Social dominance and reproduction in the Jackdaw

(Corvus monedula)

Zoological Laboratory of the University of Groningen

Martijn Salomons, November 2000

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Introduction

The existence of a social hierarchy has been described in many species and is generally accepted to be present in all bird flocks. This hierarchy manifests itself in individual differences in resource access. The observation of individual flock members having different resource access has led to the introduction of the term 'dominance'. There is a lot of discussion on the meaning of dominance and there are a lot of different definitions. The definition we use is from Drews:

'*Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate.*' (Drews 1993)

Although aggressive interactions will occur more frequently with increasing numbers of individuals present in a group, a lot of animals are still foraging in flocks. Apparently flock feeding has benefits for all members. In birds and other animals, these benefits are mainly thought to be defence against predators and increased feeding efficiency (Pulliam et al. 1984). Within a flock the existence of a dominance hierarchy is thought beneficial because it reduces repetition and/or escalation of fights over resources between two individuals (Maxim 1981).

Jackdaws (*Corvus monedula*) feed in flocks, thus a dominance hierarchy is also present in this species, and has been described in several studies (Henderson et al. 1995; Lorenz 1931; Lorenz 1955; Röell 1978). The dominance structure in jackdaws is linear. This means that one individual is dominant over all other group members, the second bird in rank is only submissive to the first, the third in rank is only submissive to the first two and so on.

The highest ranks in a population of jackdaws are always found occupied by males (Lorenz 1931; Röell 1978). Lorenz showed that females, after pair formation, attain the rank of their mate. Because of this the dominance rank of a pair within a population is almost completely determined by the rank of the male jackdaw (Lorenz 1931).

Figure 1 *Schematic presentation of the linear hierarchy within a flock of Jackdaws (drawing from Lorenz 1955)*

As mentioned above dominance relationships and hierarchies are determined by observations of interactions over a certain resource. However an individual found to be very successful in interactions over for example food-resources, doesn't necessarily have to have a high ranking regarding access to all other resources. It's possible that the amount of fights over food won by an individual is influenced by its degree of hunger, and thus it's motivation. Because of this possibility one has to look at interactions over multiple resources by the same individuals to correctly determine a dominance hierarchy within a population.

In this study a dominance hierarchy within a population of jackdaws is determined by observing interactions over an artificial food source. Earlier study on the same population by Röell showed that the jackdaws that were found to be dominant in interactions over food, also had primary access to available nestboxes and defended more nestboxes during winter (See figure 2) (Röell 1978). Because of these findings one can safely assume the birds that are dominant at the feeding pit, to be birds with an overall high ranking within the population.

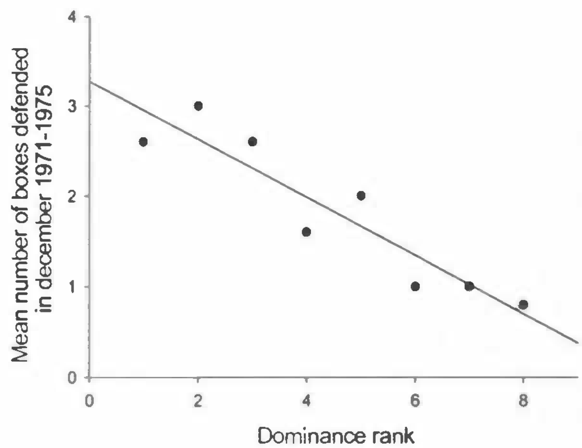

Figure 2 *Relation between dominance rank, determined at a feeding pit, and the number of nestboxes defended in December.*

As said, being able to attain a high rank can be advantageous for an individual. This can be through better access to patches that are rich in food (Slotow et al. 1997) or contain high quality food (Langen et al. 1994). Dominant individuals can also benefit from the possibility to make use of habitats that are either highly suitable for reproducing and/or safe foraging. In Great Tits (*Parus major*) for example Dhondt and Schillemans found birds that could maintain a territory, and keep it free from intruders, had the highest reproductive success (Dhondt et al. 1983). Several studies found dominant Willow Tits (*Parus montanus*) to feed in the upper parts of the canopy and monopolise space near trunks, thus being safer from predators than subordinates which foraged on the lower and outer parts of trees (Ekman et al. 1984; Hogstad 1988). Higher survival rates are also found for high ranked animals. Dominant White-throated Sparrows (*Zonotrichia albicollis*), for example, are estimated to survive 50% longer than subordinates because of their higher fatness levels (Piper et al. 1990). Finally another advantage of being dominant could lie in a higher mating success (Brodsky et al. 1988; Møller 1987).

The benefits of dominance can be diminished however, for example by more frequent involvement in aggressive encounters (Hogstad 1987). In Great Tits, dominant birds were shown to fight each other more frequently than subordinates do (Järvi et al. 1984). The higher number of fights in dominants might entail a higher energy demand and an increased risk of injuries. Elevated levels of Testosterone, associated with aggression (Beletsky et al. 1990; Wingfield et al. 1987), were also shown to have a negative effect on parental effort, decreasing reproductive success (Silverin 1980). In jackdaws reproductive success of the highest ranked birds was found to be much lower than that of birds lower in rank. This difference in reproductive success was visible in the total number of fledglings, being much lower in dominant pairs, as well as in the quality of the young produced as the young produced by dominant pairs were much lower in weight and size (Röell 1978).

The finding of a lower reproductive success in birds with a high rank is not a characteristic of the Jackdaw. This was shown in a study on a population of jackdaws in Leicestershire, England. Within this population a higher reproductive success was found for birds with the highest rank (Henderson et al. 1995), thus showing an effect of dominance on reproduction just opposite to the findings by Röell.

This study is a response to the contradictory finds by Henderson and Röell. It aims on finding possible explanations for the lower reproductive success in high ranked birds found in the population in Haren, and relate this to the findings in Leicestershire. To achieve this goal three major questions need to be answered: a) Is the reproductive success for birds with a high rank within the population in Haren lower than that of birds lower in rank? b) If the reproductive output in high ranked jackdaws is reduced, then what is the cause of this? and c) What differences between the population in Leicestershire and the population in Haren could account for the contradictory findings in these two populations?

Methods

Study area

All observations of jackdaws took place in the colony situated at the Zoological Laboratory in Haren. It consists of 36 nestboxes, of which 28 are attached to the outside wall of the building, and 8 boxes are located inside the building placed behind an opening in the wall. The space between two separate boxes is approximately 2 metres. These boxes have been used by jackdaws for breeding since 1965 (Röell 1978).

Large quantities of food are available in the outdoor pens of captive animals at the Zoological Laboratory; therefore all year round jackdaws can be seen foraging there. Not only birds from the colony at the Laboratory, but also jackdaws from other parts of Haren foraged here, resulting in a lot of unringed birds especially at the end of the breeding season (Röell 1978).

The jackdaw colony

Since 1996, after a period of less active research on the jackdaw population, great effort is put into colour-ringing the birds for individual recognition. The number of adult jackdaws at the study site during the breeding season fluctuates between 75 and 150.

Jackdaws are socially monogamous birds. This means that once a pair has formed and lasted for more than six months, partners usually stay together until one of them dies (Röell 1978). They breed in existing holes and territorial defence is limited to the nesting site. The jackdaw is a sedentary species, and can be found breeding in the same box for multiple years.

Some pairs defend their nesthole not only during the breeding season, but all year around. These are called resident pairs (Röell 1978). In some cases multiple nestholes are defended by a single pair, Röell found the number of nestboxes defended by a pair to correlate with its rank. During the breeding season (April – June) however each pair only defended one nestbox (Röell 1978).

Both parents are necessary for successfully defending the nesting site and building of the nest and the defending and provisioning of the offspring, incubation however is only carried out by the female. During incubation the female is fed by her partner. Usually when one parent dies, the other will have to give up the nestbox and the clutch (if any) will be lost (Röell 1978).

Egg laying starts in the middle of April, a clutch usually consists of 3-6 eggs. Incubation takes approximately 18 days, and after hatching the chicks stay in the nest for another 30 days. After fledging the young stay with the parents for about a month in which they gradually become less dependent.

Capturing of the jackdaws

In order to correctly study the colony it was necessary to catch the jackdaws that hadn't been ringed in previous years. Loss of rings also turned out to be a problem, in these cases the original code could be restored by means of a numbered aluminium or steel ring (present in all partially ringed birds found).

Attempts to capture unringed and partially ringed birds were made from the middle of March until the finding of the first egg on the 12th of April. This was done either by means of a cage with a trapdoor in which food was offered, or in their nestboxes. Especially the last method turned out to be an easy way to catch the desired bird. All the birds that were caught in their nestboxes were seen back at the same box within hours after release.

After they were captured the jackdaws were transported in a wooden box to a room in the Laboratory where ringing took place. Blood samples were taken from newly caught birds for DNA and sexing, and the weight as well as the wing- and tarsuslength of all the captured animals were determined. All pairs were caught five days after hatching of their first egg and a bloodsample was taken for future hormonal assay.

Ringcode

All jackdaws caught between 1996 and 1999 were given an individual ringcode consisting of three plastic rings in different colours and one ring of either aluminium or stainless steel. On each leg two rings were placed. The following colours were used: red (R), yellow (Y), mint (M), orange (O), green (G), light blue (B-) and dark blue (B+).

The individual codes are noted down by means of the abbreviations for the colours and always first the rings on the left leg and then the rings on the right leg.

Birds caught in 2000 were given only three rings: on one leg a small colour ring and a stainless steel ring were placed and on the other leg a large yellow ring with two black bands was used. The bands on the yellow ring were either thin or thick, resulting in four different options:

a) Both bands are thin (code YZ11)
b) Both bands are thick (code YZ22)
c) The upper band is thin and the lower band is thick (code YZ12)
d) The upper band is thick and the lower band is thin (code YZ21)

The hierarchy

To determine the social hierarchy within the colony, the aggressive interactions between individual jackdaws were recorded during March and the first half of April. Observations were stopped with the finding of the first egg in the colony, in order to avoid individual differences in motivation. To induce conflicts, food was offered in small pits (10 cm. in diameter). At these feeding pits only one jackdaw, or a jackdaw pair, could eat at a time. These feeding pits were only refilled during the observation period.

