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Observations on the social behaviour of semicaptive Barnacle Geese (*Branta leucopsis*)

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A five generation study of social dominance in 48 semicaptive barnacle geese (*Branta leucopsis*) showed that (a) male rank depended on father's rank the previous year; (b) male rank depended on rank the previous year as long as the individual did not gain a mate; (c) males with families were dominant over paired males, and paired males were dominant over unpaired males; and (d) rank was not correlated with age, breeding history, family size, mate rank, or rank as a gosling.

Additionally, higher ranking males exhibited a more strictly linear rank order. They also selected widows, regardless of rank, over previously unmated females in the 4 cases where widows were available for mating.

Other behaviours observed during the study include: triple copulatory behaviour (2 males and one female); grief-like behaviour over a dead gosling by an unmated male; „jealous“ behaviour by one member of a gander pair when the other member pursued a female; widowed mother/son mating; persistent and varied aggressive behaviour by unmated males towards families and individuals; and intense defense of arbitrary territories (unoccupied nesting boxes, stumps and dirt mounds) that changed frequently within the same month.

Key words: Barnacle Goose (*Branta leucopsis*), social behaviour, rank order.

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1. Introduction

The study of social behaviours in semicaptive waterfowl populations is of interest for several reasons (see KALAS 1977, 1979, LAMPRECHT 1977a, 1977b, 1984, 1986a, 1986b, SCHLAGER 1981, 1983): (1) Most heritable behaviours are more readily identified in semicaptive populations because genealogies are more easily kept. (2) Behaviours common to wild and semicaptive animals (i. e. behaviours relatively unaltered by semicaptivity) are more easily and perhaps more thoroughly studied under semicaptive conditions because of convenience of observation and relative ease of experimentation. (3) A knowledge of behaviours unique to semicaptive animals is important for understanding and properly maintaining animals in zoos and other modified habitats.

In the present study I observed the behaviour of 48 semicaptive barnacle geese (*Branta leucopsis*) through 5 generations. The following behaviours received emphasis: (1) Rank order in males was followed through several generations to detect the possible inheritance of behavioral characteristics which might affect rank. (2) The establishment of rank (presumed in this population to be relatively unaltered by semicaptivity) was studied and related to (a) rank previous year; (b) mating status (family, pair or single); (c) age; (d) breeding history (previously mated or not); (e) family size; and (f) mate's rank. (3) Behaviours were described which appeared to be unique to (or at least highly modified by) semicaptivity.

2. Study site, description of the flock, methods

The study was conducted at The KONRAD LORENZ Institute, near Grünau, Austria (65 km e. of Salzburg). The Institute is located in the forested and sparsely populated Alm Valley, on properties belonging to the HERZOG VON CUMBERLAND Stiftung. Most behavioural observations were made on a 2000 m² grassy area that enclosed a shallow pond where geese nested in boxes or on small islands (see LORENZ 1979).

The barnacle geese lived here in association with 150–200 greylag geese whose behaviour has been extensively documented and analyzed by Professor KONRAD LORENZ and his students (KALAS 1977, 1979, LORENZ 1979, SCHLAGER 1981, 1983, HUBER 1988). Both species were free to leave the area but they were fed corn and a special

wildfowl preparation to keep them in the valley throughout the year and to reduce their fear of humans. The Institute insured an additional degree of tameness by adding several hand reared (and human imprinted) individuals to the flock each year.

The geese were trapped only once during their lifetime, at the end of their first summer, when they were equipped with colored rings (leg bands) coded to the genealogical records maintained by the Institute. Institute policy did not permit subsequent trapping except to treat injuries. Thus, the flock experiences a life style intermediate to that of captive birds and that of wild barnacle geese on their arctic breeding grounds.

During the study period the size of the flock ranged from 18 to 39 as a consequence of natality and mortality. Some geese fell prey to foxes and other predators, some died of disease or conflicts with greylag geese, and some were removed by Institute personnel for various reasons.

I observed the geese for approximately 750 hours during four summers (August 22 – September 26, 1983; April 19 – May 29, 1984; June 21 – July 13, 1985; and July 3 – August 8, 1987), normally 2–3 hours in the morning and 3–4 hours in the afternoon. Individuals were identified on the basis of colored leg rings, using binoculars when necessary. Since Institute policy did not permit capturing the birds, their masses could not be taken.

