpit, is dominant over the supplanted bird (Röell 1978; Van Beek 1985; Henderson et al 1995), which gives the following outcomes:

One- the individual wins an interaction,
Two- the individual loses an interaction,
Three- the individual waits until another individual is done eating. The result of the waiting outcome was treated equal as the losing behavioral type. If an individual waits, it loses indirectly. The Jackdaws that waited at first, spurted to the feedingpit as soon as the dominant Jackdaw left, thus showing recognition of a more dominant Jackdaw.

Calculating a dominance hierarchy

The following three methods were used to calculate the dominance hierarchy, namely:

1- Making a matrix/ crosstable by arranging the interactions visually in the spreadsheet. This means checking the individual interactions between the bird and his neighbour birds and move the bird either higher, or lower in the hierarchy of the crosstable (Röell 1978; Van Beek 1985). In short this method will be mentioned as "crosstable".
2- Looking at the fraction interactions won by the bird, interaction winnings/total interactions (Lambrechts et al 1986). In short this method will be mentioned as "fraction".
3- A method following Henderson et al (1995), in which the proportion of interactions won and the proportion of individual birds supplanted by a focal bird is used. In short this method will be mentioned as "formula", the formula on page 6 describes it mathematically:

$$R = \frac{\text{No. of interactions won by x}}{\text{No. of interactions lost by x}} \times \frac{\text{No. of individuals supplanted by x}}{\text{No. of individuals supplanting x}}$$

The dominance hierarchy of the male Jackdaw was used since the rank of the females depends mostly on the rank and the presence of the male (Röell 1978). Birds must have interacted at least five times with other birds of the dominance hierarchy, to participate in dominance hierarchy. The most dominant bird was given rank 1 the second dominant bird was given rank 2 and so on.

Dominance in the Jackdaw can be related to a combination of factors, such as: age, weight, body variables like tarsus- and wing length, or the place of the box in the population. So to determine what actually correlates with dominance in Jackdaws, these variables are correlated with dominance.

Dominance in two periods

Observations of the interactions were done in the period 5/3/1998 till 10/4/1998 preceding egglaying, this period will be mentioned as before breeding season. A second period of observation was done from 27/5/1998 to 18/6/1998, this period will be mentioned as after breeding season, noted must be that in this period 21 pairs were still nourishing their young. Looking at both periods gives the opportunity to look at dominance shifts.

Reproduction

It is important to know which Jackdaws occupy the nestboxes, so reproduction parameters of these birds can be correlated with their dominance. These identities became clear by observing the nestboxes in the period 17/2/1998 to 8/4/1998, to verify these observations, observing was also done in the period 8/4/1998 to 2/6/1998.

Reproduction parameters got known by checking the nest boxes. Before hatching the Jackdaw eggs were exchanged for Quail eggs, which are approximately the same size. The female apparently does not notice the exchange. The size of the Jackdaw eggs was measured before putting them in an incubator. Eggs hatch within the next two days, the day in which the first egg of a clutch hatched was called day 1. The chicks were weighed. Blood was taken from them (determination of sex in the future), by clipping a toenail, by clipping a particular toenail the chicks can be identified later in the experiment. After these measurements the chicks were immediately returned to their nestbox and exchanged for a Quail egg. Day 5, 15 and 25 the number of survived chicks was checked. Day 10 the number of survived chicks was checked and they were weighed. Day 30, just before the young Jackdaws fledge, the number of survived chicks is checked again, they are weighed and tarsus and wing length were measured, again blood was taken from them for blood examinations in the future. The chicks got their individual colourcode. After day 30 the young Jackdaws fledged and many are found dead around their nestboxes. The aluminium ring was taken from them and their deaths were noted.

Statistics

Statistical calculations were done in the program SPSS 8.0 on the computer.

Results

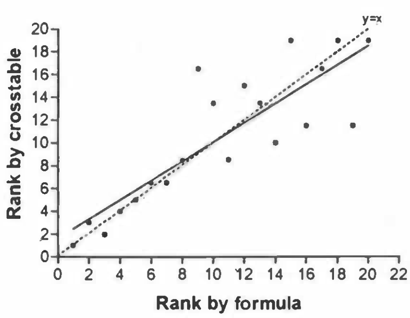
Dominance

To see if all three methods of dominance determination give the same results, the correlation between the three methods is looked at, of the two periods, before and after the breeding season. The three different methods are:
formula following Henderson et al (1995), fraction following (Lambrechts et al 1986) and crosstable following Roëll (1978).
The correlation between the three methods was in all cases significant (table 1; figure 1a, b). There is apparently no difference between the three different methods. Beside formula, fraction and crosstable are also represented in tables.

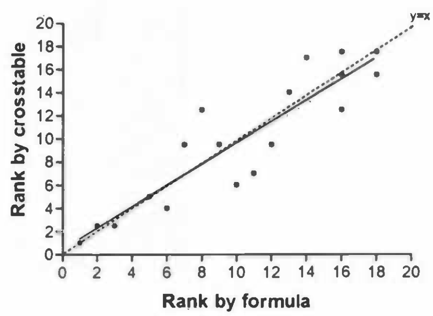
Table 1. Correlation of three rank methods: formula, fraction and crosstable.

Spearman's rank corr.	(2-tailed)	Before breeding season			After breeding season		
		formula	crosstable	fraction	formula	crosstable	fraction
formula	Corr. Coeff.		0.851	0,992		0.904	0.989
	Sig		0.000	0.000		0.000	0.000
	N		20	20		18	19
crosstable	Corr. Coeff.			0.806			0.908
	Sig.			0.000			0.000
	N			20			18

- significant



a



b

Figure 1. Correlation of crosstable and formula, before breeding season (r= 0.851, P<0.001, N= 20) (a) and after the breeding season (r=0.904, P<0.001, N=18) (b).

A perfect distribution of interactions would be, if all males have an equal amount of interactions. However, dominance correlates significantly negative with interacting at the feedingpit; dominant males interact more than subdominant ones (figure 3).

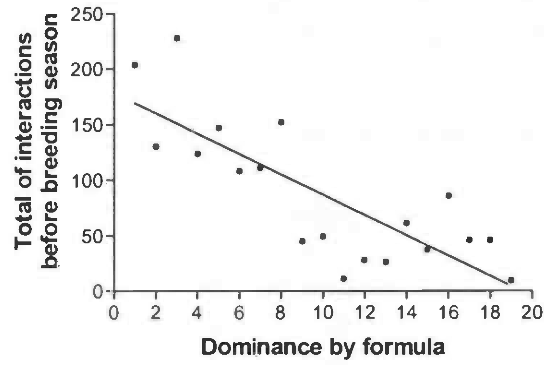


Figure 2. Correlation of dominance and total of interactions, before breeding season (r= -0,763, P< 0.001, N= 19).