Four types of interaction were distinguished:

1. *Supplanting* - a jackdaw, eating at the feeding pit, flies off in reaction to another jackdaw landing at the pit. The bird flying away is termed the loser in this conflict,
2. *Threat* - a jackdaw is chased away by another jackdaw by obvious threat postures, but no physical contact,
3. *Fight* - the opponents make physical contact, the bird flying off is termed the loser in this conflict,
4. *Waiting* - usually when a jackdaw is eating, some jackdaws are standing around showing obvious interest in the food and are waiting for the eating bird to leave. The bird eating at the feeding pit is said to be dominant over the birds waiting.

The rank of a jackdaw was then calculated on the basis of the outcome of the interactions, mentioned above, in which it participated. The outcomes of all four types of interaction were treated equally. For this calculation a formula was used based on both the proportion of interactions won and the proportion of individual birds supplanted by the focal bird (Henderson et al. 1995). The formula is:

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

Only interactions in which both participants were ringed were used in the formula and an individual jackdaw had to participate in at least four interactions before a rank coefficient was calculated. Based on the calculated rank coefficient a rank number is assigned to each bird. The bird with the highest rank coefficient, and therefore the highest bird in rank, is assigned the lowest rank number. When using data from both years in the analysis, the dominance rank is divided by the total number of birds present in the hierarchy of the specific year. The bird with the highest rank has the rank number closest to 0, and 1 represents the bird with the lowest rank.

Social dominance and biometric characteristics

All breeding jackdaws were caught at the fifth day after the first egg in their brood had hatched. All birds were weighed (± 1.0 g). Both left and right tarsus length was measured by folding the birds foot in towards the tarsus and recording the length between the notch behind the intertarsal joint and the bend of the foot (± 0.1 mm) (Svensson 1975). Wing length was determined by measuring the flattened maximum cord (± 0.5 mm) (Svensson 1975).

Social dominance and reproduction

Of all jackdaws breeding at the Zoological Laboratory the reproductive parameters were collected. This was done by checking all nestboxes daily, starting on the 7th of April. The laydate was the day when the first egg was laid in the clutch; this day was called day 1.

All eggs in a clutch were exchanged for Quail eggs 1-2 days before the estimated hatching date and then put in an incubator. Quail and jackdaw eggs are very alike, and the female jackdaws didn't seem to notice the exchange as they continued incubating. Before they were put in the incubator, the length and width of the eggs were measured. Eggvolume was estimated from Coulson's formula: $V = \pi A^2 LK/6$. Where A is width, L is length and K is a constant. A value of 0.00096 was used for K, for width and length in mm and volume in cm^3 (Soler 1988).

After hatching the chicks were weighed and a blood sample, for sexing and future DNA-analysis, was taken by clipping a toenail. The clipping of a toenail doesn't interfere with its growth. The clipped nail is identifiable later on by a blunt tip; therefore the clipping of a specific toenail or combination of two nails was at the same time used as an identification aid. After hatching the chicks were returned to their original nests as soon as possible, from which an equal number of quail eggs was then removed.

The survival of the chicks in the nest was checked every 5 days. At day 10, 20 and 30 the chicks were also weighed and tarsus- and winglength (day 20 and day 30) were measured to monitor growth. All bodyparameters of the chicks were corrected for sex before they were used in the analysis. At day 30, shortly before fledging, the remaining chicks were ringed.

Since jackdaws are strictly monogamous and extra-pair fertilisation is not found in this species (Henderson et al. 2000; Liebers et al. 1999), the total number of fledglings is considered a good measure of the total reproductive success.

Social dominance and parental care

In jackdaws both parents contribute in provisioning the young in the nest. Especially during the early nesting stages, when the female is incubating the eggs or when the chicks are very young, however food acquisition and delivery is mainly taken care of by the male. Henderson and Hart found male provisioning rate to be a strong predictor of fledging success in the jackdaw (Henderson et al. 1993).

To find out if there were differences in parental care between jackdaw pairs, and see if these differences were related to reproductive success and/or social dominance, the jackdaws were observed when their chicks were respectively 6 and 15 days old (day 6 and day 15). During these observations video recordings were made of the nestopening and all visits of the parents were noted. The duration of every observation was 90 minutes, and all observations took place between 9:30AM. and 12:30AM. The following parameters were noted for all observations:

1. Total time spent in or at the nestbox by the female
2. Number of times the female left the nestbox
3. Average time spent at the nestbox per visit by the female
4. Number of times the male entered the nestbox
5. Total time the male spent away from the nestbox
6. The average time between two feeding visits by the male

There are two major problems in observing parental care in the jackdaw. The first is caused by the fact that jackdaws are crop-feeders, this makes it impossible to determine the amount and composition of the food brought to the nestbox by the parents. The second problem is that the feeding of the young takes place inside the nestbox. Since all recordings were made outside the nestbox, there was no way of knowing whether or not the food brought to the nest was actually fed to the young.

Close observation of the video recordings made it possible to distinguish between a full crop and an empty one and every observation of one of the parents entering the nest with a full crop was noted as a feeding visit by that parent.

To be able to easily distinguish between the male and female parent during the observations, all females were marked. This marking was done by dyeing the tip of the tail-feathers with white paint, during the capture at day 5.

Statistics

The relationships between dominance rank and reproductive parameters, for the data from 1998 and 2000, were analyzed using the Spearman's Rank correlation coefficient. In this analysis each individual nest was treated as an independent observation. This was done by use of the statistical program SPSS (version 9.0).

For a combined analysis of the two years, the program MlwiN (version 1.10) was used. With this program it was possible to use a 'repeated measures, hierarchical linear model' where the possibility of an individual jackdaw breeding in both years was accounted for in the analysis. The significance of the effect of the different variables was assessed by calculating the difference in deviance (2*log-likelihood) between models including and excluding those variables, and consider it as being tested as a chi-squared statistic with one degree of freedom.

Results

In some cases it was possible to use data from a study in 1998, on the same population of jackdaws, in the analysis. If so, both the separate results from the two years and the combined results are presented.

Social dominance

To see if the dominance level of an individual jackdaw at a feeding pit is influenced by the location of this feeding pit, two separate feeding pits were used to determine the dominance rank. The space between these feeding pits was approximately 30 metres. At each pit interactions between jackdaws were observed and a dominance value for each bird was calculated. Fig. 3a shows a strong correlation between the rank of a jackdaw at feeding pit 1 and its rank at the second feeding pit (Spearman's rank correlation $r_s=0.877$, $P<0.0001$, $N=14$), indicating that the rank of a foraging jackdaw is not site-dependent.

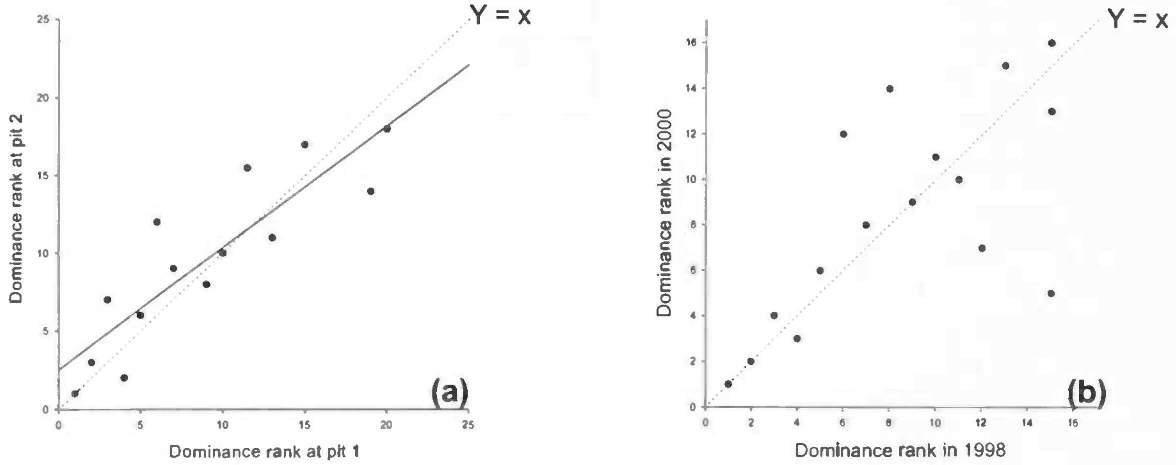

Figure 3 *Relation between (a) dominance rank measured at two distant feeding pits (r_s = 0.877, $P<0.0001$, $N=14$) and (b) dominance rank in 1998 and in 2000.*

The hierarchy within the jackdaw colony in Haren appears to be stable over multiple years. Especially the higher ranked birds were able to maintain their rank from 1998 until 2000. Shifts in rank between 1998 and 2000 occur largely in the lower ranges of the hierarchy (See figure 3b and appendix 1).

