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THE UNIVERSITY OF ALBERTA

A STUDY OF SOCIAL DOMINANCE IN CANADA GEESE

by

GARY GREGOIRE

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A STUDY OF SOCIAL DOMINANCE IN CANADA GEESE submitted by GARY GREGOIRE in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

Supervisor

Jan O. Murie

Date: April 11, 1988

Abstract

Dominance relations among Canada geese (*Branta canadensis*) were studied in the family state, and non-family state (i.e. goslings separate from adults and the converse). Males, both goslings and adults, interacted with other geese more frequently than did females; males were dominant over females. Adult males interacted more among themselves than did adult females, but in the case of goslings the proportion of interactions within each sex was similar. There was no correlation between size and dominance status among either adults or goslings. The frequency and intensity of agonistic interactions among parentless goslings declined through time, and the hierarchies established showed high stability over time. Several methods, including artificial manipulation of the number of goslings in a series of broods, were used to determine if the dominance status of a family of Canada geese is a function of the numbers of goslings it possesses. The results showed a positive relationship between family size and dominance status (i.e. large families (4 or 5 goslings) dominated small families (1 or 2 goslings) more often than the converse). Large families interacted more among themselves than did small families. The status of the family at this time was largely independent of the dominance status of the parents during the post-breeding period. Partial loss of the brood before fledging, however, had little effect on the family's previously-acquired dominance status within the group of families, but complete loss resulted in a general decrease in rank status of previously more dominant pairs. Family dominance status was not related to hatch date of goslings, but the frequency and intensity of agonistic interactions among families declined over time after hatching. Among parentless goslings, most large broods dominated small broods. More dominant families gained priority of access to resources such as food and shelter (be they limiting or not). Goslings, unlike adults, showed no apparent competition for limiting resources.

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INTRODUCTION

Throughout the animal kingdom are species that form social groups. Such groups have evolved apparently in response to the selective advantages accruing to their members through avoidance of or defense against predators, group defense of food and space, and through the exploitation of these resources (Krebs and Davies, 1978). Within such groups a hierarchical arrangement of individuals may raise feeding efficiency by reducing intra-group aggression; it may also reduce vulnerability to predators through more effective intra-group vigilance. Social hierarchies may also provide a mechanism that can limit natality locally through the regulation of the numbers of reproductively active individuals and the identification and elimination of surplus subordinate breeders (Watson and Moss, 1970).

Large flocks of geese are social groups composed of subflocks, which in turn are composed of families. Within each subflock is found a hierarchical arrangement of families based on dominance status (Raveling 1970, Bellrose 1980). Dominance behaviour is reported to influence the inclusive fitness of several species of geese (e.g. Jenkins 1944, Hanson 1953, Collias and Jahn 1959, Lorenz 1966, Raveling 1970, Lamprecht 1986a) through a positive correlation between dominance status and subsequent fledging success.

Traditionally, an explanation for dominance rank within hierarchies has been sought in the physical characteristics of the individual such as sex, weight, or some size attribute. In a summary of current knowledge on the determinants of dominance, Wilson (1975:291) reported that males usually dominate females. He added that, in multimale societies, it is typical for the rank ordering of the males to lie entirely above that of the females, or at most to overlap it slightly. Several authors have suggested this to be the relationship between the sexes in Canada geese (e.g. Boyd 1952, Collias and Jahn 1959, Raveling 1970, Lamprecht 1986a). Wilson (1975) points out that few studies have found any correlation between weight (and by implication size) and dominance status; this was supported by Lamprecht (1986a) for adult bar-headed geese (*Anser indicus*). In this study I determined the relationship between gender and dominance status, as well as the influence of body weight and structural size (tarsus length) on dominance status, in both gosling and adult Canada geese.

If dominance status is to have some selective advantage it must be shown to be stable over time. It is generally accepted that dominance hierarchies do gain stability over time. Chase (1974) argued that the frequency and intensity of aggressive interactions subside over time as the dominance status of individuals in a group of animals becomes known. Rowell (1974) noted, however, that there is little conclusive evidence in the literature to substantiate this general belief. Radesäter (1974) showed that the intensity of agonistic interaction decreased with time among goslings in broods of greylag (*Anser anser*) and Canada geese. To confirm that this relationship held true in captive Canada geese, I recorded the frequency of interaction over time among goslings in parentless broods of various size, and assessed the hierarchical linearity and stability over time within these broods.

After considering dominance relationships among goslings that had been separated from their parents, I turned my attention to the family situation, as typically represented by geese in the wild. Geese exhibit strong social bonds among members of the nuclear family; young of the year usually remain in close association with their parents until the beginning of the following breeding season (Bellrose 1980:109,158, Prevett & MacInnes 1980). Among Canada geese, families remain intact throughout the winter (Raveling 1969). Canada geese are also highly philopatric, migrating annually between their traditional natal and wintering grounds (Raveling 1979). Inexperienced juveniles may improve their chances of surviving to breeding age by following their parents to these traditional and proven roosting and feeding areas on the summer and winter ranges (Akesson and Raveling 1982). The dominance status of the family group and hence its success in agonistic encounters with other families and individuals, particularly in flocks on the wintering grounds, is reported to be directly related to family size; larger families dominate smaller families within the flock which in turn dominate pairs, and pairs dominate singles (Boyd 1953, Hanson 1953, Raveling 1970, Gregoire 1985). Although the evidence is only circumstantial, it has generally been assumed that larger more dominant families have priority of access to resources when they are in limited supply (Raveling 1970, Gregoire 1985). This would imply that the size of the family unit has survival value. It also assumes that the dominance status of the family is a function of numbers of goslings in the brood (Jenkins 1944, Raveling 1970). That the dominance status of the family reflects the dominance status of the parents, and as a consequence dominant parents raise larger broods than subordinate parents, is a possibility that has not been addressed. In this study, I performed several experiments to determine the relationship between family size of Canada geese and their dominance status in the group. This objective was expanded to determine whether the number of goslings in a brood without parents was correlated with their dominance status when interacting with other parentless broods containing different numbers of goslings.

Dominance status is not a characteristic of the individual as such but only of that individual relative to others in its group. Thus, dominance is not an absolute attribute but a probabilistic one – dominant individuals having a higher probability of gaining priority of access to contested resources than subordinate individuals (Kreveld, 1970). By allowing certain individuals priority of access to resources, including mates, hierarchies provide an unequal distribution of these advantages. Situations in which resources are not in short supply probably permit all individuals to have access to them but dominant individuals may continue to have priority-of-access to those resources of highest quality. If resources are in limited supply, however, rank position in the hierarchies may mean the difference between having access to these resources or not (Morse 1980). In this study, I considered the influence of dominance status, shown by captive Canada geese, on their ability to gain access to limited resources.

METHODS

Study of parentless goslings

This study of dominance relationships among parentless goslings of Canada geese made use of the facilities at the Brooks Wildlife Centre (hereafter referred to as BWC) located 10 km east of Brooks, Alberta. The BWC provided the facilities needed to incubate eggs, raise the goslings, and house the geese until they fledged.

