

# DETERMINANTS OF SOCIAL RANK IN GOOSE FLOCKS: ACQUISITION OF SOCIAL RANK IN YOUNG GEESE

by

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## Introduction

It is the dominant individuals within social groups that have regular access to resources in competitive situations (CLUTTON-BROCK & HARVEY, 1976). In mallards (*Anas platyrhynchos*) aggressive males monopolise food patches (HARPER, 1982) and take favoured positions in display when pairs are forming (WILLIAMS, 1983). A function of the pair-bond in geese, through increased display and agonistic behaviours, is thought to enhance a pair's ability for acquiring essential fat reserves prior to migration and breeding (BLACK & OWEN, 1987). Aggressive geese have priority at established feeding and roost sites (RAVELING, 1969) and nesting territories (COLLIAS & JAHN, 1959). Continued access to these resources must contribute to the positive relationship between dominance and breeding success. This link has been established not only for geese (COLLIAS & JAHN, 1959; LAMPRECHT, 1986a, 1986b) but for other birds (SCOTT, 1980; ROBINSON, 1986) and mammals (CLUTTON-BROCK, GUINNESS & ALBON, 1982; McCANN, 1982).

Biologists have long been intrigued by the questions—why are certain animals aggressive and not others and what makes an individual aggressive? Several studies have begun to approach these questions by establishing that young goslings raised in small broods develop different degrees of aggressiveness and establish a rank order (RADESÄTER, 1974; STAHSBURG, 1974; WÜRDINGER, 1975; KALAS, 1977). Early relationships with siblings may affect future aggressiveness. The initial aim of

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this study is to investigate the acquisition of rank by monitoring the experience birds have in rearing groups and relating this to their success when encountering unfamiliar birds.

An individual's success and order of first encounters with unknown contestants may also influence future social rank. Eight-month old chickens which were pecked initially usually lost their next encounters while those which exercised pecks tended to win (MCBRIDE, 1958). FISCHER (1965) found that goslings deprived of social contact during rearing obtained the lowest rank when introduced into a flock. We test the effect of accumulated experiences in two ways; by monitoring success in relation to previous performance and by comparing the performance of goslings which had a different breadth of experience during rearing.

PREVETT & MACINNES (1980) and RAVELING (1981) suggest that the aggressiveness of a goose is influenced by the social rank of its family. The assumption is that goslings reared in high-ranking families acquire their parent's rank and retain this later in life; there is some evidence for this in wild swans (SCOTT, 1980). To test this hypothesis we compare the performance of young goslings raised by parents with different degrees of aggressiveness. Some tests were designed in order to separate the genetic from the learning component of aggressiveness; there is evidence that aggressiveness in Galliforms is inherited (BOAG & ALWAY, 1981; MOSS, WATSON, ROTHERYE & GLENNIE, 1982).

### Methods

A flock of barnacle geese (*Branta leucopsis*) was established at the headquarters of the Wildfowl Trust, Slimbridge, in the early 1960s from several pairs taken from the wild. In successive generations the flock grew to around 200 individuals, and later hatches were allowed to become full-winged, as are nearly all the birds at present. The geese nest largely on islands in the Trust's fox-proofed enclosures, which extend to around 40 ha. An aggression index was developed for nesting birds, based on their reaction when humans visit the nest, on a scale of 1 to 6. Birds were scored as follows:

1. Initially and persistently attacked the observer with wing beating and biting.
2. Initial physical attack then stood at the nest site displaying agonistic threat postures (as described by RAVELING, 1970; RADESÄTER, 1974).
3. Stood at the nest site giving threats.
4. Stood a few metres away from the nest giving threats and immediately returned as the observer left.
5. Retreated several metres from the nest giving no threats and returned in a minute or two after the observer left.
6. Retreated several metres from the nest even before the observer got close (*e.g.* 20 metres away) and the returned was delayed.

In 1983, as the geese began nesting, we recorded their aggressiveness as we approached each nest on different days during egg-laying. The scores for the two pair members were summed so that a pair had a maximum possible index of 12. Pairs which scored nine or more were considered non-aggressive, those scoring 3 or less were aggressive. This

method allowed a quick assessment of all the breeding pairs' aggressiveness, albeit towards a human.