Correlation between the periods will give an answer to the question if rank shifts occur during the breeding season. For the males (N=15), which interact before and after the breeding season, the correlation of the rank is significant, for each of the three methods (table 2; figure 3). No significant differences in dominance hierarchy occur.

Table 2. Correlation of the periods analyzed with dominance by the three methods.

			Before breeding season correlated with After breeding season
Spearman's rank corr. (2-tailed).	Dominance by formula	Corr. Coeff.	0,714
		Sig.	0.003
		N	15
Spearman's rank corr. (2-tailed)	Dominance by fraction	Corr.Coeff.	0,682
		Sig.	0.005
		N	15
Spearman's rank corr. (2-tailed)	Dominance by crosstable	Corr. Coeff.	0.782
		Sig.	0.001
		N	15

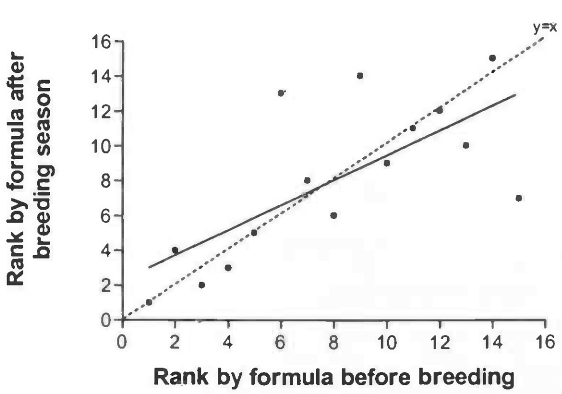


Figure 3. Correlation of the two periods, using the dominance of formula (r=0,714, P< 0.005, N= 15).

Factors determining dominance

Body parameters, of the male Jackdaw, might say something about the males place in the dominance hierarchy. However body parameters measured this year, do not show a correlation with dominance (table 3; figures 4a, b).

Table 3. Correlation between dominance and body-parameters of the male.

Spearman's Rank corr. (2-tailed).	Males	Before breeding season		
		formula	fraction	crosstable
Tarsuslength	Cor. Coeff.	,280	-,289	,171
	Sig.	,245	,230	,483
	N	19	19	19
Winglength	Cor. Coeff.	,062	-,096	-,240
	Sig.	,799	,696	,323
	N	19	19	19

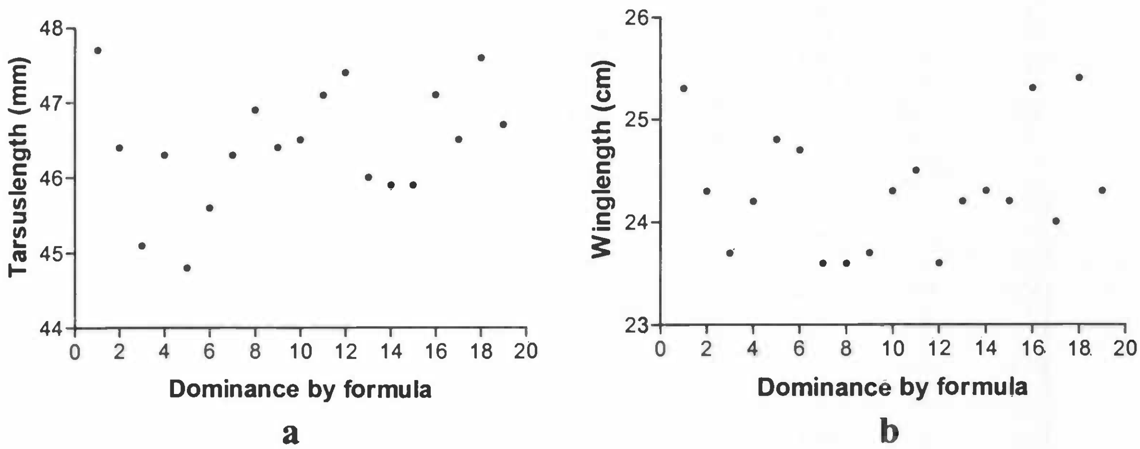


Figure 4. Correlation between dominance and tarsuslength (a) and winglength (b).

Dominance is not statistically tested with Parameters like age and owning a nestbox, because of missing or not enough data of both parameters. Visually expectancies may be taken out of figures 5a, b, but no conclusions are drawn.

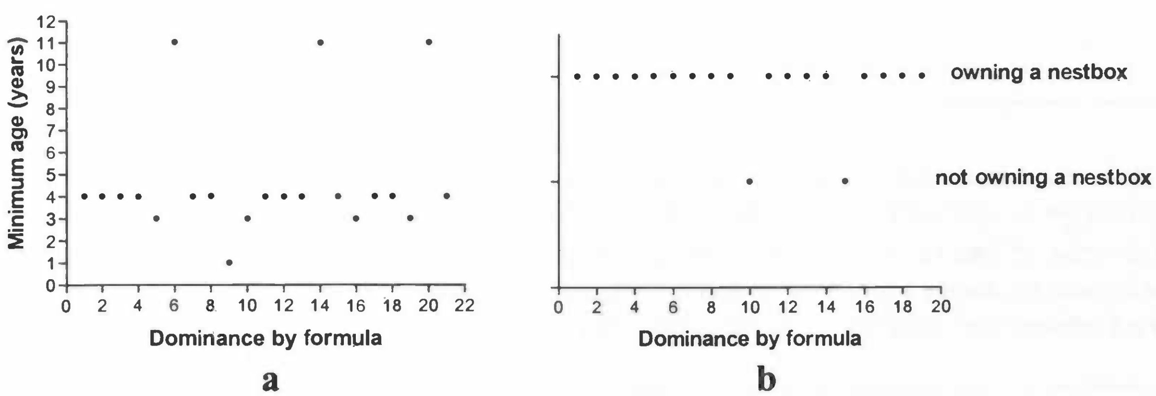


Figure 5. Dominance of the male Jackdaw and it's minimum age (a) and owning a nestbox (b).

Dominance and reproduction

The same result Roëll (1978) found on dominance and fledging, was also found this year. More dominant, leads to fewer chicks left, at different ages until fledging of the chicks. Table 4 shows significant results given by all three methods, before the breeding season. Figures 6a, b and c show the correlation of dominance on number of chicks left at respectively the ages 10 days and 25 days and fledged young. Figure 6d shows a rising of the correlation coefficient of dominance against the number of chicks left, during the period chicks are cared for.

Table 4. Dominance and number of chicks.