In 1983, 21 Canada goose eggs were collected, each from a separate nest in the wild, and upon hatching in an incubator all individuals were imprinted on me. I raised these goslings (12 males and 9 females) together as a group. Web tags and fluorescent red paint were applied as a means of individual identification of the goslings until they were old enough to wear individually identifiable coloured neckbands. According to Raveling (1969), and references therein, colour-marking has no noticeable effects on the behaviour and social relationships of Canada geese; I recorded no behavioural effects either.

After approximately 1 month at the BWC, the young geese were transferred to a new location at Bantry Lake (7 km east of the BWC). From the time of hatching (between 7 and 14 May), until the end of the study (12 July), the goslings were weighed at regular intervals of approximately 1 week and observed for an average of approximately 5 hours per day, 7 days per week. The variation in initial weights of members in the group taken on 14 May reflects mainly differences in age (up to 7 days). During the periods of observation, the outcome of agonistic interactions between individuals were recorded as wins and losses. Aggressive encounters consisted of either fights, frontally directed pecks, chases, or displacements (threat or otherwise). Fights involved birds biting each other on the head and/or neck, while beating one another with their wings. Chases involved the active pursuit of the retreating bird(s). Displacement involved a bird moving away from another's threats and/or advances in its general direction (only obvious displacements were recorded). Ranking of birds was based on the ratio of wins to losses. In order to avoid any potential bias when interpreting the outcome of interactions because of sex of goslings involved, I did not determine the sex of each gosling until the end of the study period. Furthermore, subjective interpretation when recording wins and losses was avoided by eliminating from the data set any interactions that were not obviously either wins or losses. These criteria were also used in the subsequent research in 1984 and 1985.

In each year of the study (1983 - 1985), I attempted to induce competition for resources among goslings by exposing them to food and water in containers that were small enough to allow only one gosling access at a time.

In 1984 five natural broods of siblings were obtained consisting of: seven (5 males and 2 females), five (3 males - 2 females), four (2 males - 2 females), two (2 males), and one gosling (female). These goslings hatched between May 11 - 13 from eggs produced in captivity and incubated artificially. Each brood was imprinted on me, and taken regularly for walks in the surrounding area. The broods were kept separate in visually isolated enclosures (proportional in size to the number of goslings in each brood), and interactions among individuals within broods were recorded from 11 - 30 May. The outcome of an agonistic interaction was recorded as either a win or loss; a comparison of the ratio of wins to losses among individuals was used to determine relative rank status. Observations were performed between 0800 and 1800 hours, and since all broods were given equal attention for all time periods during the observation day, this controlled for any possible time-of-day effects on interaction frequency.

In 1985, a replicate of a similar set of broods with identical sex ratios, consisting of 7, 5, 4, 2, and 1 goslings was used. However, they were composed of nonsiblings (goslings obtained from eggs taken in the wild in the vicinity of the BWC). The procedure followed for these broods was identical to that described above for the broods of true siblings in 1984. In both 1984 and 1985, the dominance status of each brood, relative to all others, was determined so as to consider the effect of brood number on its dominance status. All pair-wise combinations of larger versus smaller broods were tested. For each comparison, two broods were placed in an unfamiliar pen and observed until their relative dominance status emerged, that is, when one brood (the dominant) clearly and repeatedly displaced the other brood (the subordinate).

Data sets obtained in this study were compared using parametric statistics where assumptions about normality and equality of variances were not violated. Otherwise non-parametric statistics were used. Differences were considered significant when $P < 0.05$.

Study of family units

For this portion of the study, I used a captive flock of Canada geese maintained year around at the BWC. The primary feathers of these birds were clipped to prevent flight. In 1985, 14 pairs of captive Canada geese were used to study the influence of family size on dominance status. Each pair was kept in an separate breeding pen (10 X 10 m) containing a pond (2.6 X 2.6 m), metal feeder, and nesting structure. Each pair laid a clutch of eggs, incubated them, and successfully hatched them. Hatch dates varied from 8 May to 5 June.

Seven pairs were allowed to raise five gosling and seven pairs two goslings. The number of goslings was assigned randomly to each pair before hatching occurred. In order to have the assigned numbers, it was necessary to manipulate some of the broods by either adding or removing goslings; one gosling was added to each of two families of four, two goslings were added to one family of three, and one gosling was added to a family with one. The goslings added were hatched from eggs artificially incubated from clutches collected in the wild. Donor goslings were both hatched and introduced to the recipient broods within 24 hours of hatching of the recipient brood. This ensured acceptance of the donated young by the recipient families, as well as successful bonding among members of the family group.

In order to promote strong bonds between goslings and parents and thus eliminate the possibility of creching, each family was kept isolated in its individual breeding pen until 29 June (one family with five goslings lost one gosling during this period), when they were released into a common grazing pen of approximately 1 ha. This large pen contained a central pond (approximately 20 m in diameter), as well as two feeders (separated by several metres and thus defendable) filled with commercial food pellets. In an effort to compare the status of families with that of other potential units within the summer flock, three single adults and three adult pairs without young were placed in the same grazing pen with the families. Food was provided *ad lib* in Phases 1 (30 June to 23 July) and 2 (25 July - 12 August), but, in order to initiate interactions, in Phases 3 (2 September - 31 October) and 4 (late February - early March), food was provided only twice a day, in one feeder, for a 1.5-hour period. All adult birds were individually identifiable by the metal bands and coloured neck-collars they bore.

Observations of interactions among the families were made from a 2.5 m tower located near the perimeter of the large grazing pen. I used 10 X 50 mm binoculars on a tripod to identify individually marked birds, and a hand-held tape recorder to record interactions. During observation periods (averaging approximately 6 hours per day) the entire flock was scanned for interactions, and all aggressive encounters and displacements were recorded for all individuals involved (except those involving an individual that became separated from its family). Aggressive encounters consisted of either fights, pecks, chases, or displacements as described earlier. In determining dominance ranks of families, the win-loss records between all dyads in the group were compared (within any dyad the one with the higher win/loss ratio was called the higher-ranking or more dominant). A family's overall rank was based on the number of other families it dominated.

Weights of the adults were recorded on three occasions during Phases 1 and 2 of the study (28 June, 25 July, and 19 August); tarsus length of the adults was also recorded in early summer. The relationship between these two variables and dominance status was tested. Since food was not limited during Phases 1 and 2, it was assumed that all the birds were in relatively similar body condition, and thus variable body condition would not be a complicating factor in the analysis.

The flock, containing 14 families, was under observation between 30 June and 23 July (Phase 1) (one gosling in each of two families of two goslings died during the first week of Phase 1). On 24 July, four goslings were removed from each of the three most dominant large families (reducing the number of goslings in each to one) in an effort to determine if the dominance status of these families would change with this reduction in brood size. I did not remove any goslings from the four remaining large families, because I wished to determine whether their dominance status would increase once they had relatively more goslings than the others. The flock, so modified, was observed from 25 July to 12 August (Phase 2). After 12 August, all goslings were permanently removed from their parents in order to rank the pairs without their young. These ranks in the hierarchy were obtained between 2 September and 31 October (Phase 3). Observations were discontinued between 12 August and 2 September to allow the newly broodless pairs a period of potential readjustment in dominance status. Upon completion of Phase 3, the pairs were left over winter together in a pen that encompassed approximately 1080 m^2. In late February and early March of 1986 the hierarchy recorded among pairs the previous autumn was reassessed (Phase 4).