Social dominance and observed interactions

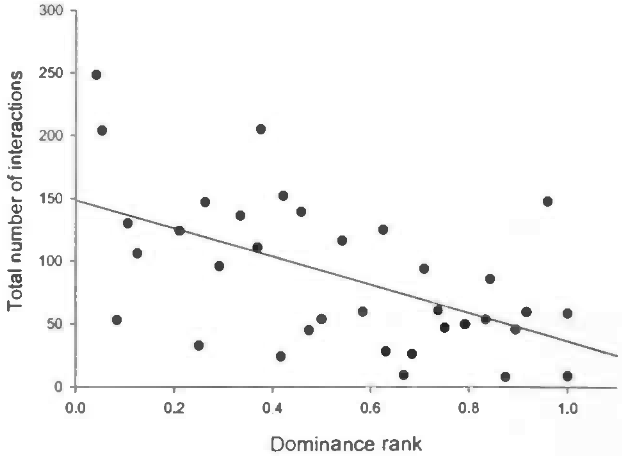

Figure 4 *The Relation between dominance rank and the total number of interactions observed at a feeding pit. (Dev. change =12.404, df=1, P<0.001, N=35)*

Data from 1998 and 2000 show a high correlation between the dominance rank of a jackdaw and the total number of aggressive interactions observed at a feeding pit in which it participated (See figure 4). As a result dominant male jackdaws and their partners will spend more time in competitive situations than subdominants.

Social dominance and biometric characteristics

No correlation was found between the dominance rank of the male jackdaws and the length of their wings and tarsi or bodyweight (See table 1 and figure 5).

Table 1 *Correlation between dominance rank and male body parameters*

Spearman's Rank correlation (2-tailed)		Dominance rank
Winglength	Corr.coeff.	.004
	Sig.	.989
Tarsuslength	Corr.coeff.	-.219
	Sig.	.369
Weight	Corr.coeff.	-.153
	Sig.	.520

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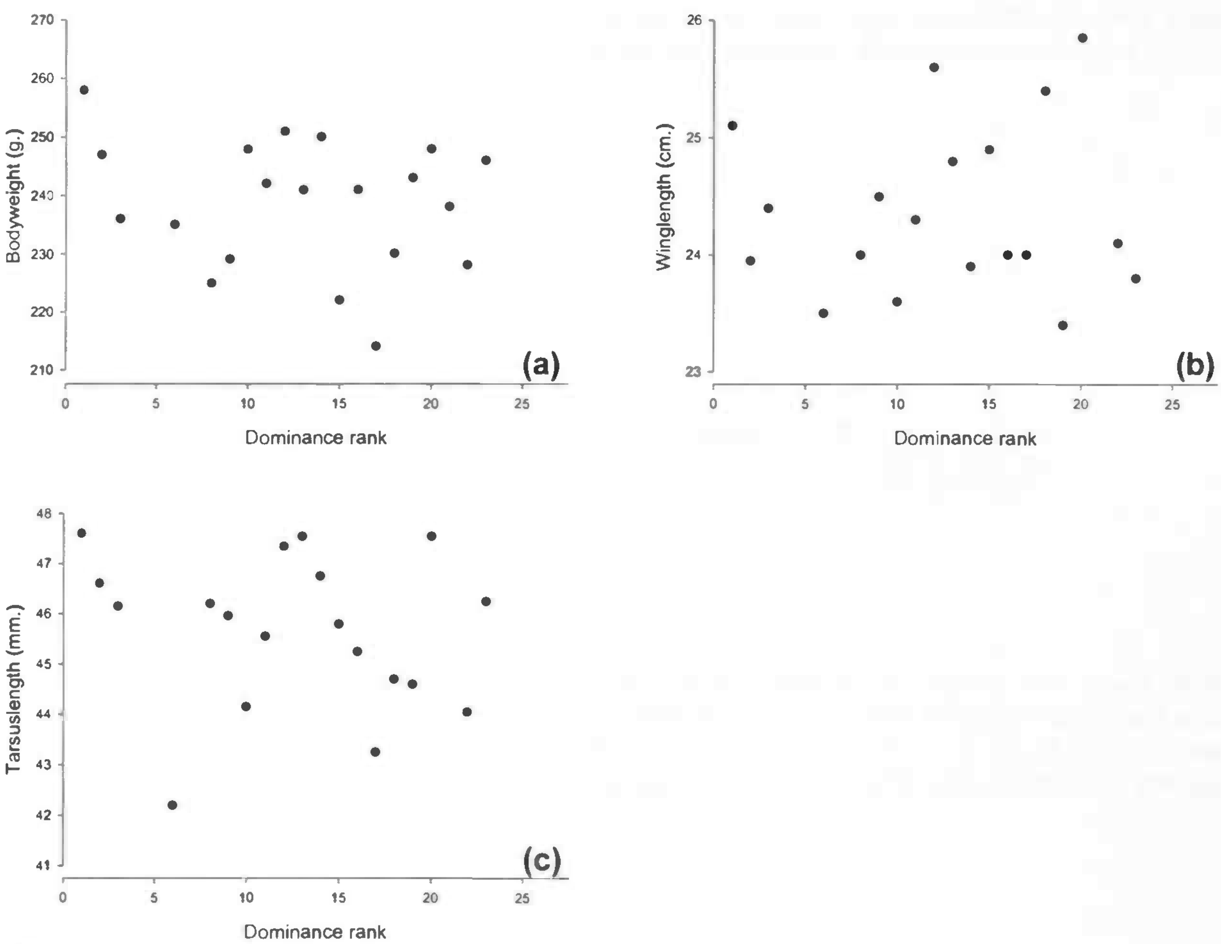

Figure 5 *Dominance rank in relation to (a) bodyweight, (b) winglength and (c) tarsuslength of a male jackdaw*

Social dominance and age

Our data show no relation between dominance rank and age (See figure 6). The age of most of the birds however is not precisely known and only an estimation of minimum age is used, a conclusion about rank and age is therefore not yet possible.

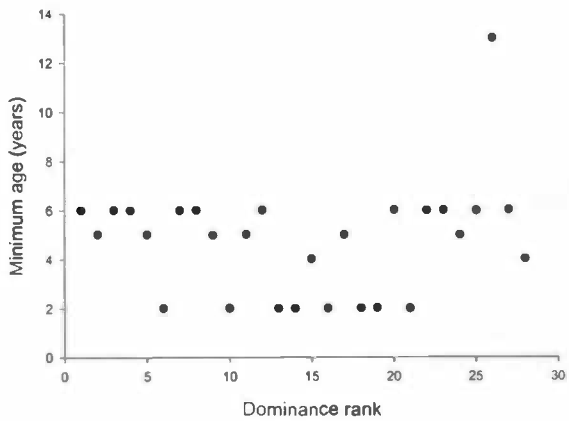

Figure 6 *The relation between dominance rank and minimum age*

Social dominance and nestbox occupation

An effect of dominance on nestbox-occupation is also not shown by our data (See figure 7). Despite the fact that the total number of jackdaws visiting the colony site, during and before the breeding season, outnumbered the available nestboxes, not all boxes were used for breeding. There is no information available on the possibility that the five jackdaws, in the graph, without a nestbox are breeding elsewhere in Haren.

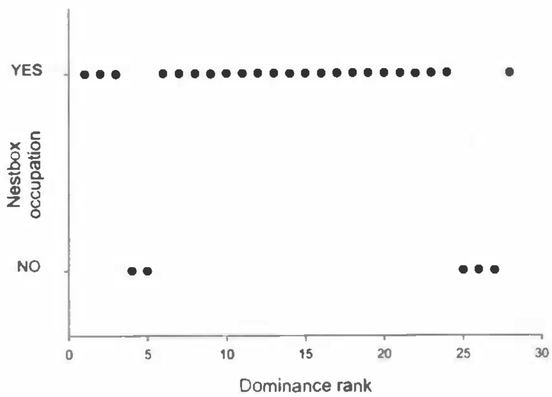

Figure 7 *The relation between dominance rank and nestbox occupation*

Social dominance and survival

No relation is found between dominance rank and return to the colony two years later (See figure 8). This suggests that there are no differences in survival between dominant and subdominant birds. Data from 1998 and 2000 show an annual survival of about 82,5% (See appendix 2). This corresponds with the findings of Röell in 1978 who found an annual survival of 80% for this colony (Röell 1978).

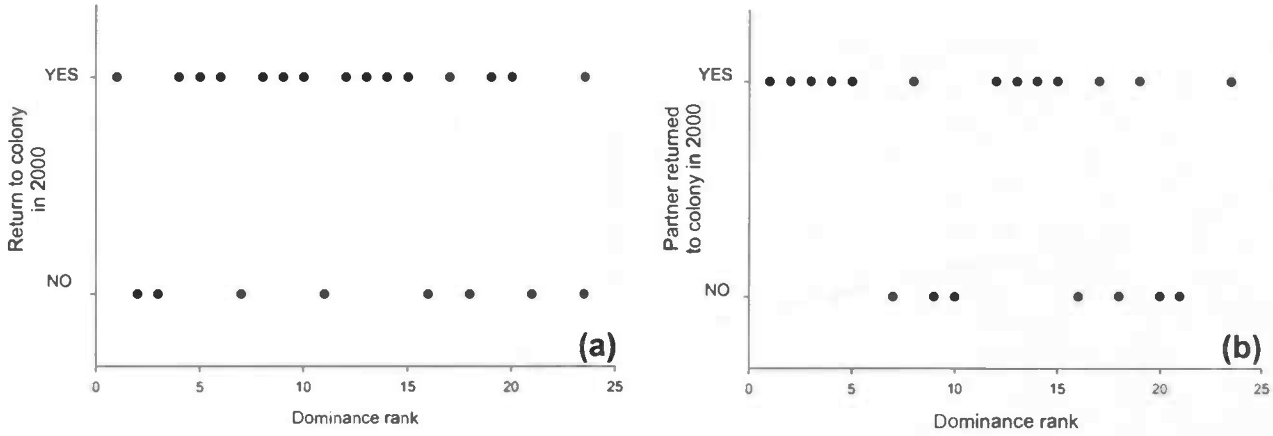

Figure 8 *The relation between dominance rank of a male jackdaw in 1998 and (a) his return to the colony in 2000 and (b) the return of his partner in 2000.*