Spearman's rank (2-tailed). corr.		Before breeding season			After breeding season		
		formula	fraction	crosstable	formula	fraction	crosstable
Clutchsize	Cor. Coeff.	,227	,185	,346	,055	,081	,093
	Sig.	,380	,478	,174	,828	,751	,722
	N	17	17	17	18	18	17
Nr. of chicks day 5	Cor. Coeff.	,056	,027	,112	,144	,208	,208
	Sig.	,832	,919	,669	,568	,408	,423
	N	17	17	17	18	18	17
Nr. of chicks day 10	Cor. Coeff.	-,037	-,096	,089	,121	,119	,033
	Sig.	,889	,713	,734	,633	,639	,899
	N	17	17	17	18	18	17
Nr. of chicks day 15	Cor. Coeff.	,123	,080	,226	,025	,041	,096
	Sig.	,637	,760	,384	,923	,873	,713
	N	17	17	17	18	18	17
Nr. of chicks day 20	Cor. Coeff.	,368	,362	,358	,079	,090	,185
	Sig.	,146	,154	,158	,756	,724	,476
	N	17	17	17	18	18	17
Nr. of chicks day 25	Cor. Coeff.	,486*	,477	,501	,167	,176	,290
	Sig.	,048	,053	,040	,509	,484	,259
	N	17	17	17	18	18	17
Nr. of chicks day 30	Cor. Coeff.	,447	,464	,361	,053	,061	,135
	Sig.	,072	,060	,155	,836	,809	,606
	N	17	17	17	18	18	17
Fledged	Cor. Coeff.	,531*	,547*	,463	,134	,156	,243
	Sig.	,028	,023	,061	,596	,536	,348
	N	17	17	17	18	18	17
Nr. of chicks day30/ clutchsize	Cor. Coeff.	,443	,497	,347	,069	,070	,151
	Sig.	,086	,050	,188	,786	,781	,564
	N	16	16	16	18	18	17

Categorical and individual ranking

Categorical dominance, by putting birds in categories following Henderson et al (1995) correlates positively with fledged young ($r= 0.651$, $P< 0.05$, $N= 16$). Dominance by individual ranking, following Roëll (1978) correlates also significantly positive, as can be seen in table 6. So there lies no difference in determining a dominance hierarchy by means of categories or ranking individual birds in our experiment, both give the same positive correlation between dominance and fledged young.

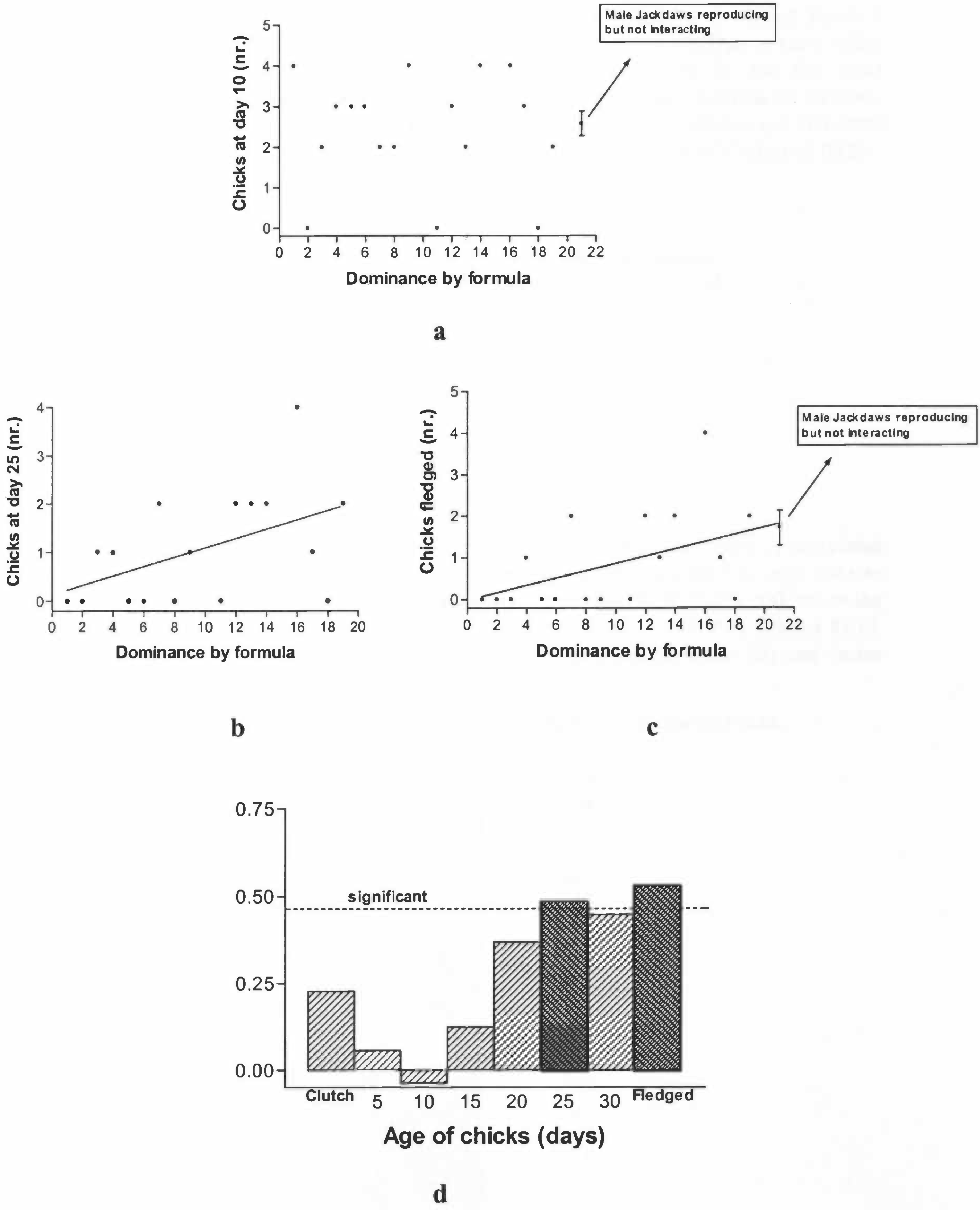


Figure 6. Correlation between dominance and chicks left at the ages of 10 days (r= -0,037, P= 0.889, N= 17) (a) and 25 days (r= 0,486, P= 0.048, N= 17) (b) and fledged young (r= 0,531, P= 0,028, N= 17) (c) and the rising correlation coefficient of dominance against number of chicks left, on different chick ages (d). The points in a and c, of the male Jackdaws that did not interact, but did reproduce were not taken into any statistical calculations.

Dominance of the male has no significant effect on fledging success (table 4), but figure 7 shows a trend towards less fledging success if a bird gets more dominant. Due to the finding that subdominant males do not interact much (figure 3). Expected is that the most subdominant males do not interact and are thus missing out of this years dominance data set. These subdominant males may have a low or high reproduction. Male Jackdaws, which bred in a nestbox, but did not interact at the feedingpit are expected to be these subdominant birds.