Five different tests were made with two groups of goslings with different backgrounds; selection was on the basis of the aggression index of pairs. All the eggs were marked as soon as they were laid. Goslings were marked initially with web-tags and then with leg-rings. The tests are listed below.

#### Sibling-rearing broods.

For this sample, eggs originating from aggressive and non-aggressive pairs were hatched in incubators. Within two hours of hatching, the total of 30 goslings were divided according to hatching order into four rearing groups each of seven or eight. They were kept in heated brooders for the first two weeks, after which they were moved into  $5 \times 12$  m pens on grass. The 4 pens were about 5 metres apart so that there was effectively no social contact between adjacent groups. Water and supplementary food were available at all times. The age of goslings in these groups varied by not more than two days except in one (D) where some goslings hatched seven days apart. All goslings in this study hatched within a period of 18 days.

These groups are termed "sibling-broods" although they contain goslings from different genetic broods. A maximum of two eggs was taken from any one pair, so that the sibling-broods contained no more than two genetic siblings. By the time ranking tests were performed, sibling-broods were reduced to the following sizes:

Progeny of aggressive pairs:            Brood A -  $n = 7$ ,            Brood B -  $n = 5$   
Progeny of non-aggressive pairs:      Brood C -  $n = 7$ ,            Brood D -  $n = 8$

*Test 1.* We determined the rank order within these sibling-broods between 21-28 days and 45-52 days (average age in each brood) by separation trials and opportunistic observations of aggressor-submissor encounters (threats and contacts). When the birds were separated in their pen they often "greeted" each other (mutual neck-stretching and vocalisations) when re-united. This gave rise to the "facing-away" posture by low-ranking birds, revealing dominance relationships established in previous agonistic encounters (RADESÄTER, 1974). It was also evident that low-ranking birds greeted more often and with greater intensity than dominants (STAHLBERG, 1974). An individual was ranked as dominant over another after eliciting at least three consecutive submissions.

*Test 2.* The next test was made at ages 53-75 days when goslings within the four broods approximated the same weight; relative growth rates in goslings stabilise between 40-90 days of age (WÜRDINGER, 1975). Goslings were placed into pens with three to five unfamiliar goslings until each had established a dominance relationship with every other gosling in the trial. The pens measured  $5 \times 6$  m and were enclosed so that groups were visually isolated.

Goslings of similar rank (according to their position within their sibling-brood) were placed together, but thereafter the duration of the tests determined which set of birds became available for new groupings. It was difficult to avoid grouping individuals together more than once. Of the 248 dyads 33 (13.3%) were repeated once and six (2.4%) twice. Some birds were either extremely aggressive or submissive, which affected the behaviour of all group members so as to hinder the development of rank order; these birds were removed from the group. When a new group was formed each individual was placed into a new pen. Two goslings from the same original sibling-brood were not placed together to avoid the possibility of their assisting each other in encounters.

#### Family groups.

This involved 23 goslings which were hatched and raised by real or foster parents in the main enclosure. These included a number from eggs collected from non-aggressive pairs which were hatched and raised by aggressive foster parents. Each brood had one or two

goslings initially, but some mortality occurred. Only four of 12 goslings hatched by non-aggressive pairs survived to fledging. On the other hand, 14 of 17 goslings fledged under the care of aggressive pairs (excluding broods of fostered goslings). This difference is significant ( $\chi^2 = 6.97$ ,  $P < 0.01$ ).

Groups raised in families, therefore, contained:

Progeny of aggressive pairs reared by them:	Group E - n = 14
Progeny of non-aggressive pairs reared by them:	Group F - n = 4
Progeny of non-aggressive pairs fostered by aggressive pairs:	Group G - n = 5

*Test 3.* The 23 goslings reared in families were separated from the adults at an average age of 75 days (S.E. 3.6) and held for a short time in three large pens. Dominance relationships were monitored in groups of three to five goslings separated in smaller pens. The trial was conducted as in Test 2; groups were held together until their rank order had been established (on average 10 hours, S.E. 1.04, range 0.5 to 28 hours). Unfortunately Group F's rank in this test included only two females; the two males were excluded half way through their groupings because they sustained an injury. We still used all group F bird's weights and measurements in comparisons with other groups as these recorded made before the injury (see below).

