

Male-male Pairs in Greylag Geese (*Anser anser*)

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Pair bonds constituted of same sex partners have been reported for most vertebrate taxa (for reviews see BEACH 1947, BRION & EY 1964, FORD & BEACH 1960, GADPAILLE 1980, MEYER-HOLZAPFEL 1961, MORRIS 1952, 1954, 1955, SCHUTZ 1966). A disproportionate number of these studies have focused on birds (ALLEN 1934, LORENZ 1935, 1940, MASOTOMI 1957, 1959, MORRIS 1954, SAUER 1972, SCHUTZ 1965a, b, WILLIS 1972). The formation of homosexual pairs was commonly attributed to one or more of the following, (1) a failure to correctly identify the sex of a prospective partner — see also “Inferiorism” (ALLEN 1934), “Rangordnungs-Ambivalenz-Theorie” (LORENZ 1935, 1940, ÖHLERT 1958); (2) acceptance of an inappropriate partner (e. g. as a sub-optimal stimulus) at times when appropriate companions are in short supply (MORRIS 1952, GREENBERG 1961); and (3) pseudo-female or pseudo-male behavior in one of the partners (ARONSON 1948, BEACH 1948, MORRIS 1952, 1955). Reports of homosexual pairs are largely restricted to animals held under captive or semi-captive conditions (SCHUTZ 1966), and only a few studies have demonstrated same-sex pairs in the wild (HUNT & HUNT 1977, SCHUTZ 1965). In part, this may be due to the fact that homosexual pairs predominantly occur in species lacking overt sexual dimorphism (DILGER 1960), which makes it also inherently difficult to recognize homosexual pairs in the wild.

In Greylag Geese, as in other members of the subfamily Anatini, both sexes exhibit cryptic feather patterns and it is virtually impossible for the human observer to distinguish sexes in the field. Species which are characterized by a significant reduction in sexual dimorphism, may largely depend on behavioral differences to identify the sex of conspecifics (WELTY 1982, MERRIT & KING 1987, HUBER 1988). This report concerns a flock of 130 free-flying Greylag Geese in which the biological sex of most individuals was known from cloacal inspection shortly after hatching. This represents a unique opportunity to study the nature of pair bonds in geese, as well as the dynamics underlying their formation and maintenance.

The social structure of a flock of geese is much more complex than might be expected from the monogamous breeding system of the species. Besides families, pairs, and single geese, one finds several other social units, including groups of juveniles, trios, and gander pairs (COLLIAS & JAHN 1959, FISCHER 1965). Gander pairs are identified as two males performing pair bonding behavior, i. e. the triumph ceremony (FISCHER 1965, LORENZ 1965), with each other. The first male-male pair bonds were identified in the Grünau flock in 1975 and gander pairs have since represented a promi-

nent social unit in this group. Bonds have been observed to form between males with very different life histories. Frequently, they develop between two brothers as a continuation of their bond as siblings. In some cases brothers who had initially paired heterosexually, formed a pairbond after the loss of their respective partners. Homosexual bonds are less frequently forged between unrelated ganders suggesting the importance of previous familiarity, as had also been suggested for other anatids (SCHUTZ 1966). Some gander pairs which formed in this flock have been found to persist for over 15 years.

The aims of the present study were twofold. Firstly, to test whether a male bias in the sex ratio of the flock favors the formation and maintenance of homosexual pair bonds in this species. Secondly, we attempted to identify the behavioral mechanisms which underlie the formation of such pairs. Homosexually paired males were subjected to a quantitative behavioral analysis in an attempt to compare the partners of gander pairs (1) with each other, (2) to the heterosexually paired gander, and (3) to the heterosexually paired goose.

Study Animals and Methods

This study was carried out at the Konrad-Lorenz-Institute in Grünau im Almtal, Austria, and summarizes data spanning the years 1973–1988. The flock of approximately 130 tame, free-flying greylag geese was established in the Almvalley in 1973 as described elsewhere (KALAS 1979). Colored leg rings permit identification of individuals in the field. For each member of the flock individual data such as age, sex, familial affiliation, pair bonds, aggressive encounters, and diseases, are compiled in a registry. Summary information for the flock, including the number of individuals, the sex ratio, and the number of heterosexual and gander pairs, was obtained from these records.