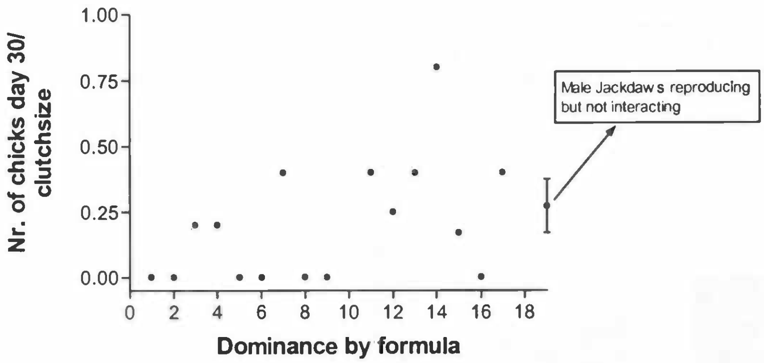


Figure 7. Dominance and fledging success.

To see if dominance of the father is reflected in chick parameters, dominance is correlated with a number of chick parameters. Dominance shows a significant effect on egg volume (table 5). Females of dominant males lay smaller eggs (figure 8a). Dominance reflects in the weights of the chicks in later stages of the chick's life, significantly (table 5; figures 8b,c). Dominance correlates also significantly with the chick wing (table 5; figure 8d) and tarsus length.

Table 5. Correlation of dominance and laydate, hatchdate and body-parameters of the chicks,.

Spearman's rank corr.(2-tailed).		Before breeding season		
		formula	fraction	crosstable
Laydate	Cor. Coeff.	-,223	-,272	-,196
	Sig.	,407	,309	,467
	N	16	16	16
Hatchdate	Cor. Coeff.	-,465	-,522	-,321
	Sig.	,094	,055	,263
	N	14	14	14
Eggvolume	Cor. Coeff.	,541	,568	,429
	Sig.	,030	.022	,097
	N	16	16	16
Hatchweight	Cor. Coeff.	,581	,546	,634
	Sig.	,029	,044	,015
	N	14	14	14
Chickweight day 10	Cor. Coeff.	,294	,224	,361
	Sig.	,354	,484	,249
	N	12	12	12
Chickweight day 20	Cor. Coeff.	,782	,864	,547
	Sig.	,004	,001	,082
	N	11	11	11
Chickweight day 30	Cor. Coeff.	,690	,714	,667
	Sig.	,058	,047	,071
	N	8	8	8
Chickwinglength day 20	Cor. Coeff.	,764	,845	,524
	Sig.	,006	,001	,098
	N	11	11	11
Tarsuslength day 20	Cor. Coeff.	,582	,691	,378
	Sig.	,060	,019	,252
	N	11	11	11

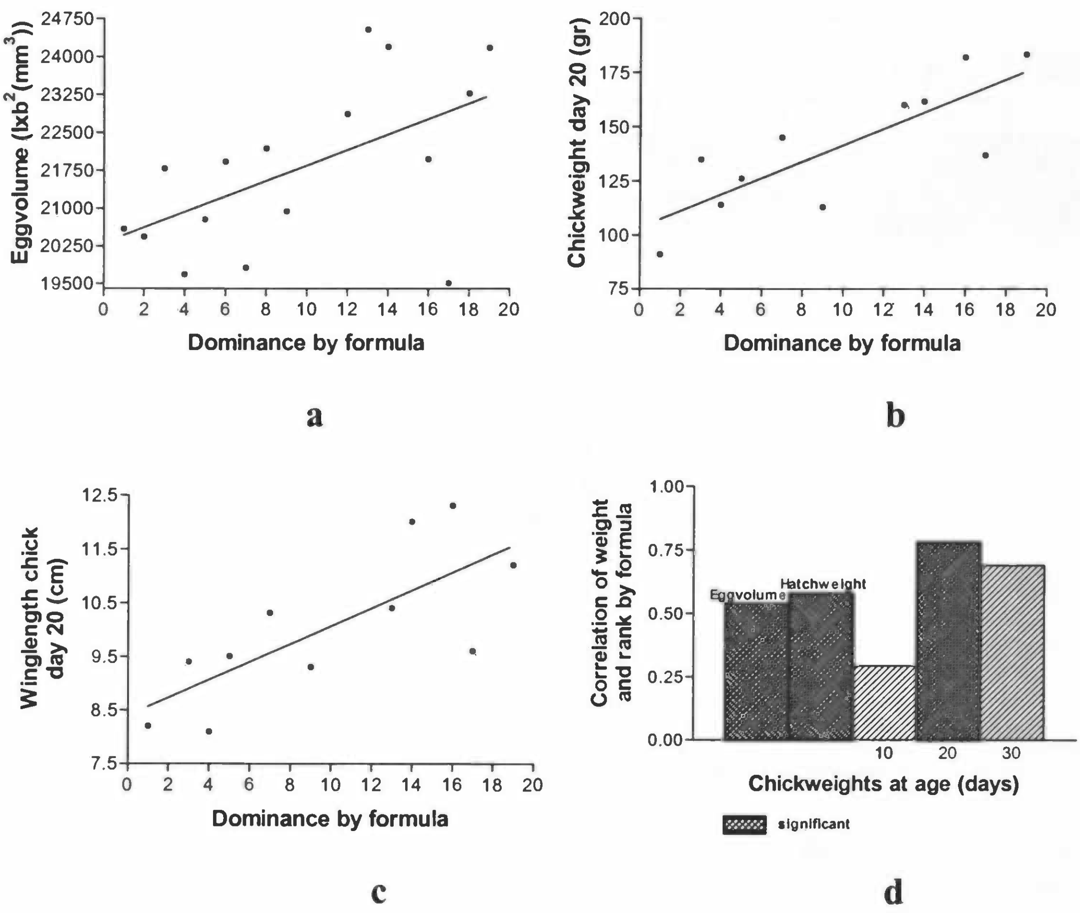


Figure 8. Correlation between dominance and average egg volume of a clutch (r= 0,541, P= 0,030 N= 16) (a) and average chick weight at day 20 (r= 0,782, P< 0,005, N= 11) (b) and average wing length of the chicks at day 20 (r= 0,764, P< 0,01, N= 11) (c). The rising effect of dominance on average weight of chicks, as the chicks get older(d).

Lay date

Lay date is another variable that can affect reproductive parameters, so to see which of these two variables, dominance or lay date does affect reproduction, lay date is correlated with reproductive parameters. If indeed lay date has an influence both variables will be controlled for.

Lay date correlates significantly with clutch size (table 6; figure 9a) and number of chicks, at different stages of the chick's live (table 6; figure 9b, c). Lay date correlates also significantly with the weight of the chick at day 20 (r= -0,478, P= 0,045, N= 18) and the tarsus length of the chick at day 20 (r= -0,469, P= 0,049, N= 18). Lay date shows a significant correlation with number of chicks at day 30/clutchsize (table 6; figure 9d).