In the same year (1985) I used seven late breeding pairs, not included in the above experiments, to create a potential crèching situation. I did this by releasing the pairs with their newly hatched goslings into a common pen immediately after hatching rather than holding them in separate pens for an extended period as in the previous experiment. The seven families included one with only the female parent. Two pairs (LM and KK) were given foster goslings to replace the number of non-fertile eggs they were incubating. Within 24 hours of their expected date of hatch, the infertile eggs were replaced with pipped eggs obtained from the wild. These two families with foster goslings each had three goslings, another (EE) had five goslings, three (AA, XX, and NN) each had four goslings, and the lone parent family (ZZ) had a single gosling. At approximately 48 hours post-hatch, each of these families were released into a second grazing pen, similar to that described above, on the following dates: ZZ and NN on 9 June, KK on 11 June, LM on 12 June, XX on 13 June, AA on 14 June, and EE on 16 June. Pairs EE and XX eventually (by 20 June) took possession of all the goslings in this group: each had nine goslings, the remaining six goslings having disappeared (known or presumed dead). On 11 July, these two families were released into the first grazing pen containing families with small (1 or 2 goslings) and large (4 or 5 goslings) broods. From this point onward these families with gang broods were included in all aspects of the study of the family groups as described earlier. The broods in these two families were also reduced to one gosling each in Phase 2, and all their goslings were removed in Phases 3 and 4.

RESULTS

Study of parentless goslings

Sex and dominance status

Considering all interactions among 21 goslings (Table 1) between 14 May and 12 July, males dominated females significantly more often than the reverse. When this time period was partitioned into halves, in an effort to determine any difference with age in the ability of one sex to dominate the other, the relative proportion of males dominant to females did not change significantly, but the actual rank position of many birds changed (Table 1). The proportion of interactions within and between sexes did not differ significantly from a random distribution (Table 2).

Relationship between weight and dominance status

There was no significant correlation between weight and dominance status among female goslings during any of the seven time intervals (Table 3). Among males, weight was correlated positively with dominance status only during the first of seven time intervals (Table 3).

Hierarchical linearity and stability within broods

Data from the relationships among Canada goose goslings in parentless broods of seven, five, and four in 1984 and 1985 were used to investigate the linearity and stability of hierarchies established in each brood. Landau's index (h) of linearity (Lehner, 1979) ranges between 0.0 and 1.0, with the latter denoting a strictly linear hierarchy. Based on this index, the hierarchies showed significant linearity in all three broods of seven (Table 4). Although brood sizes of five and four were too small to test for significant linearity, the "h" values obtained (Table 4) suggest that most of the broods exhibited a linear or near-linear hierarchical arrangement.

A comparison of the within-brood dominance relationships among the goslings in the hierarchies recorded during the first and second halves of the study period in 1985 showed that the number of rank changes occurring, relative to the number possible, was small (Table 5), suggesting a high level of stability within the hierarchies.

Frequency of interaction among goslings over time

The frequency of interaction among goslings in parentless broods of varying size was recorded over time. In 1984, and possibly in 1985, there was a trend indicating that the number of interactions among goslings (per bird per unit time) decreased over time (Figs. 1 and 2). Considering only the frequency of fights, a decrease in numbers is more clearly evident over time for each brood size (Fig. 3).

Based on the data in Table 1, which represent an average of 5 hours observations per day, 253 interactions were recorded during the first half of the study period (n = 23 days) while 148 were recorded during the second half (n = 35 days), a significant decrease in the number of interactions during the second period (X^2 (adjusted) = 92.08, $P < 0.001$).

Brood size and dominance

The outcome of interactions between parentless broods of different size was recorded. In 1984, of 10 trials in a neutral arena, larger broods won 9 (the exception being a brood of two winning over one of four). In 1985, with the replicate groups (A and B) under similar conditions, larger broods won 30 of 40 trials ($X^2 = 10.0$, $P = 0.002$) (the exceptions being 3 cases of a brood of 5 over one of 7, 2(4 over 7), 1(2 over 7), 2(4 over 5), 1(2 over 5), 1(2 over 4)).

Relationship between dominance status and access to limiting resources

Restricting access to food and water by placing them in small containers that allowed only one bird access at a time reduced the relative availability of these resources. Under these circumstances, the goslings were expected to show increased levels of agonism. I was unable, however, to detect any competition, and it appeared that all had equal opportunity to eat or drink. Since the birds had been deprived of food during the night, they were all both hungry and thirsty before the observations were made the following morning and would all immediately crowd around the introduced containers of food and water. The ones that were closest to the containers (apparently independent of dominance status) arrived first and were the first to partake. Others, though, would methodically take turns gulping down a mouthful of food or water. It did not appear that any birds actively prevented others from having access to the resources. In fact, during these experiments, it appeared that agonistic interactions ceased while the goslings were getting their fill. In short, access to the limiting resources appeared to resemble a random event among the goslings.

Study of family units

Sex and dominance status

Considering the adult paired geese over the entire study period (data for all four phases combined), males (M in Table 6) were involved in 3486 interactions with individuals or groups other than males, significantly more often ($X^2 = 64.69$, $P < 0.001$) than females (F) were (2846) with individuals or groups other than females (Table 6). Adult males were also significantly more successful (93%) than adult females (35%) in winning interactions (Table 7), and males interacted with other males much more often than did females with other females (Table 8).

During Phase 1, 20 male goslings were involved in more ($X^2 = 119.4$, $P < 0.001$) interactions (168) than 26 female goslings (46) (Table 6). During Phase 2, involving 16 males and 18 females, the difference (127 versus 12 - Table 6) was also significant ($X^2 = 109.6$, $P < 0.001$).

During Phase 1, the 28 adults were involved in more ($X^2 = 966.8$, $P < 0.001$) interactions (1768) than the 46 goslings (G) (861) (Table 6). The same was true during Phase 2 when the 28 adults were involved in 1186 interactions and the 34 goslings in 456 interactions, a difference that was again significant ($X^2 = 485.9$, $P < 0.001$) (Table 6). Thus, adults were involved in a significantly greater number of interactions than the goslings.

Weight and structural size versus dominance status

Weights of the 32 Canada geese, comprising the 16 adult pairs including pairs EE and XX with gang broods, were recorded on three occasions during the summer of 1985 (June 28, July 25, and August 19); tarsus lengths of these birds were also recorded. I compared the mean of these weights for each male and each female with its rank (shown as a pair) in the hierarchy. The same was done with tarsus length. In neither sex were these variables correlated with dominance status (Table 9).