*Test 4.* At the age of 80-85 days family-reared goslings (Groups E, F, G) were placed together with similar ranked goslings from sibling-broods (A, B, C, D). There was a total of 16 groupings, four each of high, intermediate, and low ranked birds. There were four goslings per group, consisting of two goslings of similar rank from each rearing group.

*Test 5.* Sibling-reared goslings were re-formed into their original groups and dominance rank was again monitored at the age of 85-92 days to test if encounters outside the brood affected within brood rank order.

Linear rank order was calculated by ranking individuals by a) the proportion of encounters they won and b) the outcome of specific encounters arranged in a matrix so that the least number of circularities occurred. These two methods showed a significant correlation throughout the study. Two-tailed statistical tests were employed throughout (SIEGEL, 1956).

## Results

### Index of aggression.

Two lines of circumstantial evidence were used to test whether this index was meaningful intraspecifically. We observed encounters between birds classed as aggressive and non-aggressive. Twenty one of 28 encounters were won by birds classed as aggressive (Sign test,  $P = 0.008$ ).

The density of nests on the 'colony' islands was very high, and there was considerable competition between pairs. In another study at this colony males spent more time in intraspecific aggression and lost more weight during incubation than non-colony males (OWEN & WELLS, 1979). Pairs scored as aggressive, non-aggressive and intermediate were therefore plotted according to their nest location (Table 1). As predicted, no non-aggressive pairs were able to compete within the colony ( $\chi^2$  for difference among groups in Table 1 15.43,  $P < 0.001$ ); in fact the least aggressive pairs nested in a separate enclosure where nest density was low.

TABLE 1. The relationship between nest position and aggressiveness of breeding pairs

Nest site	Number of pairs at various nest defence ranks			Percent aggressive
	Aggressive	Intermediate	Non-aggressive	
Colony	17	8	0	68.0
Non-colony	7	11	11	24.1

There is evidence for geese and swans that larger individuals from the same pair or family status are more successful in intraspecific encounters (SCOTT, 1980). Birds ranked most aggressive in this study were significantly larger and heavier than others. There is, therefore, substantial evidence that the aggression index is meaningful in terms of intraspecific competition in encounters and for nest sites.

#### Test 1. Social rank within artificial sibling-broods.

During the first few days after hatching the goslings which were earliest to hatch were the most active and the first to show signs of agonistic behaviour. A stable linear rank order among the broods was not, however, approached until the third week. Rank order in groups of four Canada (*Branta canadensis*) goslings was established in 15 days (RADESTÄTER, 1974). The difference is probably due to the fact that groups in this study contained twice as many individuals.

Table 2 shows the significance of Spearman Rank Correlations for the various factors which influenced rank order within sibling-broods at different ages. The result is given only when two or more of the four groups showed significant correlations or when the majority of non-significant correlations were in the same direction. Even though initial rank order was not significantly correlated with hatching weight, older birds tended to dominate younger ones when contestants' weights were within 10 grams ( $P = 0.011$ ,  $n = 10$ , Sign Test). Rank and age were correlated at 28-days in three of the four groups and rank correlated with 28-day and 21-day weights in two groups. The rank order at 52 days was not correlated with 45-day weights, but within each dyad, heavier birds of the same sex dominated lighter ones ( $P = 0.012$ ,  $n = 64$ , Sign Test). At 52 days, older birds won against younger goslings in dyads where sex and weight were similar ( $P = 0.035$ ,  $n = 11$ , Sign Test). Sex was not a major factor during the first two months but males did win relatively more encounters than females in the second month ( $\chi^2 = 5.5$ ,  $P < 0.02$ ).

TABLE 2. *Test 1*: Correlation between factors in social rank acquisition for sibling-reared goslings at different ages

	Age	Hatch weight	Weight 21-day	Rank 28-day	Chronology of study				Weight 85-day	Size 85-day <sup>b</sup>	Weight change <sup>c</sup>
					Weight 45-day	Rank 52-day	Rank 75-day <sup>a</sup>	Weight 85-day			
Hatch weight											
Weight 21-day	+	+									
Rank 28-day	a cd		Bc								
Weight 45-day	+++	+	+++								
Rank 52-day	cD	-	bC	bCd							
Rank <sup>a</sup> 75-day	+++	-	+++	+++	+						
Weight 85-day							A D		+		
Size <sup>b</sup> 85-day							+++				
Weight <sup>c</sup> change	-						+		+		
Rank 92-day			bC	bCd							
			+++	+++	+++	+	+	+	+	+	+