Lay date and dominance apparently both affect several parameters. Though lay date does not correlate with dominance (table 5). To find if lay date is explained by dominance or vice versa partial correlations were done.

Correlation between fledged young and dominance by formula:
r= 0,4917 N=13, P= 0,063 controlled for lay date.
Correlation between fledged young and lay date:
r=-0,4487 N=13, P=0,093 controlled for dominance by formula.

Out of these findings, one variable does not exclude the other variable's influence.

Table 6. **Correlation between lay date and reproductive-parameters.**

Spearman's Rank corr.	(2-tailed)	Clutchsize	Nr. of chicks day 5	Nr. of chicks day 10	Nr. of chicks day 15	Nr. of chicks day 20	Nr. of chicks day 25	Nr. of chicks day 30	Fledged	Nr. of chicks day 30/clutchsize
Lay date	Corr. Coeff.	-,500	-,213	-,224	-,166	-,418	-,453	-,486	-,438	-,442
	Sig.	,015	,330	,303	,448	,047	,030	,019	,036	,035
	N	23	23	23	23	23	23	23	23	23

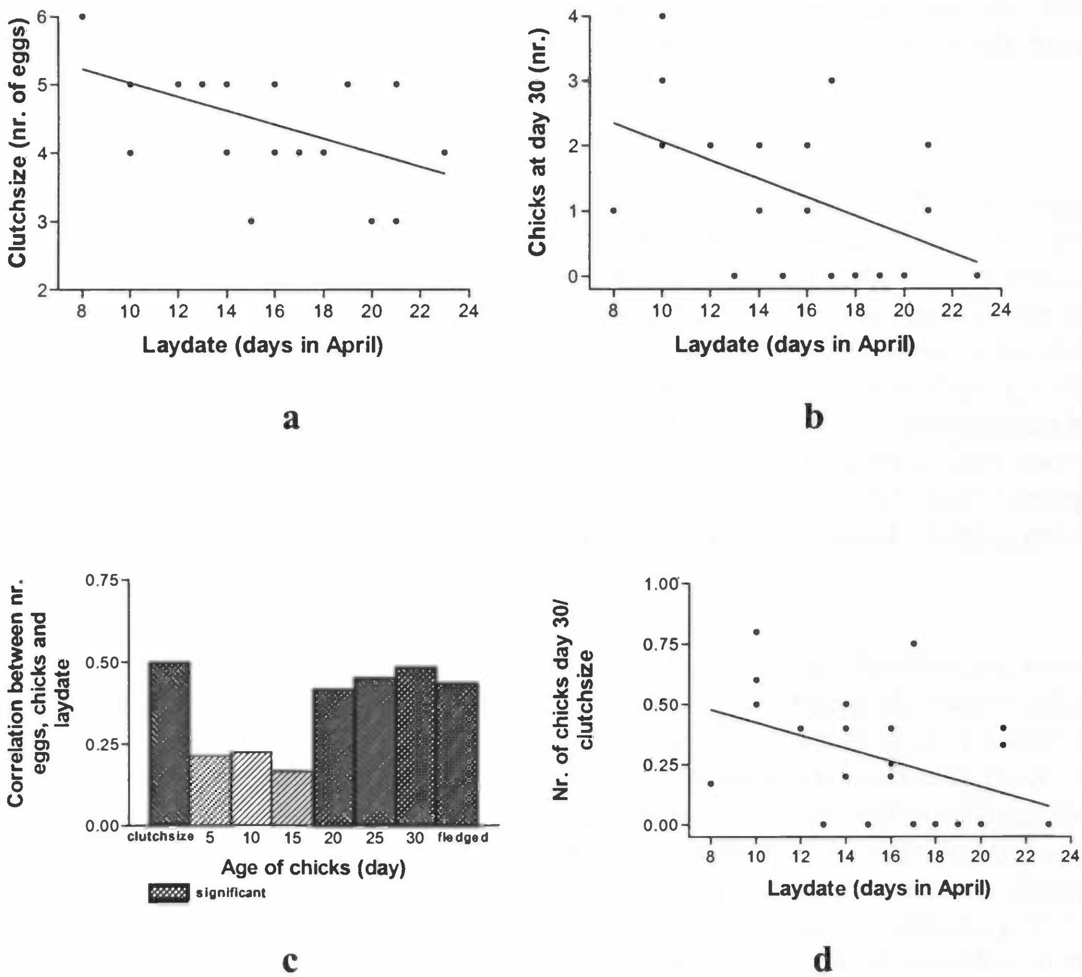


Figure 9. Correlation between lay date and clutch size (r= -0,500, P= 0.015, N= 23) (a) and chicks at day 30 (r= -0,486, P= 0.019, N= 23) (b). The correlation coefficient of lay date on the number of chicks, at different chick ages (c). Correlation between lay date and fledging success (r= -0,442, P= 0,035, N= 23) (d).

Discussion

Methods of determining dominance

The different methods for calculating a dominance hierarchy correlate significantly. All three give the same dominance hierarchy as can be seen in tables 1 and 2 (figures 1 and 2), but which method is preferable? Formula and fraction give a quick mathematical way to calculate the ranks. The formula method is a more exact way to calculate a dominance hierarchy than fraction, because formula takes individual interactions into account too. Using a crosstable is perhaps even more accurate, given individual interactions. Though making a crosstable, compared to the formula or fraction method, is not grounded on mathematical terms and more subjective errors might sneak in. A crosstable can be less orderly in a spreadsheet program and interactions can be overlooked, if the matrix exists out of many animals. Preference in this research went out to the formula method following Henderson et al (1995), because of it's individual component and mathematical grounds.

Dominance and interactions

The total of individual-interactions varies enormously (figure 4). The third dominant bird has a maximum of 228 interactions whereas some very subdominants have less than 10 interactions with 5 interactions as a minimum. More dominant birds interact more (figure 5), they can hold their position longer at the feeding pit. So this puts them in the situation to spend more time interacting. Subdominant birds keep clear of interacting with a more dominant bird, the few interactions of subdominant birds are probably due to avoiding behaviour. Because subdominant birds don't interact much, the most subdominant birds might not have interacted at all. This may have excluded male Jackdaws from our rankorder. Solutions to this problem might be to observe more interactions, use more feedingpits (food satisfaction problem, mentioned in Methods) or observation at natural foraging grounds.

Shifts in rank

Correlation between the two different periods (before and after the breeding season) is also significant (table 2). This supports Röell (1978), he found a relatively stable rank order over several years. So scoring dominance in different periods should give a stable dominance hierarchy. However Röell (1978) also found that temporary rankshifts take place. This is due to pairs, which do not nourish young bothering pairs, which are still nourishing their young. The pairs without young could hold a higher rank, temporary. In our experiment there were also rankshifts observed, which led to no significant correlation between dominance and reproductive parameters after the breeding season (table 6). These results suggest a not totally stable dominance hierarchy present. In our experiment the second period is mentioned as "after the breeding season", but some pairs were still nourishing their young. While other pairs did not have young anymore. Figure 10 shows male Jackdaws, which were still nourishing young and male Jackdaws, which had no young. The mean shift in rank does not differ between pairs with and without young in this period (two sample T-test: mean rankshift for males still nourishing is 0,0909, sem= 2,287, N= 4, for males finished nourishing young is the mean rankshift -0,25, sem= 0,939, N= 11).