Dominance status among Canada goose families

That family size was related to dominance status was evident in the significantly greater number of agonistic interactions won by large than by small families during Phase 1 (Table 10 & Fig. 4). It is noteworthy, however, that only one family won every interaction against families of a different size; this was a family with one gosling (coded G in Fig.4). In Phase 1, 12 of the 17 trials won by small families involved only two families (G and D, Fig. 4), and in Phase 2 these two families accounted for 11 of the 15. During Phase 1, large families were also involved in significantly more ($X^2 = 192.9, P < 0.001$) interactions (2412) than small families (1538) (Table 11). Moreover, during this period, large families won proportionally more interactions than small families (Table 11). As a consequence, large families generally had greater priority of access than small families to such resources as shelters and food bins. Hatch date of the young in a family was not correlated to rank status of the family in the hierarchy (Table 12). During Phase 2, after removal of all goslings but one from the three most dominant large families, these originally large families (coded as 1, 3, 6 in Figs. 4, 5 & 6) retained their original dominance status; i.e. no reversals were scored. Thus, large families continued to dominate small ones in Phase 2 (Table 10). In comparing the rank position of the 14 family units between Phases 1 and 2, a high degree of stability was found (Table 13). Of 91 possible dyadic combinations that could have changed between Phases 1 and 2 when all the families were considered, only four reversals were scored between the two phases; three of these reversals took place between large and small families, but none involved the large families from which goslings had been taken in Phase 2 (Figs. 4 & 5). Thus, the dominance relationships among the families remained stable over time. In Phase 3, after the adult pairs had been deprived of all goslings for over a month, the outcome of agonistic interactions changed significantly; those pairs that had five goslings originally no longer dominated, to the same degree, pairs that had only two goslings (Tables 10 & 13, Figs. 4, 5 & 6). In Phase 4, after the pairs had been without young for approximately 6 months, their relative dominance status was unchanged from that found in Phase 3 (Tables 10 & 13, Figs. 6 & 7).

Without exception, families dominated pairs without goslings as well as lone adults: in Phase 1, families won all 442 interactions against pairs, and all 214 against singles; in Phase 2, families won all 282 against pairs, and all 152 against singles.

In Phase 1, 1975 interactions were recorded over a 24-day observation period, while in Phase 2, 1230 interactions were recorded over a 19-day observation period. Considering an average of 6 hours of observation per day, a significantly greater number of interactions were recorded in Phase 1 (X^2 (adjusted) = 43.8, $P < 0.001$), indicating a decrease in the frequency of interaction over time. Before food was rationed during Phase 3 (i.e. during the first week), the rate fell to approximately 20% of that recorded per day during Phases 1 or 2 when goslings were present.

In the second group of seven families housed initially in a separate pen, crèching occurred with pairs EE and XX pirating all goslings present. Of the nine goslings in family EE, three were its own, two were recruited from family XX (the other two goslings of family XX disappeared and were presumed dead), and four came from the remaining families. All nine goslings in family XX came from other pairs. In no case did goslings of a given family become divided between the two crèches.

The resulting families of both EE and XX were highly successful in winning interactions with other families (Table 14). However, between Phases 1 and 2 (with goslings) and Phases 3 and 4 (in the absence of goslings) the win-loss record dropped several percentage points, a decline that was statistically significant ($X^2 = 5.62$, $P = 0.018$) (Table 14). Worthy of note is the fact that the goslings in families EE and XX were all hatched later (June 8 - 15) than those in the other 14 families (May 8 - June 5), and consequently were much younger, and hence smaller in size than any gosling in the other families. As well, they were disproportionately smaller because of slower growth in a grazing pen that contained no commercial feed. Despite this size differential, individual goslings from both families EE and XX were at times successful in dominating larger individuals (goslings and adults) of other families.

DISCUSSION

Relationship between sex and dominance status

I found that adult males interacted more frequently among themselves and that males, both adults and goslings, were in general dominant over their female counterparts; male goslings began to dominate females from the onset of life. Raveling (1970) reported (without quantification) that within various age classes of Canada geese (juvenile and older), single males dominated single females. In this study, it appeared that the rank order of families depended most highly on the dominance status of the gander. Other researchers have indicated the importance of the gander in dominance relations. For example, Raveling (1970:298) reported that families had a higher success ratio in agonistic encounters when the gander was involved. With bar-headed geese (*Anser indicus*), Lamprecht (1986a) also provided evidence that suggested the gander's strength and motivation was the main determinant of rank of a pair or family. Lorenz (1966) provided evidence from greylag geese suggesting that a female acquires the rank status of her mate. Boyd (1952) found that for both family and non-family pairs of white-fronted geese (*Anser* *a. albifrons*), males were clearly more successful in winning interactions than females, and took part in a larger share of the agonistic contacts of the unit. Interestingly, however, he noted (as did I) that the sexes were alike in the vigour of their attacks and in the threats they used. It is generally agreed that in geese, the gander invariably takes on the greatest role in defending the family unit when threatened, the goose being secondary in this capacity. Collias and Jahn (1959), Ewaschuk and Boag (1972), and Akesson and Raveling (1982), have observed that the maintenance of territory among Canada geese usually depended upon the gander's ability to dominate outsiders. The female's preoccupation with nesting activities during the breeding season probably forces the male to be mainly responsible for territorial defense.

Unlike the adults, I found that male goslings interacted among themselves to the same degree that female goslings did. Since there is no apparent differentiation in sex roles at this age, and since the young appear to make use of essentially the same resources in a similar manner, it would seem plausible that interactions be independent of gender. Nevertheless, the outcome of these interactions was asymmetrical, with males winning significantly more than females.

Relationship between both weight and structural size and dominance status

A comparison of weight, and length of tarsus, versus dominance status yielded no relationships among Canada geese. Wynne-Edwards (1962) noted for many species of mammals and birds the lack of any correlation between dominance status and size or apparent strength. According to Allee (1951), there is no correlation between weight and dominance position in the peck order of chickens. Although Raveling's (1970) data is confined to adults, he found this to be true in Canada geese – some older, larger Canada goose males that had no young were submissive to younger, smaller males with broods. It would be useful to know if the more dominant families show increased weight gains in a situation where food was limiting; unfortunately, my study design did not allow me to consider this possibility.

Hierarchical linearity and stability

Three of nine broods, in which the number was large enough to test for linearity (Appleby, 1983), showed a significantly linear arrangement in their dominance relationships. Although the other six broods were too small to test for linearity, they also had a marked tendency towards linearity. The relatively small number of reversals within the hierarchies of these broods suggests that they were stable throughout the study period, a characteristic that may be needed for linearity (Komers, 1988). Evidence for such a relationship between linearity and stability was found in the Harris Sparrow (*Zonotrichia quereula*); linear hierarchies were more resistant to reversals than nonlinear ones (Chase & Rohwer, 1987). Kreveld (1970) suggested that dominance relationships are characterized by a certain stability; after an initial period during which the relationships among individuals are settled, reversals are relatively rare, a suggestion consistent with what I observed within groups of parentless goslings, as well as among families.

Frequency and intensity of interaction with time

In addition to causing dispersion of individuals, a major function of agonistic behaviour and rank orders is to promote stability in a group (Kreveld 1970, Raveling 1970, Gauthreaux 1978). Once geese learn to recognize their position in a hierarchy, they can coexist with reduced aggressive intensity because intention movements of attack (threats) suffice to maintain the benefits of being superior (e.g. access to food and space) and constantly reinforce an individual's position relative to others (Raveling, 1970). The rate and intensity of aggression may become quite low once a rank order has been established (e.g. Chase 1974, Schein 1975, Kaufmann 1983). The decline over time in rates of interactions among gosling broodmates manifested such a phenomenon. It is generally argued that group members soon learn to recognize and accept their position in the hierarchy, and therefore there is little need for constant reinforcement of one's status. As explained by Kalas (1977), the survival function of rank order lies in diminishing the intensity and frequency of agonistic interactions, in diminishing the number of social stress situations, and in promoting a close family cohesion. A reduction in the frequency of fights with time would serve to minimize the incidence of potential injury within the group. While observing fights between individuals (in particular adult geese) it was clear to me that, at times, the intensity of biting and wing beating had the potential to inflict injury. Several authors (Altmann 1962, Kreveld 1970, Richards 1974, Morse 1980, Bernstein 1981, and Kaufmann 1983) argued that, in the absence of dominance relationships in competitive situations, a greater potential for injury would exist.