Dominant behaviour was recorded when geese competed for food. Conflicts were especially common at feeding time when grain was scattered among the flock, and frequently I provoked conflicts between specific individuals by scattering grain between them. An individual was considered dominant if it won (chased away or caused a withdrawal movement) a majority of the conflicts with another individual. Threatening movements that caused withdrawal were given the same weight as pecking or chasing. From these data the linear rank order was derived that had the fewest circularities (instances in which an individual low on the list won encounters against an individual high on the list).

Either a MANN-WHITNEY U or a SPEARMAN Correlation Coefficient test was used to establish if rank was correlated with (a) rank the previous year for birds 3 years old or older; (b) family status (pair with or without goslings); (c) age; (d) breeding history (previously bred or breeding for the first time); (e) family size (i. e. number of goslings); and (f) mate's rank. In the few cases where unmated birds were observed prior to mating, the ranks of the individuals were compared to the ranks of the mates they selected. Sample size for the different categories varied, adult males providing the largest data sets and juvenile females the smallest, since the latter entered into the fewest conflicts.

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3. Results and Discussion

3.1. Possible inheritance of behavioural traits

Males with high ranking fathers (based on the previous year) tended to have high positions in the dominance hierarchy ($P < 0.03$; Table 1), suggesting a possible genetic component in the establishment of rank. However, it is also possible that offspring from high ranking fathers receive more food resources during their development, thereby influencing size and hence rank; or they may learn aggressive behaviour either directly from their fathers, or indirectly from their position as siblings of dominant fathers (under whose protection they may win more conflicts). BLACK & OWEN (1987) reported that offspring from non-aggressive parents reared by aggressive foster parents achieved higher ranks than those reared by their own parents, though not as high as offspring from aggressive parents that were reared by aggressive parents. For a discussion of the relationship between dominance and aggression, see FRANCIS (1988).

Table 1. Correlations between rank and various factors that may affect rank. Spearman correlation coefficient test was used for all categories except family status and breeding history, for which Mann-Whitney U test was used. t. s., test statistic. Asterisk indicates significance at $P < 0.05$.

Tab. 1: Korrelation zwischen Ranghöhe und möglichen Einfluß-Faktoren. Ermittelt wurde der SPEARMANsche Rang-Korrelationskoeffizient. Nur bei 2b) und 2d) erfolgte der MANN-WHITNEY U Test. * = Signifikanz ($p < 0,05$).

Possible rank determinant	males			females		
	d.f.	t.s.	P	d.f.	t.s.	P
1. Father's rank prev. yr.	9	0.71		13	-0.35	—
2a) Rank previous year	21	0.83		15	0.19	—
b) Family status	8,6	48		8,6	25	—
c) Age	11	-0.27	—	5	-0.31	—
d) Breeding history	8,12	23	—	10,10	27	—
e) Family size	7	-0.26	—	7	-0.23	—
f) Mate rank	16	-0.02	—	16	-0.02	—
3a) Rank as gosling	9	-0.22	—	5	-0.33	—
b) Mate choice	6	0.45	—	6	0.45	—
c) Linearity	37	0.49		11	-0.04	—

3.2. Behaviours probably similar in wild and semicaptive geese

(a) Male rank was dependent on rank the previous year, except for individuals that increased in rank after acquiring a mate (Tables 1, 2). Thus, rank order of males remained the same relative to each other, even though absolute rank changed each year as newly mated males entered the hierarchy at various levels. It is possible that there was a learned component in establishing rank, with the result that lower ranking birds were less inclined to challenge higher ranking birds, even when the latter are temporarily sick or weakened. BLACK & OWEN (1987) demonstrated how previous success can shape individual performance in intraspecific conflicts among barnacle geese.

(b) Males with families were dominant over paired males ($P < 0.001$), and paired males were dominant over unpaired males ($P < 0.001$). Likewise, the gain of a mate elevated rank in males (Table 2). These relationships were shown in wild populations of barnacle geese (BLACK & OWEN 1989), as well as in semicaptive populations of bar-headed geese (LAMPRECHT 1986a). Acquiring a mate, like acquiring a territory, possibly elevates motivational level in males to give an advantage in conflicts that determine rank. LAMPRECHT (1986a) found that breeding males lost more fights with conspecifics when the female was not present.