Reproduction

- Social dominance and quantity of offspring

Table 2 *Correlation between dominance rank and number of chicks*

	Dominance rank				
	Spearman's Rank Correlation (2-tailed)			Repeated Measures HLM.	
		1998	2000		1998/2000
Clutchsize	Corr.coeff.	.227	.130	Change in deviance	1.611
	Sig.	.380	.576	Sig.	.204
Number of chicks at day 5	Corr.coeff.	.119	-.301	Change in deviance	.090
	Sig.	.650	.185	Sig.	.764
Number of chicks at day 10	Corr.coeff.	.033	-.125	Change in deviance	.008
	Sig.	.900	.589	Sig.	.929
Number of chicks at day 15	Corr.coeff.	.123	-.268	Change in deviance	.005
	Sig.	.637	.240	Sig.	.944
Number of chicks at day 20	Corr.coeff.	.368	-.222	Change in deviance	.551
	Sig.	.146	.334	Sig.	.458
Number of chicks at day 25	Corr.coeff.	.486	-.118	Change in deviance	1.890
	Sig.	.048 (*)	.612	Sig.	.169
Number of chicks at day 30	Corr.coeff.	.447	-.063	Change in deviance	2.263
	Sig.	.072	.786	Sig.	.133
Number of chicks Fledged	Corr.coeff.	.531	.111	Change in deviance	4.950
	Sig.	.028 (*)	.632	Sig.	.026 (*)

Note: *(*) = Sign. <0.05 / (**) = Sign. <0.01 / (***) = Sign. <0.001*

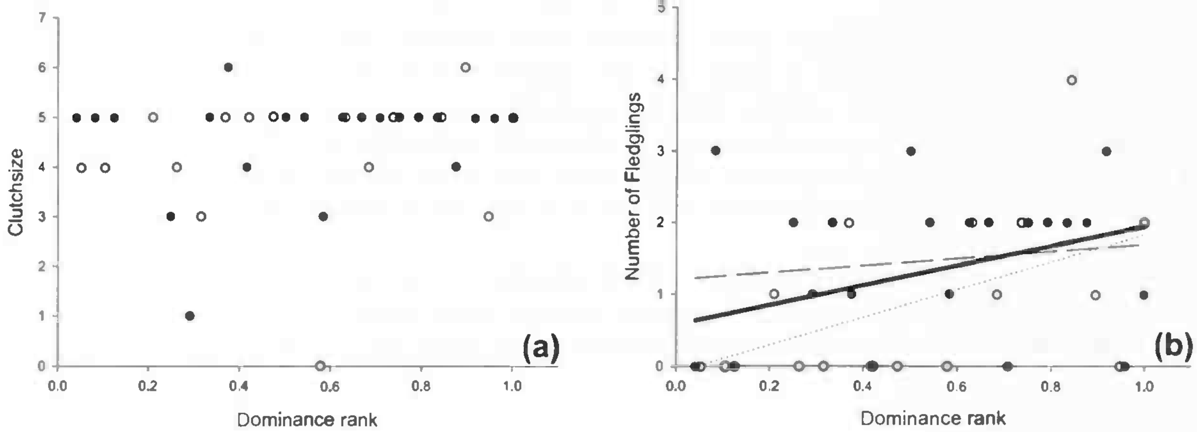

Figure 9 *Relation between dominance rank and (a) clutchsize and (b) number of chicks fledged. Closed symbols represent data from 1998; open symbols represent data from 2000. Dotted line represents correlation for data from 1998, dashed line for data from 2000 and bold line for both years combined.*

In contradiction to the findings in 1998, this year no effects of dominance rank on reproductive success, measured in number of chicks fledged, were found (See table 2). Analysis of the data from the two years combined did show a significant correlation between dominance rank and number of fledglings (See table 2 and figure 9b). Both in 1998 and in 2000 no effect of dominance rank on clutchsize was found (See table 2 and figure 9a).

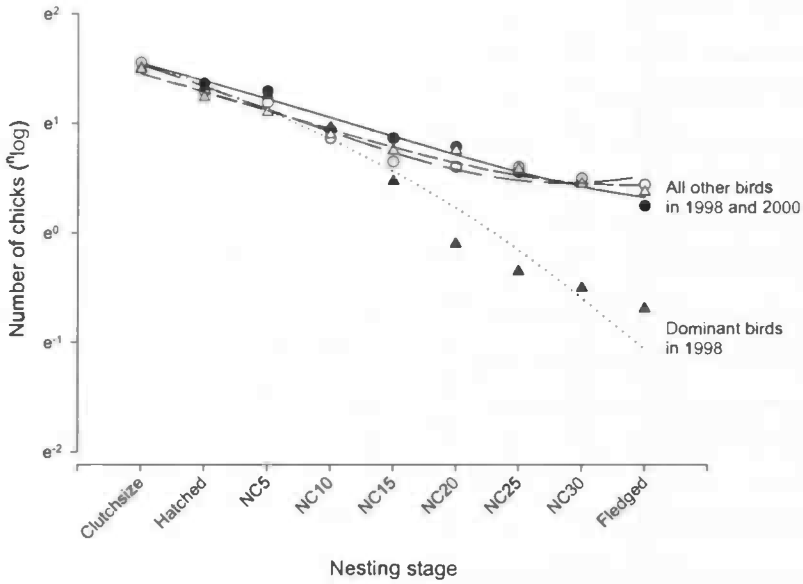

Figure 10 *Relation between nesting stage and number of chicks per nest. Closed symbols represent data from 1998; open symbols represent data from 2000.*

The rate of mortality of chicks in the nest was constant during the entire nesting stage and equal for the subdominant birds in 1998 and all birds in 2000. A high mortality of chicks was recorded in 1998 for the most dominant birds between day 5 and day 20 (See figure 10). Mortality rate, between laying and hatching and after hatching every five days, is about 15%. This value is also found in the nests in 1998 of the most dominant birds except between day 10 and day 20 where mortality was 40 – 45 %.

- Social dominance and quality of offspring

Not only do high ranked jackdaw pairs produce fewer fledglings compared to pairs that are lower in rank, the chicks that do fledge are also lower in bodyweight and size (see table 3). Apparently chicks of dominant jackdaws, in this colony, are of less quality. With an exception at day 10, this difference in weight and size between chicks from dominant pairs and chicks from lower ranked pairs was found on all the days the young were weighed and measured and is still found at day 30, 1 to 2 days before fledging (See table 3 and figure 11c).

The effect of dominance rank is already visible in the eggs, with the eggs laid by female partners of high ranked males being smaller compared to eggs from females lower in rank. And the young hatching from eggs of dominant pairs are also already smaller (See table 3 and figure 11a/b).

Table 3 *Correlation between dominance rank and eggvolume and chick-bodyparameters*

	Dominance rank				
	Spearman's Rank correlation (2-tailed)			Repeated Measures HLM.	
		1998	2000		1998/2000
Eggvolume	Corr.coeff.	.374	.555	Change in deviance	14.534
	Sig.	.209	.009 (**)	Sig.	<.001 (***)
Avg. hatchweight	Corr.coeff.	.654	.351	Change in deviance	12.837
	Sig.	.015 (*)	.119	Sig.	<.001 (***)
Avg. chickweight at day 10	Corr.coeff.	.527	-.044	Change in deviance	.505
	Sig.	.096	.855	Sig.	.477
Avg. tarsuslength of chicks at day 10	Corr.coeff.	-	-.144	Change in deviance	-
	Sig.	-	.544	Sig.	-
Avg. chickweight at day 20	Corr.coeff.	.782	.493	Change in deviance	11.346
	Sig.	.008 (**)	.032 (*)	Sig.	<.001 (***)
Avg. tarsuslength of chicks at day 20	Corr.coeff.	.636	.391	Change in deviance	6.980
	Sig.	.048 (*)	.097	Sig.	.008 (**)
Avg. winglength of chicks at day 20	Corr.coeff.	.758	.291	Change in deviance	7.259
	Sig.	.011 (*)	.226	Sig.	.007 (**)
Avg. chickweight at day 30	Corr.coeff.	.536	.604	Change in deviance	15.464
	Sig.	.215	.008 (**)	Sig.	<.001 (***)
Avg. tarsuslength of chicks at day 30	Corr.coeff.	.393	.441	Change in deviance	6.615
	Sig.	.383	.067	Sig.	.010 (*)
Avg. winglength of chicks at day 30	Corr.coeff.	.571	.350	Change in deviance	8.438
	Sig.	.180	.155	Sig.	.004 (***)