In my study of the relationships among families, the frequency of interaction declined significantly over time between Phases 1 and 2. I also noted that the intensity of aggression declined over time. In particular, fighting among adults was much more prevalent in Phase 1 than Phase 2. Like Raveling (1970), I observed that, with time, threats replaced more intense forms of interaction. This may explain in part the decline in numbers of interactions between Phases 1 and 2, because the outcome of threats were sometimes less clear-cut and consequently some of the more subtle of these may not have been noted. Bernstein (1981) suggested that there may be an inverse relationship between the frequency and intensity of aggressive assertions of dominance and the degree to which the relationship is established and stable. The low frequency of reversals among goslings (Table 5) reflected the stability of their hierarchies. Radesäter (1974) found that in groups of gosling Canada and greylag geese, the number of fights in both species showed a marked decrease after about 7 days of life, and had completely ceased to occur when the goslings reached 12 days of age. I also observed a reduction in fighting with time, but fighting continued long after the goslings reached 12 days of age (Fig. 3). Such a reduction in fighting suggests the intensity of overt aggressiveness decreased with time, and a plausible explanation for this is that, upon recognizing their position in the group, individuals no longer needed to manifest such high levels of aggressiveness to reinforce their rank position. A clear trend is evident in Figure 1 but not in Figure 2 (such a trend may have been more apparent in Figure 2 had I continued observations to a later date).

Periodic observation of these broods, beyond the date when they were released together into a large grazing pen (after 12 July) showed that agonistic interaction and fighting continued intermittently within the broods throughout the summer at least up to the time of their release in early September when observations ceased. Thus, fighting cannot be entirely related either to a space-density phenomenon, nor to a specific time period.

Fischer (1965) reported that aggression among sibling greylag goslings was seldom observed, and she was unable to find any rank order among the members of a sibling group. This contrasts with my results, as well as those of Radesäter (1974) who reported that agonistic tendencies in greylag and Canada goose goslings were first observable when they were at an age of about 2 days, and Kalas (1977) who reported fighting within greylag broods 1 day after hatching. Although there was variation among individuals and groups, I observed agonistic behaviour in some of the Canada goose goslings as soon as they were dry and could properly balance themselves on the first day post-hatch. Fights were most numerous in all broods during the first 3 days post-hatch (Fig. 3).

Family size and dominance status

Up to this point gender was the only variable shown to be positively correlated with dominance status. This finding led to the search and subsequent analysis of other variables that might help explain differences in relative dominance status shown between families.

In this study, it appeared that the initial number of goslings possessed by a pair influenced the family's dominance status during that season. That family dominance status was related mainly to numbers of goslings and not to the dominance status of the adults was supported in a number of ways: (1) when the number of goslings was allocated to each family in a random fashion (and thus eliminated the possibility that more dominant pairs raised a greater number of young than less dominant pairs), large families generally dominated small ones; (2) the dominance status of pairs deprived of all goslings was different from that with goslings, i.e. pairs from large dominant families showed a general decrease in status after complete brood removal; (3) adult pairs (and single birds) without young were always subordinate to families; (4) larger parentless broods generally dominated smaller ones; and (5) the two families with gang broods of nine goslings each dominated all other families with smaller broods, but showed some reduction in dominance status in the absence of their broods. Although these results appear to indicate a definite influence of brood size on the relative dominance status of families, they do not negate the potential that parental dominance status, independent of the apparent influence of gosling numbers, may contribute to determining the relative dominance rank of families. Some small families (particularly G and D in Figs. 4 - 7), were successful in dominating some large families (particularly 2 and 5 in Figs. 4 - 7).

These results are consistent with the literature in some respects but not in others. During the winter, Boyd (1952) who studied white-fronted geese, Hanson (1953) and Raveling (1970) who studied Canada geese, and Gregoire (1985) who studied snow geese (*Chen caerulescens caerulescens*), have reported that larger families were dominant over smaller families, which in turn were dominant over pairs, single adults, and single juveniles, respectively. Lamprecht (1986a), in a study that apparently included summer and winter, did not find a positive correlation between family size and rank in bar-headed geese, although he did find that families dominated pairs without young, and single geese.

All the above observations could be explained by the dominance status of the adults if dominant pairs tended to raise larger broods. Collias and Jahn (1959) demonstrated that higher-ranking pairs of captive Canada geese were more likely to hatch young than were lower-ranking pairs. Wundinger (1973, *cited in* Lamprecht 1986b) also found a positive correlation between estimated social rank and percent hatching success for six pairs of bar-headed geese. In that species, Lamprecht (1986b) reported that more dominant pairs in winter produced more offspring in the following summer. Thus, those pairs that did not fit the general pattern in this study may have been normally very dominant pairs that by chance received only few goslings or that were very subordinate pairs that by chance received larger numbers of goslings. It appears, then, that breeding success may raise dominance status, and that this higher rank is maintained until the next year when it may make successful breeding still more likely. Since no relationship between date of hatch and family dominance status could be detected in this study, it appears that as far as dominance relations are concerned, there is little if any advantage gained by hatching an early brood; thus, size of goslings, or length of time with a brood, do not appear to be a factors influencing dominance status.

In Phase 2, I recorded no change in the status of the three most dominant families when their broods were each reduced to one gosling. In contrast to my results, Raveling (1970) observed that dominance, as measured from relative success in agonistic interactions, was reduced immediately upon separation by as little as one immature member, increasing again only after reunification of family members. In my study, only after all the goslings were removed (Phase 3) did any significant change in the dominance relationships among the pairs occur. From my study, it would appear that the presence of one gosling was sufficient to maintain a rank-order position that had been acquired, possibly through the influence of a larger brood. These results suggest that, among families that are familiar with each other, once a stable hierarchy is formed in a group of families the status attained by each family is potentially retained until the next breeding season, or until the loss of the entire brood. The difference between my results and those of Raveling (1970) may reflect differences in the familiarity of the families in each group. Geese in my study were very familiar with each other at all times; Raveling's observations were recorded in a flock of 10,000 Canada geese, in which familiarity with other flock members may well have been reduced. However, according to Raveling, the geese were not distributed in roosting and feeding areas in a random fashion. This large flock consisted of many subflocks within which the activity and use of space by a particular family was limited. He suggested that stable rank orders may have existed in the subflocks if the birds within them had learned to recognize each other.

How goslings affect the status of a family is yet to be understood. Perhaps the motivational state of the pair is directly related to brood size. In Phase 3 (without goslings), before I began to ration the feed, the frequency of interaction among the pairs was only about 20% of that observed in Phases 1 and 2 (with goslings) among families. Since most interactions among families involved only the parents, it suggests that goslings may affect the motivational state of their parents. Perhaps parental investment is directly related to family size. Increased motivation on the part of pairs of larger families may relate to protection of a relatively greater investment; such increased motivation may be beneficial to survival by allowing these families priority of access to needed resources (such as food or shelter) in times of scarcity, possibly because larger broods would require more resources than smaller ones. As suggested by Raveling (1970), since dominance implies benefits, families of geese are served best by increased levels of agonism with increased family size. In a captive flock with limited food, Jenkins (1944) observed that more-dominant Canada geese fed first.