Six established gander pairs and six heterosexual pairs were selected for a quantitative behavioral analysis. Between September 1983 and April 1984 a total of 100 hours of observations were collected for these pairs. The behavior of heterosexual pairs has been reported in detail elsewhere (HUBER 1988) and we focus here primarily on the gander pairs. The occurrence of agonistic, social-binding, and sexual behavior, and the position of the pair relative to the flock was noted for each minute. Listing of behavior patterns and their definitions follow KALAS (1977). Agonistic behavior refers to all behavioral patterns that share the function of adjustment to situations of conflict among conspecifics, including threats, submissions, chases and physical combat (DRICKAMER & VESSEY 1982). Two categories of agonistic behavior were distinguished, (1) approach-oriented agonistic behavior which directs an individual towards an opponent (e. g. threatening postures, charges), and (2) avoidance-oriented agonistic behavior which has the opposite effect (e. g. flight, vigilant behavior). The shorter forms of "approach behavior" and "avoidance behavior" are used synonymously for these terms. All vocalized behavior that is assumed to have an effect on formation and maintenance of the pairbond comprises social binding behavior (FISCHER 1965, HEINROTH 1911, RADESÄTER 1974, WÜRDINGER 1970). Sexual behavior, i. e. courtship and mating, was observed infrequently and was excluded from all statistical analyses. Replicated goodness of fit tests (G-statistics) were used to compare the frequency of (1) approach-oriented agonistic behavior, (2) avoidance-oriented agonistic behavior, and (3) social binding behavior between the partners of the six gander pairs. For each comparison the sum of the individual G-values was partitioned into pooled G (to test for similarity in behavior between ganders of gander pairs and ganders and geese of

heterosexual pairs), and the heterogeneity G (to test how similar the ganders of gander pairs behaved to each other). The experiment-wise error rate for these 18 comparisons (three behavioral categories in six pairs) was calculated according to the Dunn-Sidak Method (SOKAL & ROHLF 1981). Replicated goodness of fit tests were used to compare the frequency of these behaviors between ganders of gander pairs and gander and goose of heterosexual pairs. For the analysis of the spatial distribution of the pairs relative to the flock a nominal response model (SAS INSTITUTE INC.) was constructed with season and type of pair as treatment effects.

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Results

Although the number of gander pairs fluctuated greatly over the observation period, regression analysis (Fig. 1) demonstrated that the percentage of males in the flock for a given year can significantly explain the percentage of gander pairs formed ($R^2 = 0.766$; $F = 35.963$; $df = 1,13$; $P < 0.001$). This suggests that a lack of single females is an important factor promoting the formation of gander pairs.

Replicated tests of goodness of fit were used to compare the two partners in each of six gander pairs with regard to the frequency of approach, avoidance, and social-binding behavior (Table 1). Two out of 18 possible comparisons proved significant indicating an overall similarity in behavior between the two partners in gander pairs (only the partners of two pairs differed in the frequency of avoidance behavior). Similarly, replicated tests of goodness of fit were used to contrast the behavior of ganders of

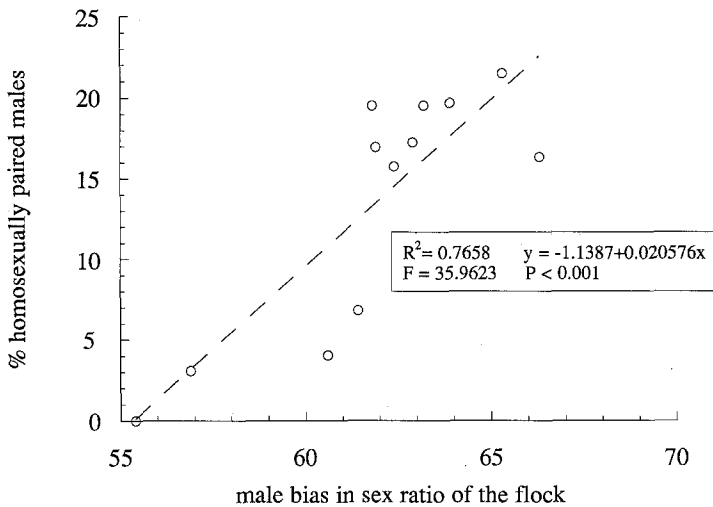


Fig. 1. Relationship between the relative number of males that were paired in a gander pair (% of total males) and the male bias in the sex ratio of the flock (50% represents an equal sex ratio) for years from 1973–1988. A regression line was fitted to the data.