<sup>a</sup> = Rank order determined outside the original sibling-broods, <sup>b</sup> = Skull and tarsus length, <sup>c</sup> = The difference in grams. A, B, C and D are the different rearing groups (see text). Upper case letters =  $P < 0.01$  and lower case =  $P < 0.05$  (Spearman Rank Correlation). The sign shows the direction of correlation for groups in the order A-B-C-D. The absence of a brood letter indicates that the direction of correlations was similar for the groups and that comparisons were not significant.

### Test 2. Social rank between unfamiliar siblings.

The factors which were correlated with the outcome of encounters between goslings from different sibling-broods (75-day rank) are summarised in Table 3. Rank order increased with weight and size, and males were more successful than females ( $\chi^2 = 42.7$ ,  $df = 6$ ,  $P < 0.001$ ). Males were also larger and heavier than females but the difference in success persisted when this was controlled for ( $P = 0.008$ ,  $n = 14$ , Sign test). Within the same sex larger goslings won a greater proportion of encounters than expected ( $P = 0.052$ ,  $n = 13$ , males;  $P = 0.04$ ,  $n = 12$ , females, Sign Test).

TABLE 3. *Test 2.* Correlation between social rank and various factors

	Rank 77-day	Age	Hatch weight	Weight 85-day	Size 85-day
Age	P < 0.001 (+)				
Hatch weight	ns (-)	ns (+)			
Weight 85-day	P < 0.05 (+)	ns (+)	ns (+)		
Size 85-day <sup>a</sup>	P < 0.001 (+)	P < 0.05 (+)	ns (-)	P < 0.01 (+)	
Weight Change <sup>b</sup>	P < 0.01 (-)	P < 0.05 (-)	ns (-)	P < 0.05 (-)	P < 0.05 (-)

<sup>a</sup> = skull and tarsus length. <sup>b</sup> = difference in grams. Tests between unfamiliar goslings from different sibling-broods ( $n = 27$ ); Spearman Rank Correlation sign shows the direction of correlation.

The rank orders established between goslings from different groups were not correlated with the ranks they held within their own broods in Test 1 nor was there a significant difference in overall success (number of wins/total encounters).

Goslings tended to lose weight during the tests (mean -72 grams,  $SE = 56$ ,  $n = 27$ ), probably owing to handling rather than as a result of encounters. The weight loss was negatively correlated with rank (Table 3). Both size and age affected weight loss: smaller and younger geese lost more weight.

If aggression is genetically controlled, the progeny of aggressive geese would be expected to be more successful than those of non-aggressive

ones, even when reared in isolation from their parents. However, no significant differences could be found in the number of successful encounters between goslings whose parents showed different degrees of aggression. Nor did goslings differ significantly in size or weight.

The results of encounters between unfamiliar birds are shown in Table 4, which indicates that the better and individual scores in one grouping the more likely it is that it will attain the highest rank in the next grouping. For most goslings these trends continued throughout the groupings with unfamiliar birds. After all groupings in Test 2, rank (at 75 days) was

TABLE 4. Probability of success of goslings with various ranks in their next encounter (*Test 2*)

Previous rank	Success in next group contest			$\chi^2$
	N <sup>a</sup>	N <sup>b</sup>	%	
Top rank	91	65	71	P < 0.001
Intermediate	33	10	30	P < 0.05
Low rank	98	13	13	

<sup>a</sup> N = total number of contests at said rank. <sup>b</sup> N = outcome of next encounter; success is defined as winning against 60% or more of the group opponents.

closely related to the goslings' success through the entire test period. Table 5 shows the repeatability of success rates for goslings of different rank. The tendency for repeated success was not as strong for parent-raised goslings, though even in those, highly successful birds were 2.4 times more likely to retain their high level of success in future encounters than the lowest-ranked birds ( $\chi^2 = 12.24$ ,  $df = 1$ ,  $P < 0.001$ ) and the overall trend still existed.