Large families interacted among themselves more often than did small families. This may indicate that large families were more aggressive than smaller families, a higher level of agonism being perhaps related to a greater investment in offspring in larger families. It could, however, reflect a spatial phenomenon. Since all families remained in a flock, and a large family takes up more space than a small family, random movement would bring large families into contact with other large families more often than with small families. Raveling (1970) found that, in wintering Canada geese, the frequency of aggressive encounters increased with brood size. This may simply reflect a tendency for the more dominant animals to be more active in securing their rank position in the group (Kreveld, 1970).

Whether there is a hormonal basis for differences in the relative level of agonism in goose families of different size is unknown. Without actual evidence, Hanson (1953) and Raveling (1970) have speculated that higher levels of reproductive hormones may be responsible for the high levels of aggression found in parents of larger Canada goose families. A good deal of research has demonstrated a positive relationship between hormonal production of androgens and aggressive behaviour, hence social rank, in other animal species (Allee et. al. 1939, Allee 1942, Hinde 1973:512-513, Moss *et. al.* 1979, Balthazart 1983:227-230). Additional research on this subject is necessary before any conclusions can be drawn for waterfowl.

Under certain circumstances, crèching is a phenomenon common in Canada geese, and very large families may result (Glasgow, 1977), but the relative dominance of such families is not well known. In this study, two families with gang broods of nine goslings each dominated all others. These two families very rarely lost an agonistic interaction with members of family units or others (paired or single adults). Upon removal of their goslings, the rank status of these pairs, relative to other pairs, was reduced (although it remained relatively high). Thus, acquisition of goslings through crèching would appear to be advantageous in augmenting the status of the recipient family.

Glasgow (1977) noted that goslings of a given family [illegible] remained together when larger groups were formed via crèching. He also found that when brood coalescing occurred donor goslings were always less than 5 days old, but goslings in the recipient broods ranged from 3 to 20 days. My observations concur with his on both these points. Like Glasgow (1977), I observed crèching to be the result of chance encounters between broods, and not the result of "stealing" on the part of the parents. In both studies, it appeared that the goslings rather than the parents were responsible for initiating coalescing. The parents of neither recipient nor donor families appeared to be involved in either preventing or stimulating these gosling transfers. Possibly, when still less than 5 or 6 days of age, goslings are more attracted to the vocalizations of their siblings and other goslings than they are to the calls of their parents. In this study, such attraction to cohorts may have functioned to prevent separation of siblings during coalescing.

Since it appears from this study that families of Canada geese benefit in status from the acquisition of goslings through crèching, then perhaps the phenomenon of crèching serves the purpose of producing a greater proportion of dominant individuals than would otherwise be realized if it did not occur. From the stand-point of inclusive fitness, a relatively subordinate pair may benefit from loss of its brood to a more dominant pair. If the donor goslings realize an augmentation in their dominance status through the transaction this may lead to greater fitness than would have been otherwise attained in the original family. Further research is needed to substantiate the above.

Dominance and limiting resources

Marler (1955) reported that when adult chaffinches in non-reproductive condition were provided with a small dish of seeds, be they starved or not, the average duration of visits to the food decreased down the dominance hierarchy, and subordinates were continually displaced from food by dominants. According to Guhl (1968), in a flock of domestic chickens (*Gallus gallus*) high dominance status gave priority at the feeders, waterers, nests, roosts and dust baths, and for males, access to mates. Radesäter (1974) limited the availability of food and water to gosling greylag and Canada geese. He found the level of aggression apparently unchanged as did I when performing the same treatment with goslings. Among adult Canada geese, however, I found that dominant individuals, pairs, and families, had priority of access to resources such as shelters and food. When food was rationed during Phases 3 and 4 of the study, more dominant pairs fed first, keeping less dominant pairs away from the feeders until they had finished feeding. Were food limited, the less dominant birds would have received less food. In situations where food is patchy in the wild, and such patches are defendable, birds of higher status may fare better. Thus, in terms of fitness, this may be one important way in which larger families benefit from their enhanced dominance status. In Canada geese, there is limited evidence suggesting that those family members which are socially dominant to pairs and single geese may enjoy the advantages of relative freedom from harassment and ready access to limited food or space (Akesson and Raveling, 1982). Gregoire (1985) reported that larger, more dominant families of snow geese feeding in salt marshes and corn fields may have benefited from their position in the hierarchy by taking over food patches (i.e. clumps of grass rhizomes (*Spartina*); corn cobs) from less dominant units. Among adult Canada geese I noted that aggression was most pronounced when families and pairs were gathered around the feeders. Raveling (1970) reported that in a flock of wild Canada geese (of mixed age, but all capable of flight and thus older than the goslings with which I performed the above experiments) that conflicts were most numerous and intense during feeding activity in fields, and especially in those areas where food was concentrated. In view of these observations, I postulate that development of rank order at a very early age in goslings (and possibly other bird species) is the result of a response which in early life contributes little toward individual fitness. In the goslings I studied, it appeared that all conflict and aggression served no other purpose immediately than to establish or reinforce one's standing in the brood hierarchy. Such conflict could not be attributed to competition for any resource, be it limiting or not. Since, however, the rank order in Canada geese is apparently retained into adulthood (Collias and Jahn, 1959), perhaps the dominance status of an individual only comes to play a significant role in its fitness later in life, once the goslings are no longer under the care of their parents.

Future needs in dominance studies of geese

Traditionally, an explanation for dominance rank within hierarchies has been sought in the physical characteristics of the individual such as sex, weight, or some size attribute. In searching for the determinants of dominance status, few studies have considered the relative influence of learned versus genetic factors in the formation of dominance hierarchies. In this study, one might speculate that a genetic component was responsible for the high success that some small families showed in dominating large families. Experiments could be designed to test if the dominance status of the parents reflects that of their young, and if so, is this status retained into adulthood. As well, does pairing of individuals relate to dominance status in any way; i.e. do individuals pair with individuals of similar status, or not? And once paired, how does the status of each individual contribute to the overall status of the pair, as well as a family with young? These are but a few suggestions for further research in an area that has scarcely been touched upon. Our understanding of waterfowl biology will certainly not be complete without a solid understanding of social behaviour.

Table 1. The rank positions of 12 male and 9 female parentless Canada goose goslings, early and late in the study period, and for the entire period in 1983 (goslings hatched May 7 - 14 and raised together in a single group).