Note: (*) = Sign. <0.05 / (**) = Sign. <0.01 / (***) = Sign. <0.001

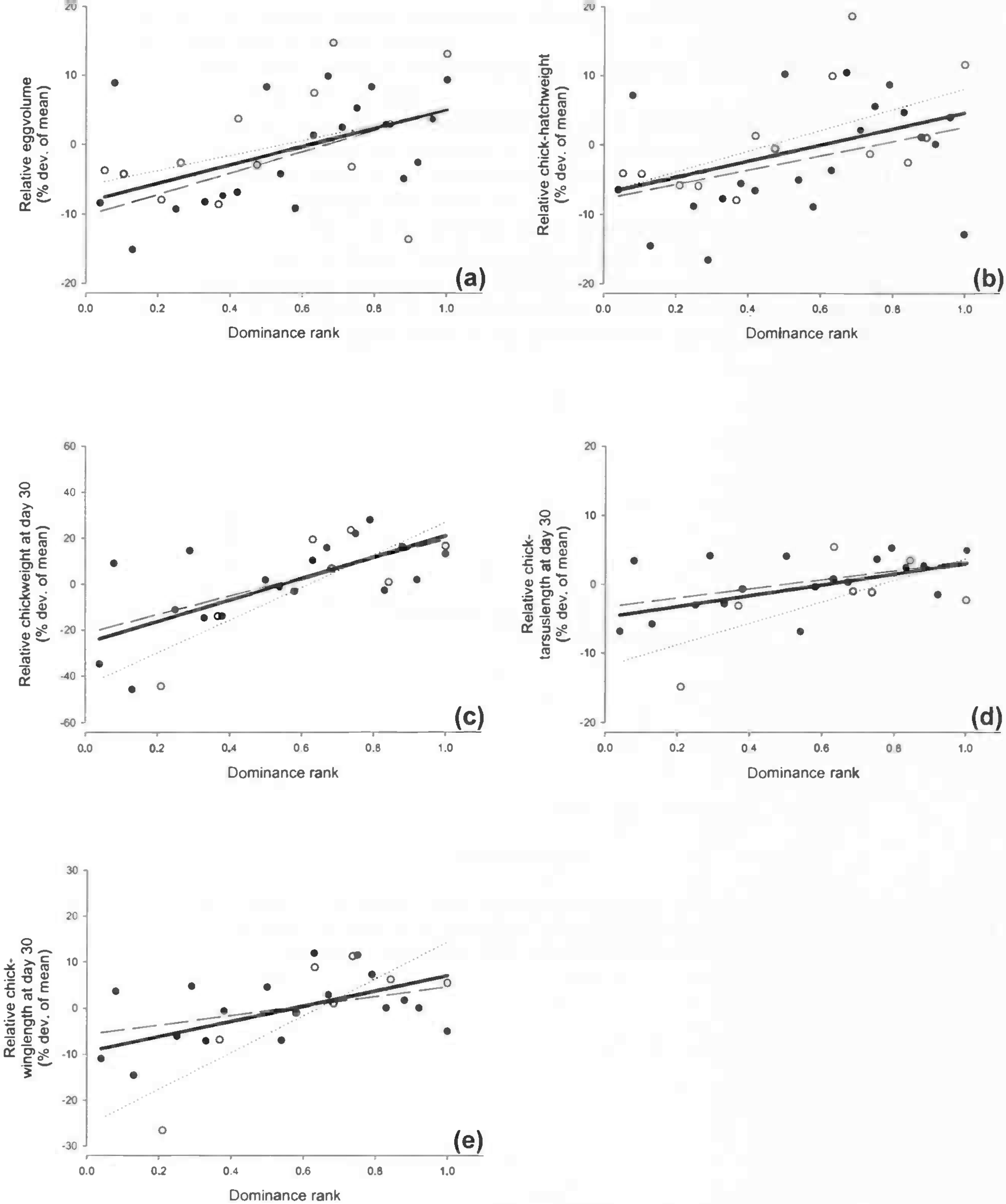

Figure 11 *Dominance rank in relation to (a) eggvolume and (b) chick-hatchweight and (c) bodyweight, (d) winglength and (e) tarsuslength of the living chicks in the nest at day 30. Closed symbols represent data from 1998; open symbols represent data from 2000. Dotted line represents correlation for data from 1998, dashed line for data from 2000 and bold line for both years combined.*

Social dominance and laydate

Figure 14 shows the relation between dominance rank and laydate. The effect of dominance rank on laydate is not significant, although a trend towards earlier laying in the lower ranked jackdaws is clearly present.

Because reproductive success can be strongly affected by laydate (Kamiñski 1989), the effect of laydate is tested for our data.

Laydate in 1998 appeared to have a greater influence on reproductive success compared to 2000. Combined data show an increase in the correlation coefficient between number of chicks in the nest and laydate in the later nesting-stages, with a significant effect of laydate on the total number of fledglings (See table 4).

To see whether the effect of dominance rank and laydate on reproductive success is explained by one or both of these variables, an analysis is done where both variables are controlled for each other. As was to be expected from the results in table 4, chicksize on day 20 and day 10 was only explained by the dominance rank of the parents. However in case of the total number of chicks fledged, none of the two variables can exclude the influence of the other (See table 5).

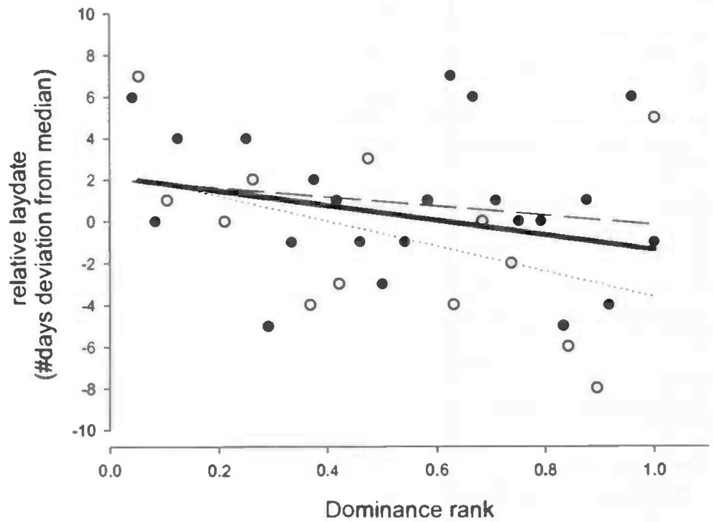

Figure 14 *Relation between dominance rank and laydate (change in deviance=2.601 df=1 sign.=.107). Closed symbols represent data from 1998; open symbols represent data from 2000. Dotted line represents correlation for data from 1998, dashed line for data from 2000 and bold line for both years combined.*

Table 4 *Correlation between laydate and reproductive parameters*

		Laydate			
	Spearman's Rank correlation (2-tailed)			Repeated Measures HLM.	
		1998	2000		1998/2000
Eggvolume	Corr.coeff.	.184	.022	Change in deviance	.365
	Sig.	.426	.924	Sig.	.546
Avg. hatchweight	Corr.coeff.	.025	-.027	Change in deviance	.034
	Sig.	.915	.905	Sig.	.854
Avg. chickweight at day 10	Corr.coeff.	.290	-.547	Change in deviance	.934
	Sig.	.228	.013 (*)	Sig.	.334
Avg. chickweight at day 20	Corr.coeff.	-.408	-.041	Change in deviance	.638
	Sig.	.104	.868	Sig.	.424
Avg. tarsuslength of chicks at day 20	Corr.coeff.	-.401	-.354	Change in deviance	2.648
	Sig.	.111	.137	Sig.	.103
Avg. winglength of chicks at day 20	Corr.coeff.	-.379	-.264	Change in deviance	2.406
	Sig.	.133	.276	Sig.	.121
Avg. chickweight at day 30	Corr.coeff.	-.154	-.298	Change in deviance	.941
	Sig.	.600	.230	Sig.	.332
Avg. tarsuslength of chicks at day 30	Corr.coeff.	-.421	-.418	Change in deviance	2.888
	Sig.	.134	.084	Sig.	.089
Avg. winglength of chicks at day 30	Corr.coeff.	-.282	-.143	Change in deviance	.046
	Sig.	.328	.571	Sig.	.497
Clutchsize	Corr.coeff.	-.519	.126	Change in deviance	.135
	Sig.	.016 (*)	.577	Sig.	.713
Number of chicks at day 5	Corr.coeff.	-.143	.208	Change in deviance	.430
	Sig.	.537	.353	Sig.	.512
Number of chicks at day 10	Corr.coeff.	-.128	.022	Change in deviance	.016
	Sig.	.581	.922	Sig.	.899
Number of chicks at day 15	Corr.coeff.	-.036	-.173	Change in deviance	.068
	Sig.	.876	.440	Sig.	.794
Number of chicks at day 20	Corr.coeff.	-.338	-.215	Change in deviance	1.494
	Sig.	.134	.337	Sig.	.222
Number of chicks at day 25	Corr.coeff.	-.388	-.197	Change in deviance	2.342
	Sig.	.082	.379	Sig.	.126
Number of chicks at day 30	Corr.coeff.	-.409	-.249	Change in deviance	3.470
	Sig.	.065	.265	Sig.	.062
Number of fledglings	Corr.coeff.	-.372	-.351	Change in deviance	5.609
	Sig.	.097	.110	Sig.	.018 (*)

Note: *(*) = Sign. <0.05*

Table 5 *Analysis of variables possibly affecting reproductive success.*

		Change in Deviance	df	*P*
Number of fledglings	Null model	105.324		
	Final model	96.425		
	Dominance rank	+ 3.131	+ 1	.077
	Laydate	+ 3.790	+ 1	.052
	Rejected terms			
	Clutchsize	- 0.059	- 1	.808
Average Chickweight at day 10	Null model	287.878		
	Final model	-		
	Rejected terms			
	Dominance rank	- 0.505	- 1	.477
	Laydate	- 0.934	- 1	.334
	Clutchsize	- 1.301	- 1	.254
Average Chickweight at day 20	Null model	256.041		
	Final model	244.461		
	Dominance rank	+ 10.942	+ 1	.001
	Rejected terms			
	Laydate	- 0.234	- 1	.629
	Clutchsize	- 0.025	- 1	.874
Average Chickweight at day 30	Null model	219.722		
	Final model	204.183		
	Dominance rank	+ 14.598	+ 1	<.001
	Rejected terms			
	Laydate	- 0.075	- 1	.784
	Clutchsize	- 2.580	- 1	.108

Note: *Null model includes the constant only. Final model includes all significant parameters. Changes in deviance and df indicate the changes when parameters are dropped from the final model one at the time (or added to the final model for rejected terms). The changes in deviance are* χ^2 *distributed (Verhulst et al. 1997).*

Social dominance and female quality

Comparison of different body parameters of the female jackdaws showed a relation between these parameters and the dominance rank of the partner. Female jackdaws paired to high ranked males turned out to have a lower residual bodyweight compared to females with a partner lower in rank, when weighed at day 4 of the nesting stage (See figure 12a). The residual bodyweight is a measurement of condition and is defined by the difference between the expected bodyweight based on the tarsuslength and the actual bodyweight. The expected bodyweight was calculated based on the formula:

$$\text{Bodyweight}_{\text{expected}} = 123.0063 + 2.3401 * \text{Tarsuslength}$$

The residual bodyweight of a female jackdaw at day 4 is correlated with the average volume of the eggs layed by this female and the weight of the chicks hatching from these eggs (See figure 12b/c). Considering smaller eggs and a lower hatchweight to have detrimental effects on reproductive success (Thomas 1983), the condition of high ranked females during breeding apparently is worse than that of females lower in rank.