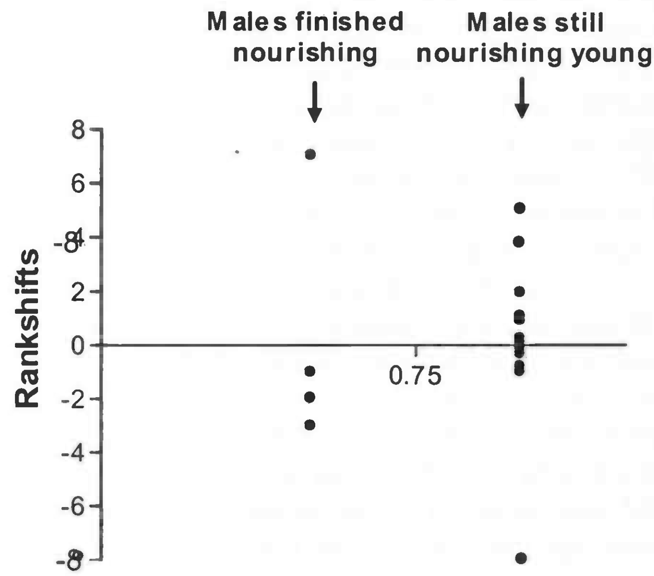


Figure 10. The relation between nourishing and rankshifts. Negative shift: the male becomes more dominant, a positive shift: means the male becomes less dominant. If the males had young from 27/5/1998 to 18/6/1998, the period after the breeding season, they were put in the group that still nourished young. If the males had no young in this period, they finished nourishing.

It is decided from the occuring rankshifts, which probably result in no significant correlation between dominance and reproductive parameters, after the breeding season, not to join both period interaction data sets. The amount of interactions observed in the period before the breeding season is larger, so the dominance hierarchy calculated from these interactions is used.

The temporary rankshifts must be looked at better, because these shifts suggest a more dynamic dominance hierarchy present in the Jackdaw colony. The same individuals and amount of interactions must be scored in the different periods. Recommended is to score interactions before the breeding season, during the breeding season and after the breeding season (when pairs are done nourishing young). However it might be difficult to score the same individuals and obtain the same amount of interactions after the young fledge, because the Jackdaws are not present much, after the young have fledged, which leads to very little interacting going on at the feedingpit.

Factors determining dominance

What makes one male more dominant than another male Jackdaw? The body parameters tarsus length and wing length did not give any correlation with dominance (table 3; figures 5a and 5b). Henderson et al (1995) also found no correlation of tarsuslength and dominance of the Jackdaw (T= 0,08, NS, n= 16). So, having larger paws or wings does not seem to affect a Jackdaw's dominance. Another body parameter, which might correlate with dominance, is the weight of the bird, found in Rooks and crows (*Corvus corone corone* L.) (Eivin Røskaft 1983; H. Richner et al 1989). However it was not possible this year to capture all the male Jackdaws and weigh them, but birds can be captured on their nestboxes or in a cage (*sketches 1 and 2*) and weighed at the time the interactions are scored, in future years.

Henderson et al (1995) found age to correlate with dominance. A male Jackdaw becomes more dominant as he ages. Roëll (1978) found shifts in the rank order because of deaths and every bird ranked below the dead bird rises a place in rank. This gives older birds higher ranks, because of a longer participation in the dominance hierarchy taking rankplaces of dead Jackdaws. Our data however cannot be used to show a relationship between age and dominance (fig 6a). Most Jackdaws in the colony are of unknown age. Minimum ages could be used (figure 6a). Minimum age is given to a bird of unknown age; minimum age depends on the state and situation the bird is in, when we see it the first time. If it has juvenile feathers, it is given the minimum age of 1 year, if the bird breeds in one of the nestboxes for the first time, it is given the minimum age of 2 years. Continues research must be done over more years to get to know real ages of Jackdaws in the colony, for instance known nestlings of past years, and give a conclusive answer about the existence of a correlation between dominance and age of a Jackdaw in our colony.

Might owning a nestbox have something to do with dominance of a bird? Figure 5b shows just two birds without a nestbox. Nothing significant can be said about owning a nestbox and dominance from this figure. Still from figure 5b raised the question, why are not more male Jackdaws, without a nestbox, interacting with birds that do own a nestbox at the feedingpit? Does the colony almost totally exist out of individuals that do own a nestbox? A group missing out of the data set is the group of unringed birds, which have been seen interacting at the feedingpit, thus giving them an unknown place in the dominance hierarchy. They may breed elsewhere close to the colony's nestboxes. The difficulty lies in the not known identities of unringed birds and the difficulty of catching them.

Dominance can also have something to do with the place of the nestbox in the colony. Out of supplement 1 (the distribution of dominance in the colony) can be concluded that there is a strange distribution of participating birds in the dominance hierarchy, in the colony. Most birds that occupy nestboxes on the C- and D-sides of the colony do not interact at the feeding pit, whereas birds of the A- and B-sides do interact at the feeding pit. An explanation would be that the birds of the C- and D-sides have a very subdominant status and might because of their low status not interact with the more dominant birds of the A- and B- side. It may also be the case that the further away the Jackdaw nests, the lower it's dominance as was found in Great tits (Drent 1983). A third explanation would be the existence of a subdivision of the colony, two sub-colonies that both have a territory not to be entered by a member of the other colony. To find out if these males at the C- and D- sides are subdominant or if a distance effect or subcolonys exist, the feeding pit must be moved for example from the A- side to the D- side and it could be moved further away from the colony as well. The place in the dominance hierarchy of the males of the C- and D- sides can also be determined by scoring interactions at their natural forage grounds.

Dominance and reproduction

There were no contrary findings in our experiment for the three different methods of determining a dominance hierarchy. So the contrary findings of Röell (1978) and Henderson et al (1995) are not due to the two different methods used.

From clutchsize to day 20 there is no significant effect of the male's dominance on remaining chicks (table 6). Though looked at the number of chicks at the age of 25 days or fledged young, a significant effect of the male's dominance on the number of the chicks (figure 6) is present. More dominant males have fewer chicks left, at the chick's age of 25 days. More young of subdominant birds fledge, which are probably of better quality too, if looked at chick parameters (weight, tarsus and wing length). Figure 7c shows how the correlation coefficient of dominance and chicks left, rises and gets significant, the older the chicks get. Fewer chicks raised can be the result of lower paternal care due to fights to maintain the pair's social status. Suggesting a trade-off between social status and paternal care (Qvarnström et al, 1998).