Rank[a]	First half May 14 - June 6			Second half June 7 - July 12			Entire period May 14 - July 12		
	Code[b]	Sex	W/I[c]	Code	Sex	W/I	Code	Sex	W/I
1	A	M	22/22	C	M	6/6	B	M	23/23
2	B	M	18/18	B	M	5/5	C	M	18/18
3	C	M	12/12	G	M	5/5	E	M	5/5
4	D	M	11/11	I	M	5/5	A	M	30/32
5	E	M	1/1	E	M	4/4	G	M	18/20
6	F	M	11/12	A	M	8/10	F	M	12/14
7	G	M	13/15	J	M	6/8	I	M	12/14
8	H	M	6/[illegible]	K	M	2/3	H	M	6/8
9	I	M	7/9	S	F	3/5	J	M	10/14
10	J	M	4/6	F	M	1/2	D	M	15/22
11	K	M	9/14	U	F	5/12	K	M	11/17
12	L	F	2/4	D	M	4/11	L	F	5/13
13	M	F	5/12	L	F	3/9	M	F	10/28
14	N	M	4/10	M	F	5/16	O	F	4/14
15	O	F	3/8	O	F	1/6	N	M	6/27
16	P	F	1/4	R	F	1/8	P	F	1/5
17	Q	F	1/5	N	M	2/17	S	F	4/21
18	R	F	4/39	H	M	0/1	U	F	5/31
19	S	F	1/16	P	F	0/1	R	F	5/47
20	T	F	0/9	Q	F	0/7	Q	F	1/12
21	U	F	0/19	T	F	0/7	T	F	0/16
Probability[d]	P < 0.001			0.001 < P < 0.01			P < 0.001		

[a] Ranking of individuals based on the proportion of wins during interactions with goslings of the opposite sex; ties were ordered according to total number of interactions

[b] Each letter refers to an individual gosling

[c] The number of wins divided by the number of interactions in which each individual was involved

[d] Based on a Mann-Whitney test using ranks of individuals of the two sexes

Table 2. The frequency of agonistic interactions within and between the sexes of 21 Canada goose goslings (12 males and 9 females) raised together in 1983. Expected values based on random interaction.

	Total number of interactions	Expected values[a]	Difference[b]
Male - Male	140	135.6	P = 0.129
Female -Female	88	73.9	
Male -Female	203	221.6	

[a] Calculated according to Levine's exact Chi-square test for small sample size (Li, 1955:13-14)

[b] Based on Chi-square test; $X^2 = 4.09$

Table 3. Rank correlation analysis of the relationship between weight and dominance status in a group of 21 Canada goose goslings (12 males and 9 females) raised together in 1983 (hatch dates spanned May 7 - 14).

Date weights recorded	Females		Males	
	Rho	P[a]	Rho	P[a]
May 15	0.492	P > 0.10	0.615	P = 0.03
May 24	0.312	P > 0.10	0.494	P > 0.10
May 31	0.184	P > 0.10	0.543	P = 0.07
June 21	0.084	P > 0.10	0.241	P > 0.10
June 28	0.242	P > 0.10	0.098	P > 0.10
July 5	- 0.349	P > 0.10	0.324	P > 0.10
July 12	- 0.089	P > 0.10	0.117	P > 0.10

[a] P based on Spearman's coefficient of rank correlation test

Table 4. A measure of the linearity of the hierarchies in broods involving varying numbers of parentless goslings of Canada geese.

	Brood size	'h' value[a]	Probability[b]
1984 Group 1	7	.98	0.01 < P < 0.05
	5	.80	—[c]
	4	1.0	—
1985 Group 1	7	.93	0.01 < P < 0.05
	5	.80	—
	4	1.0	—
Group 2	7	.86	0.01 < P < 0.05
	5	1.0	—
	4	1.0	—

[a] 'h' value based on Landau's index of linearity (Lehner, 1979:217-218)

[b] Based on the table of critical values provided by Appleby (1983)

[c] Sample sizes too small for statistical analysis

Table 5. The number of reversals within broods of parentless Canada goose goslings when comparing dominance hierarchies from both halves of the study period (first half – May 17 - 30; second half – May 31 - June 12) (1985).

	Brood size	Number of reversals recorded[a]	Number of possible dyadic combinations
Group 1	7	2	21
	5	0	10
	4	0	6
Group 2	7	5	21
	5	3	10
	4	0	6

[a] A reversal was scored when the dominance ranking between individuals forming a dyad reversed over time

Table 6. A breakdown of the number of wins and losses recorded during aggressive interactions among 14 families of Canada geese: seven large families (four or five gosings), and seven small families (one or two goslings).

Winner/Loser[a]	Phase 1[b]	Phase 2	Phase 3	Phase 4
M/Fa	427	370	176	1
M/M	133	72	736	709
M/F	64	61	952	738
M/G	292	165	—[c]	—
F/Fa	220	182	25	0
F/M	30	24	84	75
F/F	51	21	324	229
F/G	253	86	—	—
Fa/Fa	283	105	20	0
Fa/M	3	1	5	0
Fa/F	0	0	27	0
Fa/G	5	4	—	—
Gm/Fa	79	46	—	—
Gm/M	7	10	—	—
Gm/F	9	13	—	—
Gm/G	73	58	—	—
Gf/Fa	21	5	—	—
Gf/M	0	1	—	—
Gf/F	1	2	—	—
Gf/G	24	4	—	—

[a] M - paired male adult, F - paired female adult, Fa - family, G - gosling (sex unknown), Gm - male gosling, Gf - female gosling; categories based on my best estimate of which individuals were involved, in the case of "Fa" it appeared that all individuals in the family acted in unison

[b] See text for a description of the phases

[c] These combinations did not exist

Table 7. The win-loss record for paired adult Canada geese (14 males and 14 females) during interactions with family units, paired adults of the opposite sex, and goslings, during Phases 1 - 4 (see text).

Sex	Wins	Losses	Difference[a]
Males	3246	240	$P < 0.001$
Females	979	1867	

[a] Based on a 2 X 2 contingency table; $X^2 = 2432.9$

Table 8. Frequency of agonistic interactions within and between the sexes of adult Canada geese (14 males and 14 females - data combined for Phases 1 - 4 (see text)) compared with the expected values based on random interaction.

	Total number of interactions	Expected values[a]	Difference[b]
Male - Male	1650	993.2	
Female - Female	625	993.2	$P < 0.001$
Male -Female	2028	2317.5	

[a] Calculated according to Levine's exact Chi-square test for small sample size (Li, 1955:13-14)

[b] Based on Chi-square test; $X^2 = 607.0$

Table 9. A comparison of weight (mean of June 28, July 25, and August 19 weights), and length of tarsus, with dominance status (during Phases 1 and 2 (see text)) of the goose and gander (as a pair) in a group of 16 families of Canada geese.

		$\bar{X}$ wt. in kg.		Tarsus l. in cm.	
Pair code	Pair rank[a]	Male	Female	Male	Female
1	6	4.95	3.36	11.44	11.22
2	9	4.26	4.45	11.11	10.71
3	4	4.08	3.43	11.55	10.36
4	12	4.70	3.49	10.87	10.68
5	14	4.18	4.05	11.73	9.97
6	6	4.72	3.67	11.85	10.40
7	8	4.90	3.75	12.08	10.66
A	11	4.67	4.68	11.31	10.42
B	16	4.53	3.89	12.31	10.85
C	15	5.44	3.72	11.57	10.33
D	6	4.32	3.93	11.28	11.12
E	10	4.32	3.40	11.42	10.45
F	13	4.30	2.99	11.68	9.49
G	3	5.12	4.67	11.84	9.70
EE	1.5	4.33	4.23	11.83	10.89
XX	1.5	4.30	3.64	11.08	10.51
Spearman's Rho		0.045	0.084	0.103	-0.158
P		0.87	0.76	0.70	0.56

[a] Based on the outcome of interactions during Phases 1 and 2 (mean of ranks obtained in each phase)

Table 10. Win-loss record of the outcomes of agonistic encounters between seven large families (four or five goslings) and seven small families (one or two goslings) of Canada geese, considering all 49 possible dyadic combinations between large and small families (see text for a description of the phases).