### Test 3. Parent-reared birds after separation.

Goslings raised by aggressive parents (group E) were significantly heavier and larger at 75 days than those raised by non-aggressive parents (group F) (T test,  $P < 0.05$  for both measures). Weight and size were correlated, and rank at 77-92 days was positively correlated with both ( $P < 0.05$  for weight,  $P < 0.001$  for size). Males were larger and heavier than females but ranked higher even when size had been taken into account.

The results of tests involving cross-fostered goslings are shown in Table 6, and suggest that both genetics and environment contribute to

TABLE 5. Repeatability of success and defeat in agonistic encounters in relation to individuals' rank order outside the original sibling-broods (*Test 2*)

Group rank during testing	Gosling's final dominance status					
	Top ranking		Intermediate		Low ranking	
	N	%	N	%	N	%
Top ranking (>60%)	69	79	35	41	2	2
Intermediate (=50%)	11	13	24	28	15	17
Low ranking (<40%)	7	8	26	31	72	81
Total	87		85		89	

TABLE 6. *Test 3*. The proportion of wins by goslings raised by parents of different degrees of aggressiveness

Parents' status rearing status	Success rate in encounters		
	N	%	$\chi^2$
Dominant <sup>a</sup> raised dominant	128	59	P<0.05
Subordinate <sup>b</sup> raised dominant	40	45	
Subordinate <sup>c</sup> raised subordinate	11	26	P<0.05

<sup>a</sup> = 7 females and 7 males (group E). <sup>b</sup> = 3 females and 2 males (group G). <sup>c</sup> = 2 females (group F).

the acquisition of social rank. These results should be viewed with caution, however, because samples were too small to control for size, weight or sex.

#### Test 4. Sibling-reared and Parent-reared gosling relationships.

Changes in weight occurred during the testing periods in the later part of this study. Goslings from sibling-broods lost significantly more weight (T test,  $P < 0.001$ ) than those raised with parents (Fig. 1). In fact, the 21 parent-reared young gained on average 71 grams. Low-ranking birds in the sibling-broods lost more weight than both birds of high and intermediate rank (T-test  $P < 0.01$  in both comparisons). Of those raised

by their parents, the low-ranking goslings gained least weight, though the difference was not significant. Parent-reared goslings, though of similar size and weight, dominated sibling-reared birds more frequently in all categories ( $\chi^2 = 11.5$ ,  $df = 1$ ,  $P < 0.001$  for those of high rank;  $\chi^2 = 14.3$ ,  $df = 1$ ,  $P < 0.001$  intermediate rank;  $\chi^2 = 5.1$ ,  $df = 1$ ,  $P < 0.05$  low rank).

#### Test 5. Stability of initial rank order and rank reversal.

When siblings were reunited they were 85-92 days old. The rank order of goslings in three of the four broods was still significantly correlated with the 28-day Test 1 rank (Table 2). In two of the sibling-broods, the final rank order was correlated with the 21-day weight rather than weight or size at 85-92 days.

Of the 14 (of 187, 7.5%) reversals which did occur within sibling-broods after the reunion five (36%) were linked to weight and five others

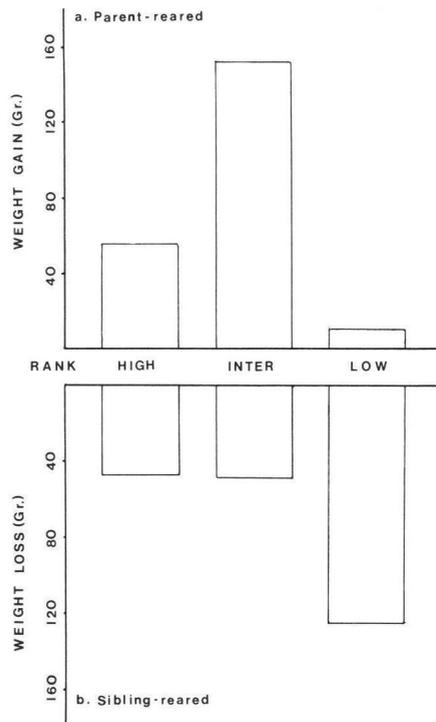


Fig. 1. Change in weights between 45 and 85 days for (a) parent-reared goslings (groups E, F, G) and (b) sibling-reared goslings (broods, A, B, C, D).

to body size plus success (wins/total encounters). This contrasted with the 18 changes in rank which occurred between the 28-day and 52-day assessments (Test 1). Rank changes at this earlier age were positively related to both differences in weight ( $P = 0.018$ ,  $n = 14$  of 18) and success ( $P = 0.0005$ ,  $n = 15$  of 18, Sign Test).