Table 1. Table summarizing the frequency of approach behavior, avoidance behavior, and social behavior observed for 12 individuals (A—L) of six gander pairs. Frequency is equal to the number of minutes in which the behaviors occurred. The total observation time (Obs.) for each pair is given in minutes. The frequency of these behavioral categories among the partners in each pair was compared with replicated goodness of fit tests and the heterogeneity G-statistic (G) is reported. Comparison-wise error rate was adjusted according to Dunn-Sidak and significant values are indicated (** $0.01 \geq p > 0.001$, *** $0.001 \geq p$).

Individuals	Pair 1		Pair 2		Pair 3		Pair 4		Pair 5		Pair 6	
	A	B	C	D	E	F	G	H	I	J	K	L
Approach Behavior	24	19	28	25	14	15	34	21	47	31	34	25
G	0.633		0.184		0.036		3.330		3.687		1.486	
Avoidance Behavior	12	36	33	36	36	44	94	82	90	24	92	73
G	13.729**		0.145		0.931		1.051		47.558***		2.753	
Social Behavior	24	21	12	12	16	16	39	37	25	24	35	32
G	0.218		0.000		0.000		0.058		0.022		0.147	
Obs. (min)	270		345		287		398		375		405	

gander pairs to that of heterosexually paired males and females (Table 2). Individually, ganders of homosexual pairs showed less approach-oriented agonistic behavior than did heterosexually paired males, but were significantly more aggressive than females. However, as pairs, ganders exhibited much more approach behavior than did heterosexual pairs, giving the impression of two geese "terrorizing" neighboring individuals. Social binding behavior and vigilance behavior was found to be significantly higher in homosexually paired ganders (Fig. 2) than in either partner of heterosexual pairs.

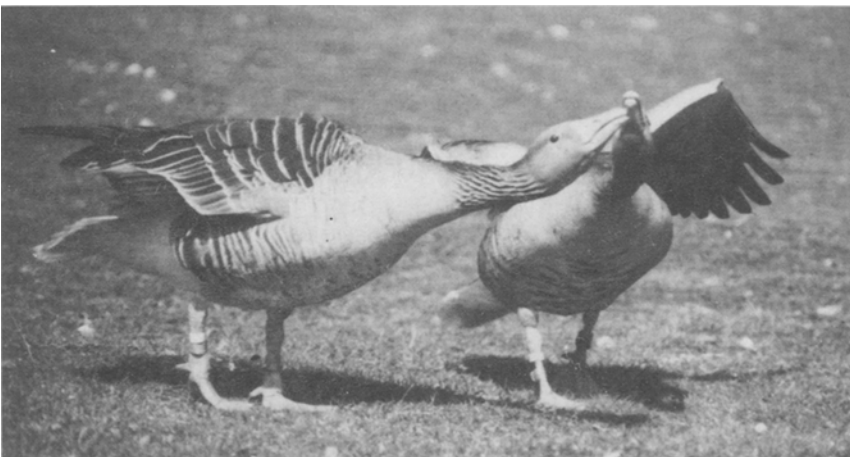


Fig. 2. A gander pair performing the triumph ceremony. This social-binding behavior is performed by both individuals with an intensity equal to that of the heterosexual male.