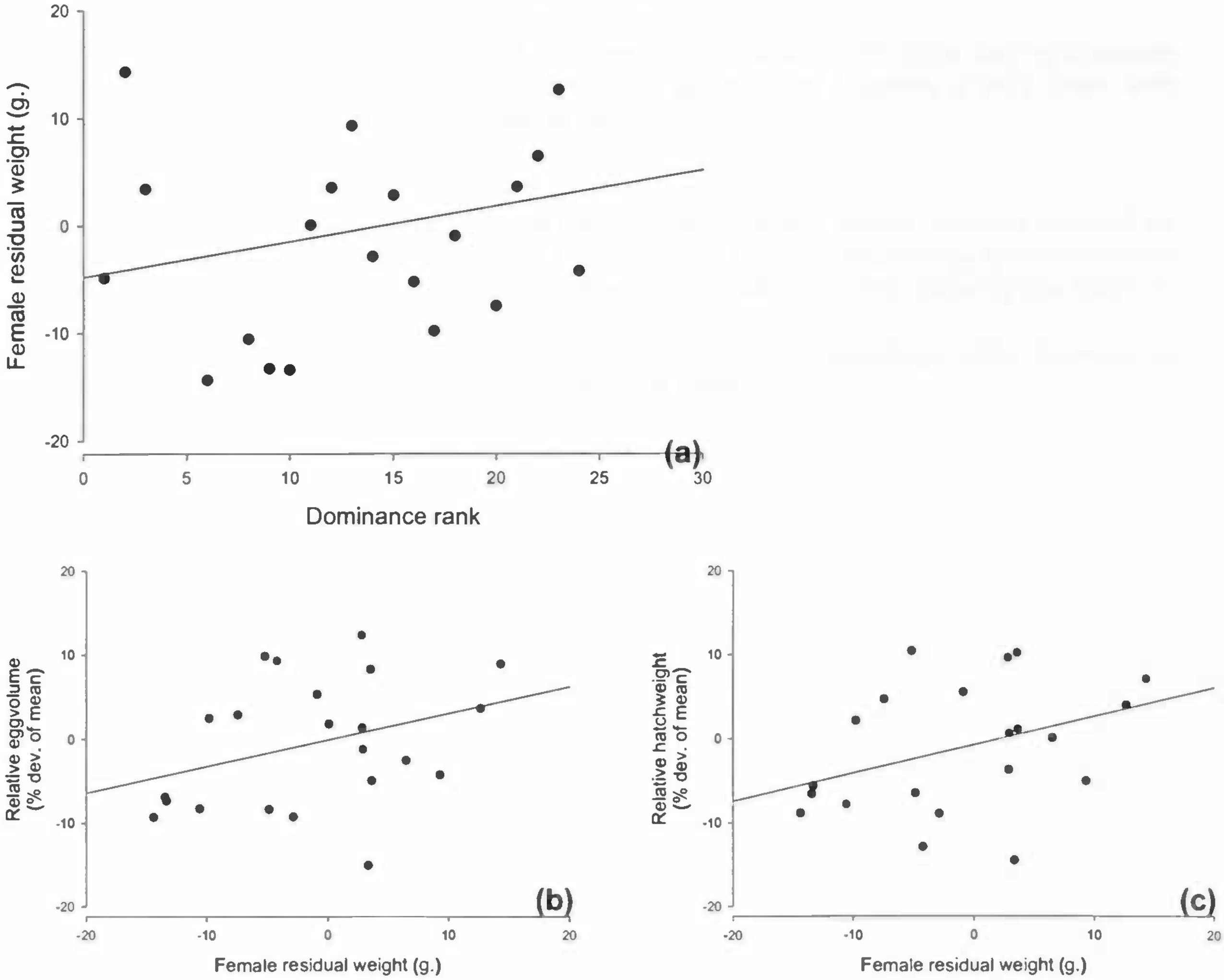

Figure 12 *Relation between (a) dominance rank and female residual bodyweight (r_s=0.296, P=0.205, =20), (b) female residual bodyweight and eggvolume (r_s=0.399, P=0.066, N=22) and (c) female residual bodyweight and hatchweight (r_s=0.435, P=0.043, N=22)*

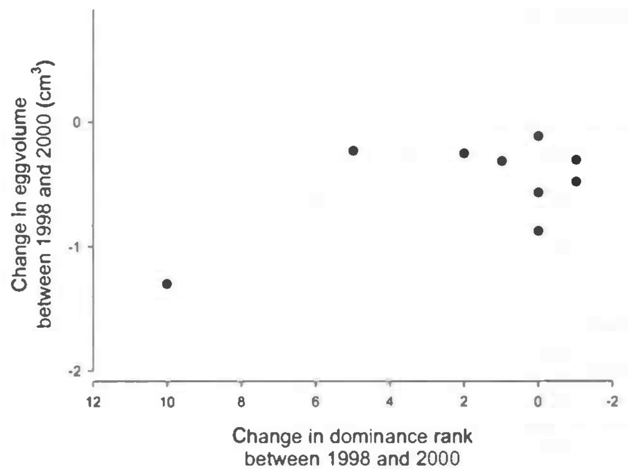

Figure 13 *Relationship between change in dominance rank, from 1998 to 2000, and the difference in eggvolume between these two years*

The data presented in figure 13 suggest a decrease in volume of the eggs laid by a female with the rise in dominance rank of her partner. The sample size however is very small, with only two birds with a considerable change in rank.

Social dominance and parental care

Analysis of the observations of parental care by the male and female jackdaw showed no effect of dominance rank on parental effort (See table 6). At day 5 the female spends most of her time in the nestbox, provisioning of the young at this time is mainly done by the male. At day 15 both parents contribute in the provisioning of the chicks.

Average chickweight at day 30 and the total number of fledglings also showed no correlation to the different variables of parental effort observed.

Table 6 *Correlation between dominance rank and parental care*

		Dominance rank	Number of Chicks fledged	Average chickweight at day 30
Female presence at day 5	Corr.Coeff.	.222	-.040	.456
	Sig.	.376	.876	.076
Female number of exits per hour at day 5	Corr.Coeff.	-.329	-.214	-.068
	Sig.	.182	.393	.801
Duration of visits at day 5	Corr.Coeff.	.263	-.221	.476
	Sig.	.291	.379	.062
Number of visits per hour by male at day 5	Corr.Coeff.	-.152	.103	.322
	Sig.	.548	.684	.223
Male absence at day 5	Corr.Coeff.	-.011	-.158	-.242
	Sig.	.964	.530	.367
Time between two feeding visits at day 5	Corr.Coeff.	-.110	-.057	-.248
	Sig.	.673	.829	.373
Female presence at day 15	Corr.Coeff.	-.287	.012	-.063
	Sig.	.264	.962	.817
Number of exits per hour by female at day 15	Corr.Coeff.	.098	.196	.090
	Sig.	.707	.450	.742
Duration of visits at day 15	Corr.Coeff.	-.400	-.028	-.037
	Sig.	.112	.916	.893
Number of visits per hour by male at day 15	Corr.Coeff.	-.371	.293	-.016
	Sig.	.143	.253	.952
Male absence at day 15	Corr.Coeff.	.422	.046	.264
	Sig.	.092	.861	.324
Time between two feeding visits by the male at day 15	Corr.Coeff.	.265	-.360	-.017
	Sig.	.305	.155	.951

Discussion

The hierarchy

Both in 1998 and in 2000 a dominance hierarchy was observed in the colony (See appendix). Although some shifts in rank of individual jackdaws, between 1998 and 2000, were observed, the hierarchy turned out to be highly stable over these two years. This was especially the case in the high ranked animals. These findings are in accordance with the findings by Röell who also found a stable order of ranking over multiple years (Röell 1978).

Because of the fact that jackdaws win all interactions at their own nestbox (Röell 1978), it is important to check whether determining the social structure by means of observations at a feeding pit is influenced by the location of this. Since no differences in the hierarchies, determined at two separate feeding pits, were found, the dominance rank of a foraging jackdaw is assumed not to be site-dependent. Since Röell found dominance rank determined at a feeding pit to correlate with the total number of nestboxes defended outside the breeding season and primary access to available nestboxes, the hierarchy determined in this study is thought to be a good representative of the actual hierarchy within this colony.

Analysis of possible factors determining dominance rank showed no correlation with the position of an individual within the hierarchy. In Great Tits (*Parus major*) social status is signaled by the width of the breast-stripe (Järvi et al. 1984) and tarsuslength (Garnett 1981), and in male pied flycatchers (*Ficedula hypoleuca*) a correlation between dominance rank and the degree of pigmentation of the plumage on the head and back is found, black males being the most dominant (Røskaft et al. 1985). Our data show no correlation between dominance rank and tarsus- or winglength. Bodymass is also not related to dominance rank. Apparently in jackdaws such morphological signals and correlates of social status are not present.

Henderson found a relation between the age of a jackdaw and its placing in the hierarchy, where the rank of an individual increased as he grew older (Henderson et al. 1995). Röell however stated that the dominance rank of a jackdaw was not so much influenced by its age, but more so by the length of residency at the study-site (Röell 1978). Our data show no correlation between age and dominance rank. This however does not mean that such a relation does not exist, since most of the jackdaws in this colony are of unknown age and only an estimation of minimum age is given. A definite conclusion about rank and age within this colony is therefore not yet possible.