In brood D, associations between goslings seemed to affect reversals during Test 5. The top ranked male (HE) and the third ranked bird, a female (FC), assisted one another within their sibling-brood during the final tests. This may explain the high rank of FC, who was the second smallest bird in the group. Similarly, a male (FA) and a female (HO) were usually in close proximity and both birds simultaneously held submissive postures even when one was threatened. After they avoided their aggressor the pair usually greeted each other. These goslings attained the lowest rank. HO was the smallest bird in the group and the associated FA, a male of average size, dropped three places in rank. These associations may have been rudimentary or trial pair-formation even at this very early age.

In dyads duplicated in different groupings during Tests 2-3 only 6 of the 39 ranks were different. In four of these the change was related to changes in body size and success.

## Discussion

Early development of social rank.

Body weight does not determine the initial rank in artificial broods, rather rank appears to affect weight (see also WÜRDINGER, 1975). There is some evidence that dominance relationships are initiated by goslings which were hatched first, which is reflected in the correlation of age and 28-day rank. Similarly, the initial rank of young chicks is dependent on the age at which they first showed aggression (RUSHEN, 1982). However, hatching sequence in real broods is closely synchronised, so discrepancies in age would be minimal. Since growth rate is not dependent on weight at hatching (ANKNEY, 1980), we conclude that the very young active goslings which dominate their siblings in the first days gain more and/or better quality resources and thus put on more weight. ANKNEY (1980) suggested that in captivity where environmental conditions are stable genetic differences among goslings from eggs of similar size determined differences in weight and size, but he did not test for behavioural causes.

The development of the submissive "facing-away" posture and the resulting sibling rank order (RADESÄTER, 1974) gives low-ranking sibl-

ings a chance of using resources without continued harassment and of gaining as much and in some cases more weight than their dominant siblings if food is abundant. Changes in weight, however, do not always bring about changes in rank among birds reared together. Dominance relationships which are formed during the first month are highly stable and will only change if the difference in size or weight becomes very great. At about 36 days when female growth rate declines some of the smallest females dropped in rank, but rank reversals were for the most part independent of the sex of the contestants. It is possible, therefore, that even though an individual is dominated by its siblings it may be more successful against other conspecifics in a flock.

In encounters outside the rearing group, size, weight, age and success, but not previous rank within the group, were important in rank development. Only in exceptional cases was rank the same in and out of sibling-broods.

#### The influence of previous success.

Previous success is a strong factor in shaping individual performance. A bird which was successful initially is less likely to adopt submissive postures in the next encounter than one which failed. We agree with RUSHEN (1982) who concluded that subordinate individuals "accept" their role as the submissor so that subordinates are responsible for maintaining stability in relationships (also see ROWELL, 1974).

The finding that subordinate goslings lost more weight than intermediate and dominant birds indicates a fluctuating relationship between weight and rank outside the rearing group. There was, however, a tendency for smaller birds to lose more weight under test conditions and this influenced future rank. There is evidence from several vertebrates that individuals who suffer various degrees of fatigue and malaise increase their susceptibility to declines in rank and fitness (CLUTTON-BROCK, GUINNESS & ALBON, 1982; CHAPAIS, 1983). Body size has been seen throughout this study as slightly more closely related to success than weight.

The finding that rank order correlated with age for the goslings raised under controlled conditions supports the concept that animals accumulate information which helps them to predict the behaviour of conspecifics and to modify their behaviour accordingly (see BATESON, 1983; ROPER, 1983; ARCESE & SMITH, 1985).

The age effect may suggest that selection will favour early nesting attempts. On the other hand, the timing of nesting in barnacle geese is limited by arctic conditions; nest initiation is related to snow-melt (PROP, VAN ERDEN & DRENT, 1984) and nesting is highly synchronised. For example, in white-fronted geese (*Anser albifrons frontalis*), which breed in Alaska, about 80% of the nests were initiated within 10 days of each other and hatching chronology was even more synchronised; about 90% within ten days (ELY & RAVELING, 1984). So the age affect between birds of the same year will be negligible (see also ARGESE & SMITH, 1985).