Table 2. Comparison of three behavior categories for homo- and heterosexual pairs of *Anser anser*. Total observation time (Obs.) for each pair is given in minutes. The frequency (f) represents the number of minutes in which 12 homosexually paired individuals (A-L) demonstrated approach, avoidance, and social behaviors. Observed frequencies were compared to the probability of occurrence (HeteroP) of these behaviors for heterosexual pairs (HUBER 1988). The behavior of homosexually paired ganders was compared to that of heterosexually paired males (G♂) and females (G♀) using replicated goodness of fit tests. Comparison-wise error rate was adjusted according to Dunn-Sidak and significant values are indicated (* 0.05 ≥ p > 0.01, ** 0.01 ≥ p > 0.001, *** 0.001 ≥ p, df: degrees of freedom).

HeteroP	Approach Behavior			Avoidance Behavior			Social Behavior			df	
	σ	G♂	G♀	σ	G♂	G♀	σ	G♂	G♀		
Ind. Pair	f	f	f	f	f	f	f	f	f		
A	270	24	3.878	28.262***	12	15.468***	1.319	24	18.750***	32.337***	1
B		19	9.088**	15.916***	36	1.232	51.894***	21	12.781**	23.934***	1
C	345	28	7.343*	29.137***	33	0.914	30.543***	12	0.056	2.273	1
D		25	10.693**	21.953***	36	0.182	37.912***	12	0.056	2.273	1
E	287	14	20.019***	5.520*	36	0.543	48.275***	16	4.085	10.811**	1
F		15	18.009***	7.022*	44	4.597	73.933***	16	4.085	10.811**	1
G	398	34	6.874*	37.981***	94	49.176***	234.397***	39	35.758***	58.725***	1
H		21	24.592***	10.052**	82	29.603***	182.417***	37	31.179***	52.523***	1
I	375	47	0.008	81.862***	90	48.947***	227.332***	25	10.756**	22.866***	1
J		31	7.429*	33.103***	24	9.914**	10.066**	24	9.291**	20.590***	1
K	405	34	7.535*	37.089***	92	43.636***	222.249***	35	26.024***	45.593***	1
L		25	18.679***	16.631***	73	16.651***	143.955***	32	20.101***	37.236***	1
Total		134.148***		324.527***		220.864***	1264.291***		172.921***	319.973***	12
Pooled Heterogen.	4160	317	110.476***	300.855***	652	77.444***	1120.872***	293	143.892***	290.944***	1
			23.672*			143.420***			29.029**		11

The spatial distribution of the entire flock covered a greater area and appeared less defined during the spring, the annual breeding season, than during the remainder of the year. The partners of both homo- and heterosexual pairs spent more time on the periphery or away from the flock than during the rest of the year (Wald chi-square = 371.024, $df = 2$, $P < 0.001$). Independent of the season, gander pairs spent significantly more time on the periphery or away from the flock than did heterosexual pairs (Wald chi-square = 143.220, $df = 2$, $P 0.001$) as is evident in the pie chart summaries (Fig. 3).

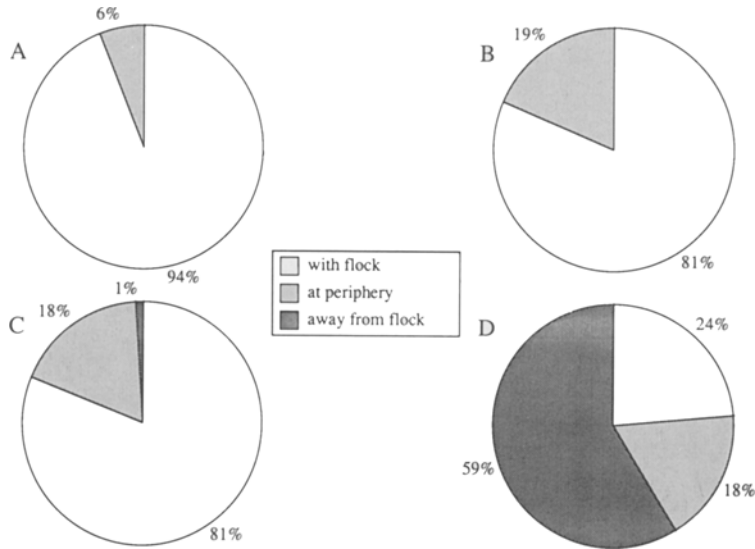


Fig. 3. Pie diagrams summarizing the amount of time spent in the flock, at its periphery, and away from the flock for (A) heterosexual pairs during the year excluding spring; (B) gander pairs during the year excluding spring; (C) heterosexual pairs in spring; (D) gander pairs in spring.