Since not all nestboxes were occupied, all birds, represented in the social hierarchy, with an intention to occupy a nestbox essentially were able to do so sooner or later in the breeding season. Therefore, as was to be expected, no differences in nestbox-occupation between higher and lower ranked birds were found.

The number of times a jackdaw was observed in interactions at a feeding pit is highly influenced by its rank. The higher in rank a particular bird was, the more interactions were scored for this animal. This is caused by the fact that birds that are high in rank can eat at the feeding pit for longer times, without being chased away by another bird. Avoiding behavior, thus preventing hopeless fights that could cause injury, by jackdaws lower in rank is thought to be another explanation of the difference in the number of interactions observed between jackdaws higher and lower in rank.

Because high ranked animals have easier access to resources, differences in survival rates are to be expected. Survival rates could be higher in high ranked animals through access to more and better food (Slotow et al. 1997) or safer foraging opportunities (Ekman et al. 1984; Hogstad 1988). However a higher ranking may result in a higher number of fights an animal is encountered with, as is the case in jackdaws, and consequently induce a higher risk of injury, lowering chances of survival. Our data from 1998 and 2000 show no difference in survival over the last two years between jackdaws higher or lower in the hierarchy.

Social dominance and reproduction

This study, in accordance to the findings by Röell, shows an opposite effect of social dominance on reproductive success compared to the study in Leicestershire by Henderson. Again was shown that the higher the ranking of a jackdaw pair within the colony at the Zoological Laboratory was, the lower its reproductive success, measured in the number of fledglings produced, turned out to be.

There are several hypothesis holding possible explanations for the reduced number of fledglings in high ranked individuals:

1. High ranked jackdaw pairs do produce fewer fledglings a year, but they can live and reproduce for more years resulting in a higher overall reproductive success;
2. The young from high ranked pairs that do fledge, are of better quality and thus have better chances of survival and/or a higher future reproductive success;
3. Increased territoriality in the higher ranked jackdaws interferes with their reproduction;
4. Jackdaws lower in rank are better parents; high ranked birds put less effort in parental care. Possibly through a trade-off between territorial effort and parental effort (Qvarnström 1997);
5. There are differences in physical quality between higher and lower ranked jackdaws that could influence the reproductive success;
6. Jackdaws that win a lot of their interactions, and therefore are placed high in the hierarchy, do so because they are frustrated by their reproductive failures;
7. Extra-pair fertilizations are more frequent in dominant male jackdaws, resulting in a higher reproductive success than is actually found in this study.

There are several studies showing a correlation between dominance rank and survival (Kikkawa 1980; Piper et al. 1990), however we didn't find any differences in survival rate between the different social classes. Since in our study survival was only based on two years, it's too soon to completely discard the first hypothesis based on our findings. More convincing proof against the first hypothesis comes from Röell, who found that the jackdaw pair highest in rank failed to produce any fledglings over a period of five years (See table 7) (Röell 1978). Because this is quite a long period in the life of a jackdaw, it is highly unlikely that this couple can compensate for the complete lack of reproduction in the remaining part of their life.

Table 7 *Correlation between rank and breeding success in June (breeding seasons from 1972 to 1976 inclusive)*

Rank	1	2	3	4	5	6	7	8
Number of fledged young (1972-1976)	0	1	2	5	5	9	4	7

In Great tits (*Parus major*) body size and weight of fledglings has great influence on juvenile survival and future reproduction (Garnett 1981). Also in Carrion *crows (Corvus corone corone L.*) growth rate and body size were shown to correlate with future social status (Richner et al. 1989). Although at the moment no evidence is available for the jackdaws in Haren, this effect is probably also present in this colony. As was shown in the results chicks from high ranked jackdaws were significantly smaller and lower in bodyweight compared to chicks from pairs lower in rank. This difference was found from hatching until fledging, with an exception at day 10. Based on the assumption that juvenile survival and future reproduction is influenced by body size and weight, chicks produced by jackdaws with a high ranking apparently are of lower quality. As a result the second hypothesis has to be rejected.

Territoriality can have great benefits for an animal. Through defending a certain area against intruders, it can monopolize for example a food resource or suitable nestsite. However increased territoriality often also means an increase in aggressive interactions.

Besides having higher chances of injury, more aggressive animals also differ from more docile animals in their hormone levels, especially in the level of testosterone (Wingfield et al. 1987), which might have negative effects for its reproduction or the animal itself(Beletsky et al. 1990).

Testosterone (T) is shown to circulate in high concentrates during periods of territory establishment and mate guarding, when a lot of male-male interactions occur, but levels decline rapidly thereafter (Wingfield et al. 1987). The decline in T levels is shown to be particularly crucial during the nesting stage of the breeding season, since a lot of studies revealed a negative effect of this hormone on the expression of parental care (Hunt et al. 1999; Ketterson et al. 1992; Silverin 1980). Aggressiveness, and dominance rank, also influence metabolic rates, resulting in higher oxygen-consumption and thus higher energetic costs (Hogstad 1987; Røskaft et al. 1985).

The breeding density at the Zoological Laboratory in Haren is supposedly very high, since nestboxes are only 1-2 meters apart. T levels were shown to be higher in areas with a high breeding density (Ball et al. 1987; Beletsky et al. 1990). Furthermore, as was shown in figure 4 of the results, the number of aggressive interactions observed during foraging is higher in jackdaws in the top of the hierarchy than in jackdaws lower in rank. Therefore individual differences in T levels are very likely to play an important role in the reproductive success of the jackdaws at our study-site.

Because of the above-mentioned relationship between territoriality, testosterone and parental care and because parental care was shown of great influence on individual reproductive success (Henderson et al. 1993), we investigated the parental effort of the different jackdaw-pairs at our colony. Analysis of our data however showed no difference in parental care between the different social classes. This is in contrast to the findings by Henderson who found an increase in parental care with dominance rank (Henderson et al. 1995). A relation between reproductive success and parental care was also not found in our data.

However a relation between parental care and social ranking can not be excluded. It is possible that the largest effect of the ranking of a jackdaw on parental care is found in another period of the day, probably in the early morning, when the males return from their overnight roosts and feeding trips are supposedly more frequent (Henderson et al. 1993), or in the evening.

The dominance rank of a male jackdaw showed no relation to his body parameters. When looking at the condition of his partner (estimated by means of her residual weight based on the length of her tarsus) at day five of the nesting stage however, we found an effect of a male's position in the hierarchy. It was shown that high ranked females at this time had lower residual weights. Furthermore we found an effect of social ranking on the average volume of the eggs in a clutch, since the eggs of high ranked jackdaws were smaller compared to eggs from jackdaws lower in rank. Because eggsize was shown to correlate with parental quality (Goodburn 1991; Reid et al. 1990), this also suggests that females paired to high ranked males are of low quality.

An explanation as to why high ranked females are in worse condition, compared to females lower in rank, is not available. One explanation may lie in a difference in provisioning by the male during incubation and the period when the chicks are still very small, at which time the female stays mostly on the nest and is fed by her partner (Goodburn 1991; Lifjeld et al. 1986). Normally females lose only 5.6% of their body mass during the breeding season, and may actually increase their body masses during the incubation phase (Henderson 1991). The condition of a female jackdaw might also be influenced by an increase in aggressive encounters either by her partner, as was observed by Röell (Röell 1978), or by other jackdaws, through the larger number of conflicts she's involved in when she has a partner with a high social position. A third explanation of the lower condition of high ranked females could be that these females simply are of lower overall quality. The idea of a choice effect during pair forming in the jackdaws was already proposed by Röell (Röell 1978). It is possible that female jackdaws of low quality choose dominant males to bond with to increase their chances of reproduction and might be more motivated and persistent than other females to do so. It is also possible that more dominant males are not the preferred partners in the jackdaw, because of possible influences of rank on for example paternal care (Qvarnström et al. 1998). Unfortunately data on the choice-determining factors in the jackdaw is not yet available. Finally senescence might be a factor affecting the quality and thereby the reproductive success of jackdaws high in rank, as Henderson found jackdaws with a high ranking to be older than those lower in rank (Henderson et al. 1995). However senescence is not likely to be such a limiting factor in high ranked jackdaws, because the effect of dominance rank of a particular jackdaw on his reproductive success is present in multiple years and an expected higher mortality caused by old age is not found.

Differences in quality between females may also account for the observed trend towards a delayed onset of egglaying in the high ranked pairs. If this is the case, the negative effect of laydate on reproductive success observed in our study may be caused not so much by timing but more so by quality. Such a relation between laydate and parental quality and age was already shown in several other studies (Soler et al. 1991; Verhulst et al. 1995).

The possibility exists that the reproductive success of a jackdaw is not influenced by its social position within a colony, but that reproductive success itself influences the ranking of a jackdaw. This can either be caused by motivational aspects, or through increased aggression caused by frustration. No data on this is available yet, but in the future this could be investigated by looking at the effect of removing all chicks from a nest, thereby lowering reproductive success, on the rank of the parents the following year.

The last hypothesis stated that the reproductive success of a jackdaw with a high position in the hierarchy might actually be higher through extra-pair fertilizations. Parentage analysis has not yet been performed within our colony, but two other studies showed no extra-pair fertilizations to occur in jackdaws (Henderson et al. 2000; Liebers et al. 1999). Therefore it is not likely to be of any importance in our colony.

So far our data suggest the decrease in reproductive success of high ranked jackdaws in the colony at our study-site to be caused by a combination of increased territoriality and aggression on the one hand and quality of the parents on the other. Whether or not the effect of dominance rank on reproductive success is mediated through differences in circulating hormone levels should be investigated in the future.

Social dominance and reproduction in Haren and Leicestershire

As was already shown by Röell, within the colony at the Zoological Laboratory reproductive success is impaired in the jackdaws occupying the top positions in the hierarchy. As mentioned earlier, these findings are in contrast with results from a study in Leicestershire, England. Within this colony reproductive success was greatest in jackdaws of high ranking.