#### The influence of learning and heredity on aggression.

This study provides evidence that goslings raised by aggressive parents are dominant over conspecifics of similar age that were raised by non-aggressive parents. There are two lines of evidence that suggest that a gosling's rank is influenced more strongly by learning than by a genetic predisposition. The first is that the progeny of non-aggressive pairs fostered by aggressive parents achieved higher ranks than those reared by their own parents. The second is that the progeny of pairs at opposite ends of the scale of aggressiveness who were raised apart from their parents were equally successful. Parent-reared goslings won more encounters against sibling-reared goslings; so it is the parental role rather than that of brood-mates which is important. This interpretation parallels rank acquisition in primates (see Berman, 1983).

Wild goslings from high-ranking families spend significantly more time threatening conspecifics and are themselves threatened less than single goslings and goslings from low-ranking families (BLACK & OWEN, 1984). SCOTT (1980) showed that wild cygnets from dominant families were still dominant a year later among swans of the same age. However, the fact that the fostered offspring (progeny of non-aggressive pairs raised by aggressive pairs) did not score as well as the progeny of aggressive pairs raised by aggressive pairs suggests that there is a genetic component.

#### Implications of parental quality.

The marked difference between parents ranked as either aggressive or non-aggressive was their ability to provide appropriate care for their nest and their young. Non-aggressive pairs not only readily fled their nests, but only reared 33% of their offspring to fledging compared to 82% for aggressive parents. The surviving goslings were also smaller and in

poorer health. This difference was not a feature of nest position; competition between families was less outside the colony and food quality similar. It is clear, therefore, that aggressiveness in parents is linked with parental quality which influences the social status and ultimately the survival of their young (see also McCANN, 1982).

Once geese become paired, social rank is complicated by the mate's behaviour (LAMPRECHT, 1986a). In Test 5 we found that even "rudimentary" relationships effect individual's rank. Observations of birds at Slimbridge showed that when an aggressive female repaired with a male, whose previous mate was not aggressive, the male's nest defence index increased considerably. AKESSON & RAVELING (1982) deduced that females direct and perpetuate males' aggressiveness and triumph ceremony displays with supportive responses. INGLIS (1977) reported that only the females which actively defended their nests against intruders or predators were successful in hatching young. We know that experience outside the rearing brood affects a bird's aggressiveness more than that gained within broods. Further investigations may, however, find that a high-ranking female who experiences more successes with her brood (but who is not as successful by herself because males are more dominant) may be more inclined to support her mate in conflict situations.

In the wild, offspring reared in large broods have more opportunities to acquire wins than goslings from small families and orphaned goslings (BLACK & OWEN, 1984). Evidence in foraging barnacle goose flocks show that large families use the best feeding stations. Since this relationship also occurs on post-hatch feeding stations (PROP, VAN ERDEN & DRENT, 1984) high growth and fattening rates for juveniles should result. Another important factor which may prejudice future social rank of offspring is inherited size. Both culmen and body weight show high heritability in snow geese (*Anser caerulescens*) (COOKE & DAVIES, 1983). However, this correlation could have been linked to the quality of parental care. We speculate that brood size will remain a very influential factor on social rank acquisition in young geese for three reasons: a) because of the variation in the amount and quality of food; continual access to quality food increases growth and size of young; b) the opportunity to experience success in encounters—success yields more success; c) appropriate tactics for conflict situations are learned. Thus aggressive parents with larger than average broods may provide offspring with the best possible equipment and experience with which to acquire a mate and compete in their reproductive lives.

### Summary

The paper describes a study of social rank acquisition in goslings reared from eggs taken from a full-winged flock of barnacle geese (*Branta leucopsis*) at the Wildfowl Trust, Slimbridge. Eggs were taken from pairs of known history and the adult's aggressiveness was ranked according to their reaction to humans. This rank was shown to be meaningful intraspecifically both by the outcome of encounters between geese and by the fact that no pairs scored as non-aggressive were able to nest in the preferred colony. A group of goslings reared by their own parents and cross-fostered goslings were also examined.