Discussion

To date there has been no published record of gander pairs in wild flocks of greylag geese. The present study indicates that both males of a gander pair in *Anser anser* are characterized by a high level of agonistic and social behavior. Particularly aggressive pairs that "terrorize" the rest of the flock have also been observed in snow geese (SCOTT pers. comm.) but the true sex of these individuals was not confirmed.

As the number of gander pairs was found to be highly dependent on the sex ratio, a lack of available females is suggested to enhance homosexual pair formation. Gander pairs were only observed when the male ratio exceeded 55%. In a similar flock at the Max-Planck-Institute for Behavioral Physiology in Seewiesen, which tended to be biased towards females (ST. PAUL pers. comm.), homosexual pairbonds were observed in only a few instances.

The hypothesis that the male-male pairbond is facilitated by pseudo-female behavior of one of the partners, was not supported. Both ganders of a homosexual pair were similar in behavior and no similarities to the behavior typical of females was detected. This is in accordance with the behavior of homosexually paired male mallards (SCHUTZ 1965 a, b), where both partners exhibited male behavior, treating the respective partner as if he were female. A potential instability of this pair bond may account for the increased frequency of social-binding behavior. Moreover, several instances were observed in which a gander, having launched an attack on bystanding geese or returned with an initiation of the triumph ceremony, was subsequently attacked by its own partner (see also RADESÄTER 1974).

The increased amount of vigilance behavior and the lower frequencies of agonistic interactions detected in homosexually paired ganders were due to the fact that gander pairs spent significantly more time apart from the flock or at its periphery. Indeed, while with the flock, the frequencies of approach behavior and vigilance behavior were not significantly different between males of gander pairs and those of heterosexual pairs.

All sexual acts of gander pairs, particularly attempted and successful copulations, began with precopulatory displays of both ganders such as "head-dipping" and "Koggenhaltung" (FISCHER 1965, HEINROTH 1911, JOHNSGARD 1965), followed by attempts to mount. In pairs where the size discrepancy is large, the smaller gander was frequently forced into the female position and mounted. In pairs of similar size attempts may (1) continue for some time until one animal succeeds in mounting of its partner (reversals of the male position on consecutive days were observed in several such pairs); (2) increase in intensity and culminate in a fierce fight; or (3) one gander may mount inanimate objects, such as logs, or a bystanding female or male goose which had joined in with the precopulatory display (COLLIAS & JAHN 1959). In either case, the post-copulatory display is always directed towards the true partner, and not towards the animal or object it copulated with.

The apparent lack of female-female pair bonds is notable and several reasons may be advanced for this. Females may not demonstrate sufficient pair-bonding behavior to form and maintain a viable pair bond (HUBER 1988). Moreover, the fact that females are the limiting sex in the flock (i. e. the sex ratio is male biased) does not favor the formation of female pair bonds.

There are a number of (non-exclusive) hypotheses which may explain the presence and function of gander pairs in *Anser anser*. (1) As gander pairs are frequently positioned at the periphery of the flock with vigilance behavior, they may serve a guardian function for the flock as a whole. (2) Male aggression is usually directed towards other males in the flock. A large portion of homosexually paired ganders may succeed in forcing unpaired ganders out of the flock, thereby controlling an excess of males and enhancing social stability. (3) A pair bond with any other individual may be a superior strategy to remaining single, as the latter have a higher rate of predation and reduced access to resources. (4) A sociobiological perspective might contend that gander pairs

represent a "buffer system" for males in the flock at times when the sex ratio is strongly biased towards them, enhancing both individual and inclusive fitness and maintaining breeding potential. Alternatively, gander pairs may represent merely an epiphenomenon in the social structure of a male biased flock of greylag geese.