Although, the fledging efficiency of dominant males is not significant lower (r= 0,443, P= 0,086, N= 16), there is a trend present. This seems to point towards a selection to be subdominant. Males that reproduced but did not interact in the colony might be the most subdominant males, if we assume that not interacting male Jackdaws are very subdominant (figure 2). Data of male Jackdaws that did not interact, but did reproduce was put in figure 6a and 6c as well as in figure 7. In figure 6c it seems, that this data fits on the line perfectly, however because no interactions were scored of these males, this data was not taken into any statistical calculations. No conclusions can be drawn from this data, it is important for future research to score interactions from this group of male Jackdaws so it becomes clearer where these males, missing out of our dominance data, can be placed in the dominance hierarchy.

Dominance is correlated with age (Henderson et al 1995). This could mean that age is the factor determining the production of fewer young by dominant males. Senescence should than be looked at; however data on age of the Jackdaws is not available, only minimum ages could be given to a number of Jackdaws.

Still, perhaps the few young that grow to maturity are of high quality. Higher quality though does not express itself in body parameters of the chicks, like volume of the eggs and the weight of the chicks at different ages of the chick, wing length and tarsus length (table 5). The more dominant the smaller the offspring. If quality is measured in body parameters, dominance is surely an indicator for low quality chicks. Though there might still be an effect of hormones on the chicks. The little amount of chicks raised by dominants in a lifetime can still be of a better quality due to hormones, which could help them in dominating later in life and thus making it possible to conquer a nestbox and reproduce. Data of hormone levels in chicks is necessary to find a hormone effect present.

Another explanation of fewer young raised by dominant males, might be that there is a choice effect present, lousy females may choose dominant males or vice versa. Röell (1978) found dominant male Jackdaws to behave more aggressive towards their mates. This aggressive behaviour might be induced by behaviour of his female. An additional effect could be a rising of hormone levels, thus making him more dominant. If indeed the female is lousy, this might not only affect her mentally but may also affect her reproduction, thus explaining the fewer young raised. The assumption would be: A lousy female makes her male more dominant indirectly, by irritating behaviour. This however lies within behaviour patterns of the Jackdaws, such failing behaviour by the female is probably difficult to determine in the eyes of the observer. Although dominant males are more aggressive towards their females, the females of dominant males, can benefit from their males social status by foraging longer on food (Röell 1978). If a female is of such low quality that she can nearly survive, let alone reproduce, she would choose a dominant male, so she can at least keep her condition on a suitable level. This could lead to lousy females choosing dominant males. To find if a possible choice effect is present, young Jackdaws must be observed just before pair bonding takes place; because Jackdaws being monogamous birds this is the time in their life to choose a mate.

The findings of dominance and reproduction are in accordance with findings of Röell. (1978), though in contrast to the findings of Henderson et al (1995). Where lies the difference between these two colonies? Why has the dominant bird at the Zoological Laboratory fewer fledged chicks than the subdominant has? Perhaps they can get older at the Zoological Laboratory due to the availability of geesefood. Senescence instead of dominance might than affect reproduction. Older birds are more dominant according to Henderson et al (1995). The influence of senescence might in that case overrule the influence of being dominant. This would explain the difference between the two Jackdaw colonies. Egg volume of females of dominant males is smaller ($r= 0,541$, $P< 0,05$, $N= 16$), implying that senescence could play a role in the quality of eggs females lay. However a maternal effect may also be because of a low quality mother, suggesting, like said above, that low quality females make dominant males, or dominant males end up with low quality females; or aggressive behaviour in females can induce physiological changes, affecting egg production.

Another explanation might be a combination of a trade-off between social status and reproduction and the availability of geesefood. Geesefood might benefit subdominant birds in their condition, which in turn could benefit their reproductivity, whereas the trade-off effect would give a dominant Jackdaw a disadvantage in reproduction, due to putting too much effort in social status.

Nestbox density is a variable, which differs between the colonies of Röell (1978) and Henderson et al (1995). Calculated out of data from Henderson et al (1995), the mean distance between two nestboxes in the colony of Henderson et al (1995) is approximately 23,15 meters, whereas nestboxes at the Zoological Laboratory are about 1 meter apart from the neighboring nestbox. So the effect of having neighbors as close as in our colony might increase fights, time spend fighting could reduce time spend nursing chicks. Also an increase in fights might increase the testosterone level in males and females. To find such an effect of nestbox density, the nestboxes must be placed at particular distances from each other and testosterone levels of the Jackdaws must be measured.

Lay date and reproduction

Dominance might not primarily determine survival of offspring. Lay date has also an effect on the amount of chicks left starting from the age of 20 days (table 6).
Lay date shows a significant negative correlation with clutch size. Birds that lay later in the season have smaller clutches and a significant effect of lay date on number of chicks at day 30/clutchsize (reproductive efficiency). Laydate correlates with a number of reproductive parameters. This raises the question if dominance and lay date are correlated, however there is no correlation between dominance and lay date (table 5).
If the correlation between dominance and chicks at day 30 and fledged chicks left is controlled for by lay date or vice versa than both variables dominance and laydate do not correlate significantly with fledged young. However the P-values show an obvious trend, as was said in the results this suggests a combined effect of dominance and laydate on reproductive parameters.

More data is required to establish which relationship exists between the effects of dominance and lay date on reproduction of the Jackdaw. Perhaps dominance is a consequence of an age effect and such an age effect could again affect the laydate, it may be that older Jackdaws are more dominant and start laying eggs later than younger subdominant ones.