1. Within a rearing group of goslings (sibling-reared broods), the oldest and heaviest birds ranked highest in the first month and males performed better in encounters than females of the same size in the second month.

2. In encounters between unfamiliar goslings from different sibling-broods in the third month of life, the most important determinants of the new rank were body size, weight and sex. Previous experience also influenced rank; previous success yielded continued success. Goslings lost weight during the test; loss was negatively correlated with rank. The performance of goslings reared without adults bore no relationship to their parent's aggressive score.

3. In the semi-captive flock, parents that scored as "aggressive" reared more and larger goslings than non-aggressive pairs. The rank of these in the third month correlated with their size and sex (independent of size). The cross-fostering experiment suggested that there was a genetic as well as an environmental influence on rank acquisition.

4. In encounters between goslings of similar rank from sibling-broods and parent-reared ones, the latter ranked significantly higher. Parent-reared goslings, though less familiar to the experimental regime, gained weight and goslings from sibling-broods lost weight.

5. Once established, rank order remained stable; the few reversals related either to changes in size or to cooperation between goslings in confrontations.

6. Parental quality clearly affects, through learning and heredity, the physical and social development of goslings, and consequently their chances of survival and reproduction. We suggest that these effects are reinforced by brood size; larger families gain better resources in competitive situations. In wild geese, competitive ability is crucial both to survival in winter and to the acquisition of nesting sites and rearing areas for the young.

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### Zusammenfassung

In einer Schar freifliegender Nonnengänse (*Branta leucopsis*) im Wildfowl Trust in Slimbridge wurde die Ausbildung einer sozialen Rangordnung zwischen handaufgezogenen Gänsekücken untersucht. Die Eier stammten von Paaren mit bekannter Vorgeschichte. Die Aggressivität der adulten Gänse wurde gemäss ihres Verhaltens gegenüber Menschen gemessen. Es zeigte sich, dass der daraus resultierende Rang sowohl intraspezifische Bedeutung hat, als Mass für die Interaktionen zwischen den Gänsen, als auch die Tatsache widerspiegelt, dass die bevorzugten Nistplätze von aggressiveren Paaren benutzt wurden. Es wurde auch eine Gruppe von den Eltern aufgezogene Gössel untersucht, als auch kreuzweise zwischen 2 Paaren vertauschte Gössel.

1. Innerhalb einer geschwistergeprägten Gruppe (sibling-broods) hatte im ersten Monat der älteste und schwerste Vogel den höchsten Rang, im zweiten Monat waren männliche Tiere erfolgreicher, auch gegen weibliche der selben Grösse.

2. Bei Begegnungen einander unbekannter Gössel von verschiedenen Geschwistergruppen im dritten Lebensmonat waren die wichtigsten Determinanten des neu erlangten Ranges Körpergrösse, Gewicht und Geschlecht. Auch Erfahrungen während früherer Zusammentreffen hatten Einfluss auf den Rang: früher erfolgreiche Tiere waren weiterhin erfolgreich. Die Gössel verloren während des Tests an Gewicht. Der Gewichtsverlust war negativ korreliert mit dem Rang. Das Auftreten der Gössel, die ohne Eltern aufgezogen wurden, stand in keiner Verbindung zur Aggressivität ihrer Eltern.

3. In der halbwilden Schar zogen Eltern, die als "aggressiv" eingeschätzt wurden, mehr und grössere Gössel auf als nicht-aggressive Paare. Der Rang dieser Gössel war im Alter von drei Monaten korreliert mit ihrer Grösse und dem Geschlecht (unabhängig von der Grösse). Das Vertauschungsexperiment legt nahe, dass es sowohl genetische als auch umweltbedingte Einflüsse auf die Ausbildung des Ranges gab.

4. Bei Zusammentreffen geschwistergeprägter und elternaufzogener Gössel ähnlichen Ranges hatten die letzteren einen signifikant höheren Rang.

5. Einmal aufgestellt, blieb die Rangordnung stabil. Die wenigen Umkehrungen waren entweder mit Änderungen in der Grösse verbunden, oder mit Kooperation zwischen den Gösseln während der Konfrontationen.

6. Der elterliche Status beeinflusst deutlich, durch Vererbung und Lernen, die physische und soziale Entwicklung der Gössel und folglich deren Überlebenschancen und