Summary

For almost two decades a flock of 130 free-flying Greylag Geese (*Anser anser*) has been the focus of detailed ethological investigations at the Konrad Lorenz Institut in Grünau im Almtal, Austria. Gander pairs, i. e. male-male pairs, represent a prominent social unit in this flock and were the subject of a detailed behavioral investigation. Analysis of the composition and dynamics of the flock over a 15 year period indicated that the incidence of homosexual pairings closely paralleled the male bias of the sex ratio. The behavior of ganders in gander pairs was investigated and compared to that of gander and goose in heterosexual pairs. The behavior of the two males in a gander pair (1) was comparable in most aspects, (2) was similar to the behavior of the gander in heterosexual pairs, and (3) differed greatly from that of the heterosexually paired goose. Therefore, pseudo-female behavior in one partner cannot account for the formation of a pairbond between two males. As a unit, gander pairs were characterized by a higher frequency of offensive agonistic behavior compared to heterosexual pairs and spent significantly more time peripheral to, and away from the flock than did heterosexual pairs.

Zusammenfassung

Das Sozialgefüge einer Schar Graugänse ist weitaus komplizierter, als es das monogame Fortpflanzungssystem erwarten ließe (COLLIAS & JAHN 1959, FISCHER 1965, KALAS 1979, RUTSCHKE 1982). Ganterpaare, die häufig über Jahre hinweg bestehen bleiben, sind für tiersoziologische Untersuchungen interessant, weil ihre Funktion nicht im Rahmen der Fortpflanzung gesehen werden kann. Welche Bedingung begünstigen die Bildung von Ganterpaaren, und welche Verhaltensmechanismen tragen zum Entstehen und zur Aufrechterhaltung dieser Verbindung bei? Die Zusammensetzung der Grünauer Graugansschar 1973—1988 zeigt, daß die Anzahl der Ganterpaare von einem Überschuß von Männchen in der Schar abhängt. Das Verhalten von 6 Ganterpaaren wurde untersucht und mit dem von heterosexuellen Paaren verglichen. Innerhalb eines Ganterpaares entsprachen sich die Partner in der Häufigkeit von agonistischem sowie sozial-bindendem Verhalten. Homo- und heterosexuell verpaarte Ganter zeigten sich im Verhalten vergleichbar. Der Ganter eines Ganterpaares unterschied sich jedoch in der Häufigkeit aller untersuchten Verhaltensweisen von dem der heterosexuell verpaarten Gans. Folgende Schlußfolgerungen und Hypothesen bieten sich an: (1) Pseudo-weibliches Verhalten bei einem der Ganter scheint nicht die Bildung von Ganterpaaren erklären zu können. Beide Ganter verhalten sich rein männlich und behandeln den Partner so, als ob dieser ein Weibchen wäre. (2) Ein Mangel an gegengeschlechtlichen Schargenossen fördert die Bildung von homosexuellen Paaren und aufzuchtsbekannte Vögel werden dabei vorgezogen. (3) Ein Zusammenschluß mit einem gleichgeschlechtlichen Artgenossen sollte, verglichen mit der Möglichkeit alleine zu bleiben, eine überlegene Strategie darstellen, da unverpaarte Gänse geringeren Zugang zu Futterquellen haben und eher Raubtieren zum Opfer fallen. (4) Homosexuelle Paare könnten als ein „Puffersystem“ für Ganter angesehen werden, vor allem zu Zeiten in denen das Geschlechtsverhältnis in Richtung der Männchen verschoben ist. (5) Aggression des Ganters richtet sich generell gegen andere männliche Schargenossen. Die Bildung von Ganterpaaren, also besonders aggressiven Paaren, könnte daher dazu beitragen, Ganter aus der Schar zu

vertreiben und ein Übermaß von Männchen in der Schar zu verhindern. (6) Da wir zeigen konnten, daß sich homosexuelle Paare oft am Rande der Schar aufhalten und dabei häufig sichern, könnte solchen Paaren eine Art Wächterfunktion zukommen. (7) Andererseits ist es durchaus möglich, daß Ganterpaare bloß ein Epiphenomen einer Graugansschar mit einem Überschuß an Männchen darstellen.

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