In addition, that rank and mating status might affect each other reciprocally is suggested by LAMPRECHT's (1986a) „casual evidence that high-ranking males are more likely to obtain a mate.“

(c) Rank was not dependent on age, in contrast to other observations of semicaptive barnacle geese where age had at least a secondary effect on dominance relationships (BLACK & OWEN 1989), a tendency these investigators observed in sibling-broods as well (BLACK & OWEN 1987). On the other hand, rank was highly correlated with age in semicaptive bar-headed geese (LAMPRECHT 1986a).

(d) Rank was not dependent on breeding history. In this regard, observations by BLACK & OWEN (1989) may be pertinent, even though the relationship between aggressiveness and dominance is not clear. These investigators reported that parental male barnacle geese that had bred more than once in the past were more aggressive than those breeding for the first time.

(e) Family size had no effect on rank. Nor was such a relationship found in semicaptive flocks of greylag geese (SCHLAGER 1981) or bar-headed geese (LAMPRECHT 1986a). However, in wild

Table 2: Ranks of 1983 males from 1983 through 1987. Until 1986, when LZ, AL, AD and DAM died, relative rank (in parentheses) remained the same except when a male gained a mate (+). In these cases, the male's rank, relative to the other 1983 males, increased.

Tab. 2: Ranghöhe von 9 ♂ in den Jahren 1983–1987. Bis 1986 (als LZ, AL, AD und DAM starben) blieb die relative Ranghöhe (in Klammern) gleich, außer nach Verpaarung (+). In diesen Fällen nahm die Ranghöhe im Vergleich zu den anderen ♂ zu.

Male	Rank			
	1983	1984	1985	1987
LZ	1	1(1)		
BZ	2	2	1	1
AL	3	3	2	
JK	4	4	4	2
BT	5	5(+)	3	12(5)
MO	6	6	6(5)	6(4)
AD	7	7	9(7)	
LU	8	9(+)	8(6)	5(3)
DAM	9(+)	8	12(8)	

populations of wintering barnacle geese (BLACK & OWEN 1989) and Canada geese (*Branta canadensis*) (HANSON 1953), large families dominated over small families.

(f) Rank was not dependent on mate rank. Although all 4 widows in this study remated with high-ranking males, their own rank did not change consistently (2 increased and 2 decreased). Interestingly, the widow of the alpha male mated with one of her own offspring, who had dominated her even as a 6-month old gander. Among the very few observations or remating in geese is LAMPRECHT's (1986a) report of a widowed bar-headed goose that lost rank when she mated with a lower-ranking male.

3.3. Behaviours that may be unique to (or highly modified in) barnacle geese living in semicaptivity

(a) A character trait in a young bird apparently persisted into adulthood. One gosling [BIM] was described during his first year as „eccentric, easily intimidated, feeding by himself, often on unusual plants, and frequently wandering off from the family to feed and rest by himself.“ As an adult he always ranked very low, never mated, and frequently associated with his sister (BAM) and her mate (LU), who accepted him as a third member of their family. This may be an example of a character trait in a young goose that persisted into adulthood and affected rank.

(b) Males available for mating did not select mates on the basis of the age or rank of the available females (Table 1: mate choice). On the other hand, the female's previous mating status may have been important, as all 4 widowed females remated with the highest ranking male available at the time (Table 3). Thus, these males, at least, chose previously mated females over previously unmated females if they could successfully compete for them. In an extreme case of a male's choosing an older mate, OLhb, who had paired with a previously unmated female (Nbg) in July, 1985, left her the following April and mated with a widow (MIT), whose mate had just died. In another case a high ranking but previously unmated male (LZor) mated with his widowed mother.

Whereas mates may be selected like this in the wild, presumably only relatively small populations of geese living in relatively confined circumstances could have knowledge about the previous rank of potential mates. On the other hand, the 4 males' clear preference for widowed females as mates could represent adaptive behaviour in the wild, since the probability of passing genes to

Table 3: Ranks of available widows and males. Numbers in bold-faced type indicate ranks of individuals that mated.

Tab. 3: Zur Ranghöhen-Situation männlicher und weiblicher Nonnengänse bei der Neuverpaarung von 4 Witwen (Ranghöhe der verpaarten Individuen durch Fettdruck hervorgehoben).