Because the two populations are completely isolated from each other, a genetic component can not be excluded as a determining factor. However environmental influences are far more likely account for the contradictory findings obtained at the two sites. A brief summary of the some obvious environmental differences is shown in table 8.

The most striking difference between the two study-sites is found in the distance between the separate nestboxes. Although the amount of nestboxes in the study area is about the same, at the site in Haren they are much closer together, resulting in a higher breeding density. Higher breeding density means more individuals close to each other, undoubtedly leading to more aggressive interactions and territorial behavior (Silverin 1998). This increase in aggressive interactions is thought to influence the highest ranked jackdaws the most, because of the higher frequency of fights in these animals and the possible avoiding behavior of the subdominant jackdaws. It is possible that the 'trade-off' in birds, between being aggressive or being a better parent, is no longer profitable to the highest ranked jackdaws in Haren because of the high number of interactions they are confronted with. The high number of interactions may also increase the levels of circulating hormones, in particular testosterone (Silverin 1998), to levels that could possibly deteriorate the health of a jackdaw. This can, for example, be through its effect on metabolic rates (Hannsler et al. 1979) and/or the immune system (Saino et al. 1995).

Another difference between the two sites is the year-round availability of artificial food offered to the captive animals at the Zoological Laboratory. This could lead to better overall survival chances for all jackdaws, thereby lowering the advantage high ranked birds could have through better access to food resources. Although this could explain a possible increase in the reproductive success of low ranked jackdaws at our study-site, it does not explain the reduced or even complete lack of reproduction in the higher rankings.

Finally the amount of human disturbance could be a distinguishing factor, through a possible heightened sensitivity to stress in the high ranked jackdaws. However this is unlikely, because human activity at the study-site is fairly constant throughout the year so high ranked jackdaws wouldn't occupy a nestbox at this side in the first place if it influenced them that much.

Table 8 *Differences between the study-sites in Haren and Leicestershire*

Study-site	**Haren**	**Leicestershire**
Habitat	Open field between buildings	1.5 ha of wood
Number of nestboxes	36	40
Proximity of nestboxes	1-2 meters	+/- 8 meters
Food availability	High (artificial food in animal pens)	Normal
Human disturbance	Higher ?	Lower ?

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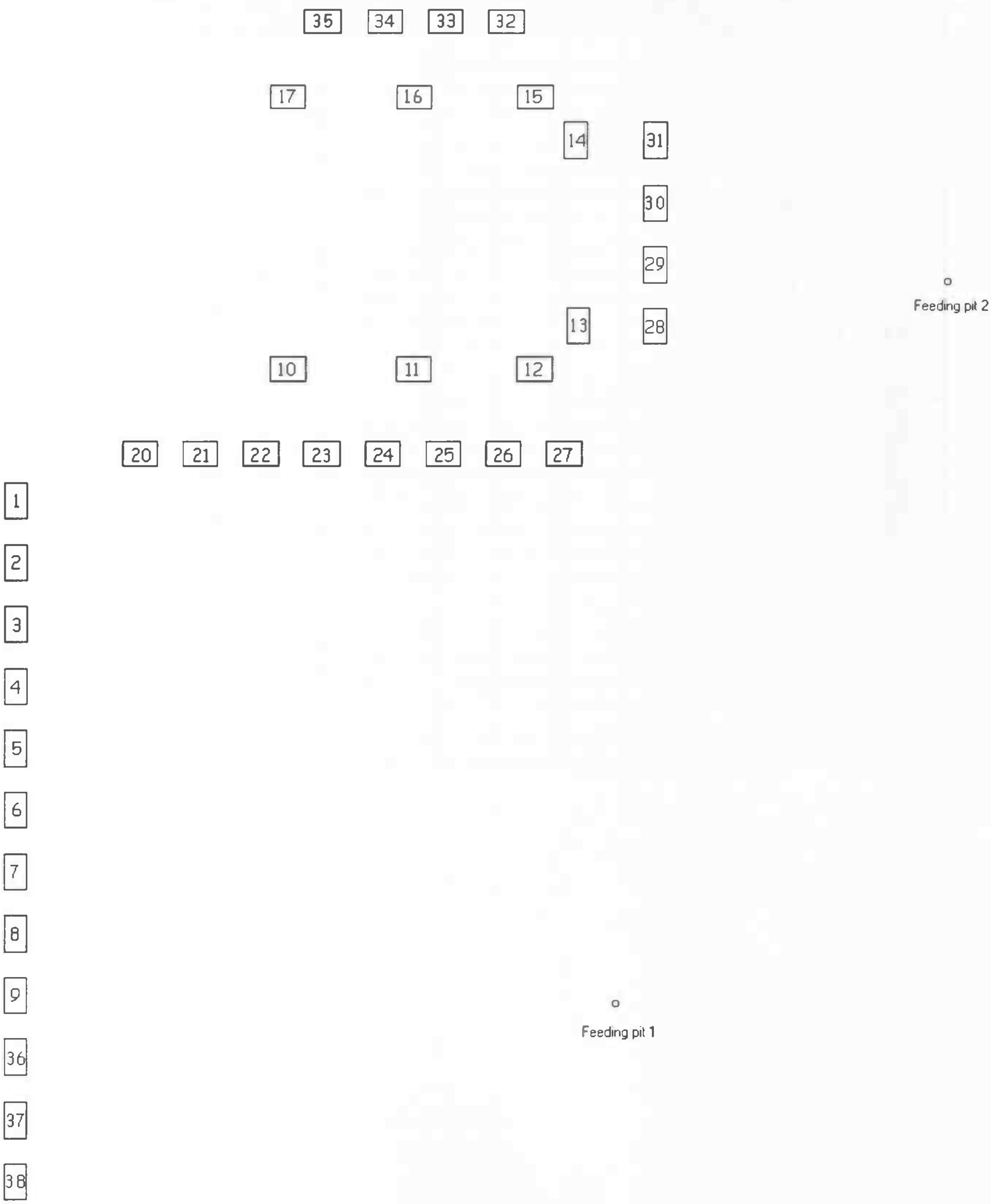
Appendix 1 *Rankshifts between 1998 and 2000.*

Bird Ringcode	Rank in 1998	Rank in 2000	Bird Ringcode
3522807	1	1	3522807
3522787	2	2	3522850
3522814	3	3	3522765
3522765	4	4	3522761
3557701	5	5	3557701
3522761	6	6	3584655
3447359	7	7	3522789
3522803	8	8	3522803
3522771	9	9	3557709
3557716	10	10	3584658
3522800	11	11	3557716
3522785	12	12	3522791
3522791	13	13	3557769
3447360	14	14	3557762
3522795	15	15	3557752
3557708	16	16	3580089
3522811	17	17	3557702
3522793	18	18	3584651
3557709	19	19	3557766
3447378	20	20	3522811
3522796	21	21	3580085
3522762	23.5	22	3522795
3522781	23.5	23	3522771
3522789	23.5	24	3557705
3557705	23.5	25	3522785
		26	3447378
		27	3522781
		28	3522815

Appendix 2 *Relation between dominance rank in 1998 and return to the colony in 2000*

Male Ringcode	Rang98	Seen in 2000	Partner seen in 2000
3522807	1	YES	YES
3522787	2	NO	YES
3522814	3	NO	YES
3522765	4	YES	YES
3557701	5	YES	YES
3522761	6	YES	-
3447359	7	NO	NO
3522803	8	YES	YES
3522771	9	YES	NO
3557716	10	YES	NO
3522800	11	NO	-
3522785	12	YES	YES
3522791	13	YES	YES
3447360	14	YES	YES
3522795	15	YES	YES
3557708	16	NO	NO
3522811	17	YES	YES
3522793	18	NO	NO
3557709	19	YES	YES
3447378	20	YES	NO
3522796	21	NO	NO
3557705	23.5	YES	YES
3522762	23.5	NO	YES
3522781	23.5	YES	-
3522789	23.5	YES	YES

Appendix 3 *Schematic representation of the study area*



Appendix 4 *Summary of data from the observations in 2000*

Rank by formula	Ringnr.	# won	# lost	# supplanted	# supplanted by	Dominance value by formula	Rank by Crosstable	Box in 2000
1	3522807	205	9	83	6	315.09	1	YES
2	3522850	39	3	27	5	70.20	11	YES
3	3522765	82	13	49	8	38.63	4	YES
4	3522761	131	28	57	15	17.78	3	NO
5	3557701	79	15	29	9	16.97	12	NO
6	3584655	24	6	13	4	13.00	7	YES
7	3522789	54	13	38	14	11.27	9	YES
8	3522803	94	31	48	22	6.62	5	YES
9	3557709	128	46	56	27	5.77	2	YES
10	3584658	13	6	14	7	4.33	18	YES
11	3557716	79	38	53	27	4.08	6	YES
12	3522791	22	12	19	12	2.90	16	YES
13	3557769	46	38	30	25	1.45	10	YES
14	3557762	31	27	19	22	0.99	20	YES
15	3557752	51	61	32	35	0.76	8	YES
16	3580089	2	3	2	2	0.67	28	YES
17	3557702	32	37	26	35	0.64	13	YES
18	3584651	17	20	19	26	0.62	15	YES
19	3557766	14	19	15	22	0.50	19	YES
20	3522811	19	33	13	19	0.39	22	YES
21	3580085	2	3	2	4	0.33	27	YES
22	3522795	19	36	17	29	0.31	17	YES
23	3522771	37	104	27	41	0.23	14	YES
24	3557705	14	35	13	26	0.20	21	YES
25	3522785	10	34	11	21	0.15	23	NO
26	3447378	4	21	3	12	0.05	26	NO
27	3522781	9	72	7	51	0.02	25	NO
28	3522815	7	74	8	55	0.01	24	YES