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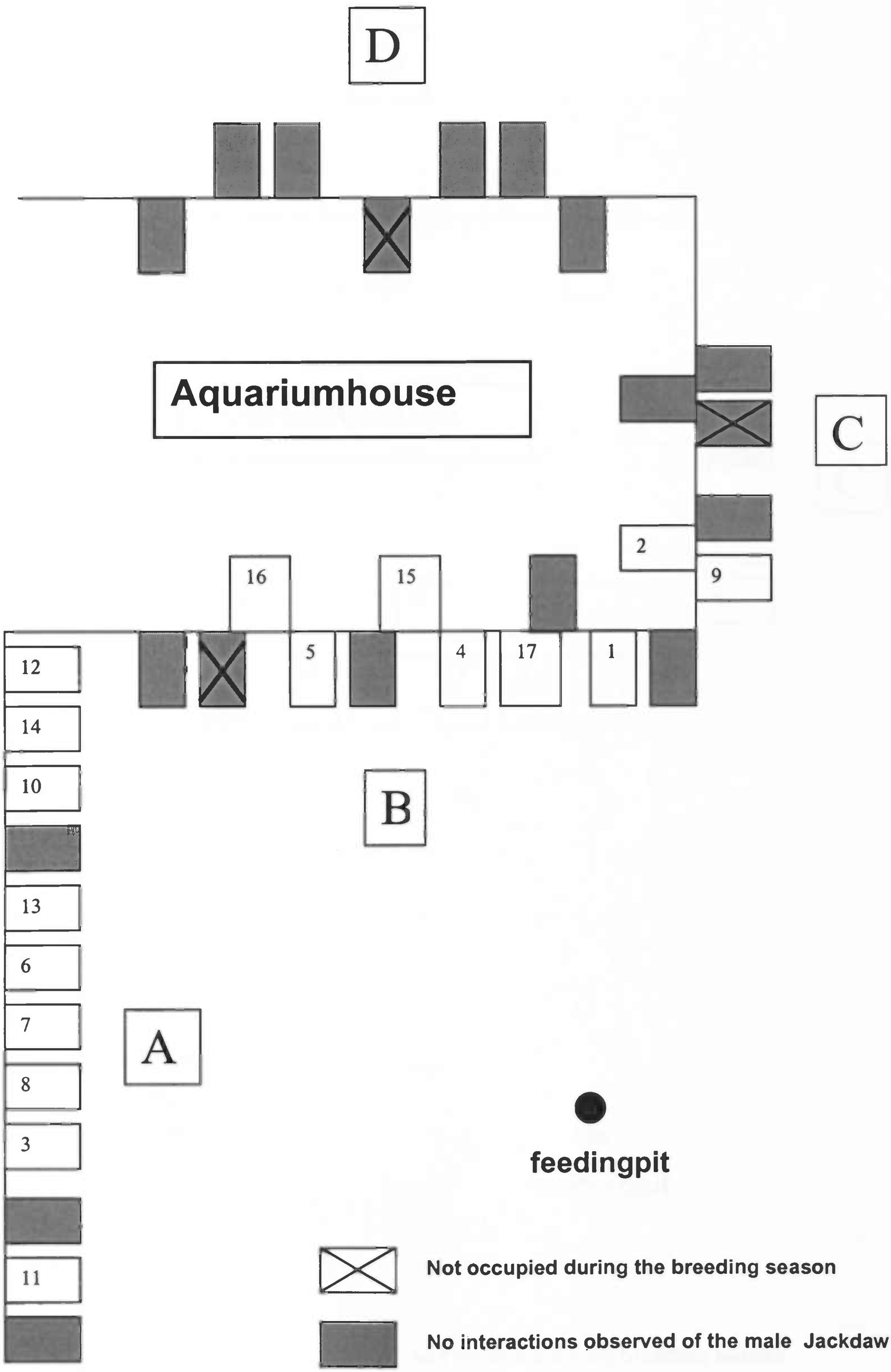
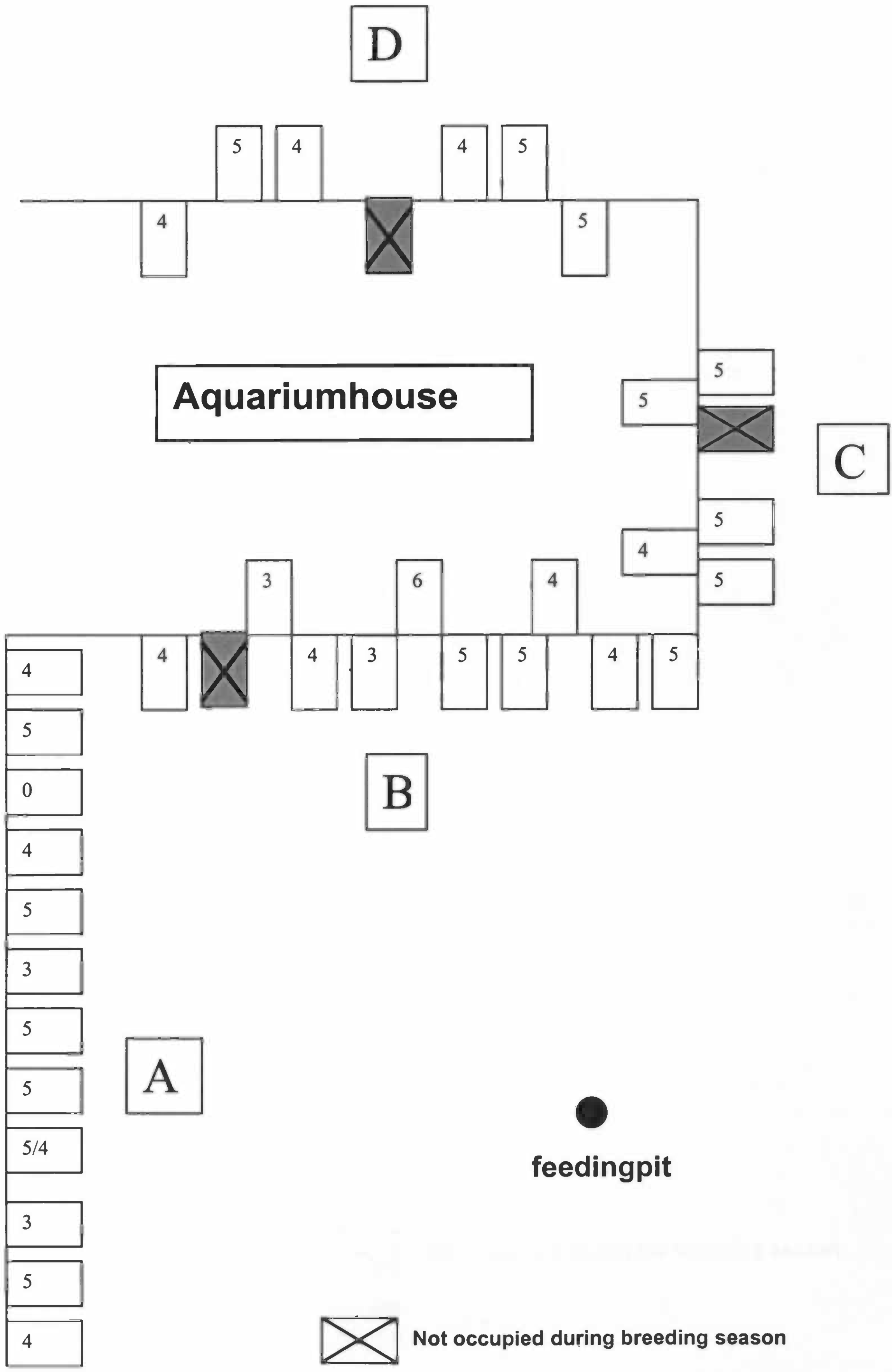
Supplement 1: Place of Henderson's dominance (in nestbox) in the colony



Supplement 2: Clutchsize present in each nestbox in the colony



Supplement 3: Number of chicks day 30/clutchsize (in nestbox) and it's distribution in the colony