Ranks			
1 Widow (her rank: rank of prev. mate)	2 Rank of new mate	3 Ranks of avail. males	4 Avail. females for male in col. 2
OL (18; 1) [1984]	5	5, 6, 7, 9, 10, 12, 13, 14	15, 18 , 20, 21, 22
BUM (17; 11) [1985]	10	10 , 12, 13	14, 15, 17 , 18, 19
MIT (28; 8) [1987]	3	1, 3, 14, 15, 16, 18, 19	22, 25, 27, 28 , 29, 36
SAR (29; 2) [1987]	1	1 , 3, 14, 15, 16, 18, 19	22, 25, 27, 28, 29 , 36

offspring should be greater when males mate with females whose fertility has already been demonstrated. Also, previously mated females should have a more effective courtship display.

(c) A gander pair regularly exhibited aggressive behaviour. In 1983 and 1984, in the absence of available mates, two low-ranking ganders (MO and AD) formed a gander pair. MO, who had never been mated, was dominant and behaved in a normal male fashion, whereas AD, a widower, consistently exhibited typical female behaviours. For example, AD tolerated being „bullied“ by MO at the feeding trough, but only up to a point, when he would abruptly leave the area. This is a typical response of females to being bullied by males. Realizing that AD was no longer present, MO would appear anxious and give the same distress call that male barnacle geese give when their mates temporarily desert them.

For a large part of each day MO and AD tormented the flock by loudly and frequently vocalizing, nervously running through the area for no apparent reason, and attacking subordinate geese without provocation. Once they so relentlessly pecked the head of an unpaired goose while she incubated her sterile eggs that she would have died from the wounds if Institute personnel had not destroyed her nest. On another occasion these two ganders acted with seeming wile. MO approached JK near his nest, pecked at him until JK chased MO about 25 meters from the nest, at which time AD viciously attacked JK's goslings in front of their helpless mother.

(d) A gander exhibited „jealousy“ and bisexual behaviour. In 1984, AD left MO to pursue BUM as a mate. Initially, MO followed these two geese during long chases through the forest. When he caught up with them he ran past AD and attacked BUM, a behaviour resembling human jealous behaviour. He later pursued them with less intensity, and often when they were resting next to each other, he would sit several meters away. He always left the area when they began courtship display, except on one occasion when he joined them and all three head-dipped together. After a few seconds, AD mounted BUM and began copulating with her. Immediately, MO mounted AD, but when the combined weight of the two males pushed BUM beneath the surface of the water, she swam from under the males and went to shore, leaving only AD beneath MO. After a few seconds of copulatory-like movements, MO dismounted and presented the typical male postcopulatory display (stretching his neck upward and lifting his wings); AD showed the typical female postcopulatory behaviour by sitting quietly and preening.

MO's „jealous“ behaviour, in which he attacked the female that AD was chasing, may have functioned to maintain his pair bond with AD. However, it is possible that MO's attack on BUM could have been his own sexual response to her that was distorted by his heightened state of excitement. Another possibility is that if it was, in fact, an aggressive act that normally would be

directed towards AD, he might have chosen BUM as a substitute (displacement behaviour), since attacking a fleeing female is less risky than attacking a male in pursuit of a female.

AD's bisexual behaviour suggests that, at least in males, both the male and female repertoires of sexual behaviour are functional and capable of being elicited by appropriate circumstances. Such flexibility with respect to sexual behaviour suggests that geese may also be adaptable with respect to other social behaviours, such as dominance and submission. Flexibility on the dominance hierarchy could be beneficial by allowing an animal to quickly, and with minimal stress, function in a different rank if the hierarchy's integrity were disrupted.

(e) An unmated gander demonstrated grief-like behaviour. When a gosling died in 1984, most geese (including its parents) ignored the carcass, although some pecked at it and pulled out some feathers. Curiously, DAM, the lowest ranking (and at that time unmated) male, seemed extraordinarily preoccupied with the dead gosling, standing over it with his neck outstretched and calling loudly. Since „grief“ is usually regarded as a response to loss, it is possible that DAM was simply annoyed or upset by a novel circumstance, much as a dog, for example, barks at a strange object.

About a minute later he left the carcass and fed, but soon returned to „grieve“ again, repeating this behaviour at least 5 times.

The next day his behaviour toward the dead gosling was different. He began calling loudly about a meter before he arrived at the carcass, but instead of stopping and „crying“ over the dead gosling, he walked past it, hardly glancing at it, and ceased crying as soon as he had passed it. Whereas his behaviour the previous afternoon suggested a sincere, grief-like state of mind, his behaviour at this time appeared ritualistic and vacuous – as though he were just „going through the motions.“

(f) Unmated ganders spent considerable time in conflicts over territories. After all incubating pairs had abandoned the 4 nesting boxes in 1984, 3 unmated (and low ranking) males (LU, MO, AD) and occasionally other males spent considerable time flying excitedly and noisily from box to box, chasing each other off of the boxes as though trying to claim any and all boxes as territories. Sometimes MO and AD claimed a box together, MO standing on top and AD sitting inside on the nest as though incubating eggs. About two weeks later, these 3 males turned their attention to a small grassy mound in the forest, spending as many as 4 hours a day squabbling for a place on top. Daily competition for this mound persisted for about a week, after which they ceased playing such territorial games altogether. This behaviour contrasts with the typical behaviour of the other non-incubating geese in this flock, which defended only their resting sites, normally small patches of ground that changed at least once a day.

3.4. Other behaviours

(a) Linearity in rank order. A negative correlation ($P < 0.045$) was found between the ranks of the males and the number of circularities, indicating that rank order is stricter in higher ranking individuals (and hence males with families).

Linearity might be less strict in lower ranking individuals because they are generally younger and have had less time to firmly establish rank; or because birds destined to be lower ranking may still be „acting like a dominant until proven subordinant“ (cf. JACKSON 1988).

(b) Aggressive behaviours in families. DITTAMI (1977, 1979) studied breeding populations of barnacle geese in Spitsbergen and reported several behaviours that differed from the ones observed in this study. He found that (a) males rarely attacked females; (b) the only attacks within families occurred between goslings; (c) after an attack, the two males assumed a sleeping posture near the territory borders; and (d) non-nesting geese always were driven away. In the present study, I found frequent instances of males attacking females; attacks within families occurring

between parents and young; the subdominant male sometimes leaving the area altogether after losing in a conflict; and non-nesting geese generally tolerated and allowed to remain quite close to nesting birds. Some of these differences might be due to stresses imposed by this number of geese living in a concentrated area where nesting, feeding and resting territories are small and surrounded by steep, forested mountains – a habitat that contrasts markedly with their normal nesting areas on the tundra (cf. CRAMP 1977). Also, the geese were continually subjected to stresses from competition with the larger and more numerous greylag geese, which always dominated them. One of the greylag ganders, in fact, killed the top ranking barnacle goose male in 1985 while the latter was defending his nesting box.

4. Zusammenfassung

Beobachtungen zum Sozialverhalten halbwilder Nonnengänse (*Branta leucopsis*). Beobachtungen zur sozialen Dominanz von 48 halbwilden Nonnengänsen in 5 Generationen zeigten, daß die Ranghöhe eines ♂ vom Rang des Vaters und – solange der Vogel noch unverpaart war – auch vom eigenen Rang im Vorjahr abhängt. ♂ mit Familien sind gegenüber den lediglich verpaarten und letztere gegenüber unverpaarten dominant. Die Ranghöhe ist nicht korreliert mit Alter, Brut-Vorgeschichte, Familiengröße, Ranghöhe des Partners und Ranghöhe als Gössel.

Männchen höherer Rangstufen ließen eine stärker lineare Rangordnung erkennen. In allen 4 Beobachtungsfällen wurden verwitwete ♀, unabhängig von ihrer Ranghöhe, unverpaarten ♀ vorgezogen.

Einige ungewöhnliche Verhaltensweisen werden geschildert: Eine Dreierbeziehung (2 ♂, 1 ♀); trauerähnliches Verhalten eines unverpaarten ♂ nach dem Tod eines Gössels; „Eifersucht“ bei einem der ♂ eines Ganter-Paares, wenn das andere ♂ ein ♀ verfolgte; Verpaarung verwitwete Mutter/Sohn; beharrliche Aggression unverpaarter ♂ gegenüber Familien und Einzelgänsen; intensive Verteidigung willkürlicher und innerhalb eines Monats oft wechselnder Territorien (z. B. unbesetzte Nistboxen, Erdhügel).

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