	No. of dyadic combinations won		
	Large families	Small families	Difference[c]
Phase 1	32	17	$X^2 = 4.59$; $P = 0.032$
Phase 2[a]	33	15	$X^2 = 6.75$; $P = 0.009$
Phase 3[b]	26	23	$X^2 = 0.18$; $P = 0.668$
Phase 4	24	25	$X^2 = 0.02$; $P = 0.888$

[a] Four goslings were removed from the three most dominant large families; does not include one combination in which the outcome was a tie

[b] All goslings removed

[c] Based on Chi-square test

Table 11. The total number of wins and losses recorded during agonistic interactions involving seven large families (four or five goslings), and seven small families (one or two goslings) of Canada goslings during Phase 1 (June 30 - July 23).

Family size	Wins	Losses	Difference[a]
Large	1279	1133	$P < 0.001$
Small	696	842	

[a] Based on a 2 X 2 contingency table; $X^2 = 22.70$

Table 12. A comparison of hatch date (day on which the greatest number of goslings in each family was hatched) with dominance status of Canada goose families during Phase 1 (June 30 - July 23).

Pair code[a]	Family rank[b]	Date of Hatch[c]
1	4	1
E	8.5	5
F	11.5	6
2	7	7
3	2	8
4	10	10
5	11.5	13
A	8.5	14
B	13	16
6	4	20
C	14	21
7	6	25
D	4	25
G	1	29

Spearman's Rho = -0.157; P = 0.59

[a] Numbers represent large families (4 or 5 goslings); letters represent small families (1 or 2 goslings)

[b] Based on the outcome of interactions during Phase 1 (see text)

[c] Days after May 7

Table 13. The rank orders of the 16 families of Canada geese during Phases 1 - 4 (see text for a description of the phases).

Pair[a]	Phase 1	Phase 2	Phase 3	Phase 4
1	6	5.5	6.5	4.5
2	9	9	11	12
3	4	5.5	8.5	4.5
4	12	11	12	14
5	13.5	15	13.5	16
6	6	5.5	6.5	10
7	8	8	5	7
A	10.5	12	10	12
B	15	16	16	12
C	16	13.5	15	8.5
D	6	5.5	2.5	6
E	10.5	10	8.5	8.5
F	13.5	13.5	13.5	15
G	3	3	1	3
EE	2	1	4	1.5
XX	1	2	2.5	1.5

[a] Numbers represent families with four or five goslings, single letters represent families with one or two goslings, and double letters represent families with broods of nine goslings

Table 14. The combined win-loss record for two families of Canada geese with gang broods of nine goslings each when interacting with 14 families of Canada geese with one to five goslings (Phases 1 and 2), and zero goslings (Phases 3 and 4).

Phase[a]	Wins	Losses	Total	Percent success
1	390	29	419	93
2	292	23	315	93
3	637	89	726	88
4	662	135	797	84

[a] See text for a description of the phases

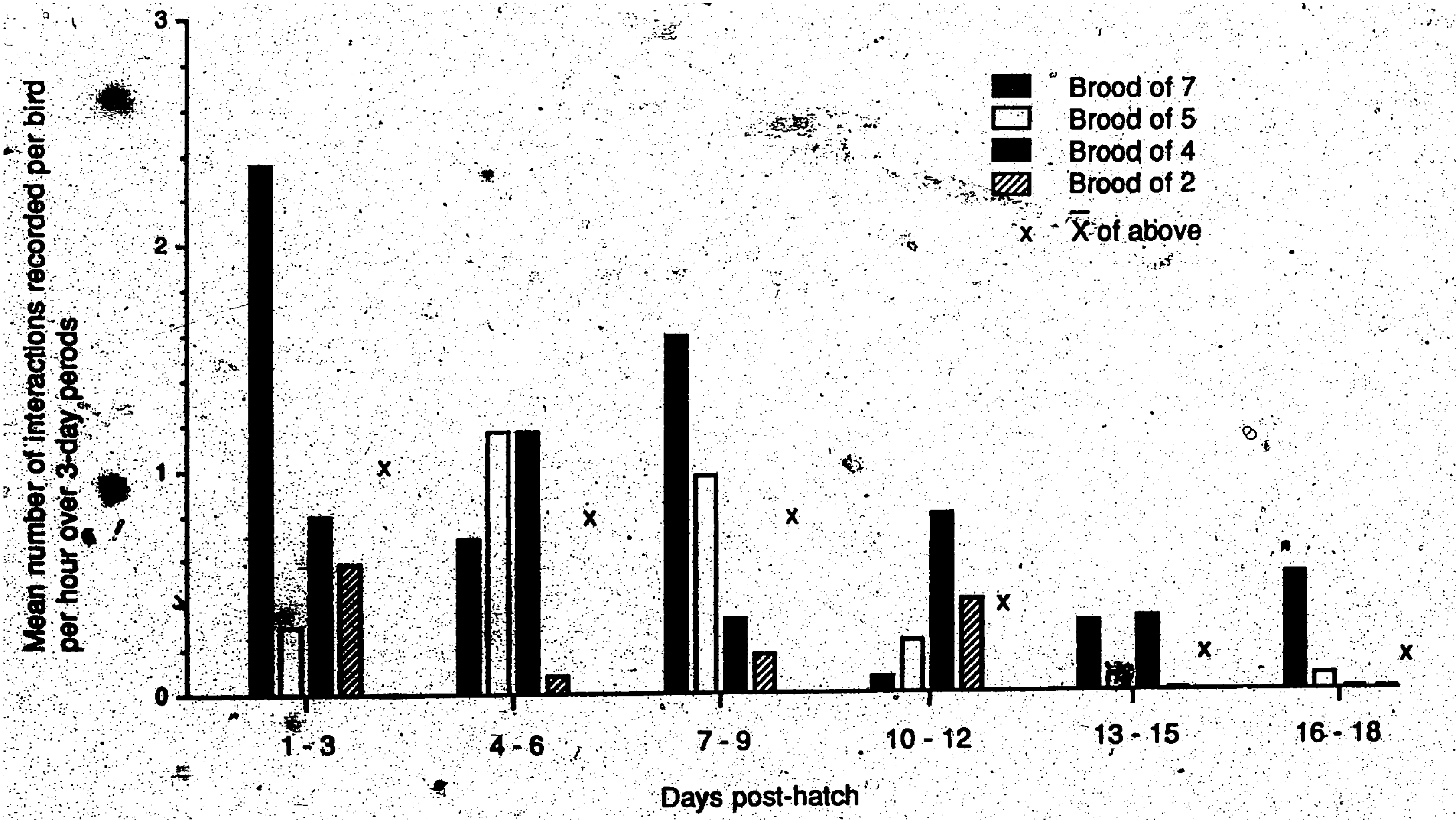

Figure 1. The frequency over time of agonistic interactions among goslings of Canada geese in broods of different size, in 1984 (each brood observed for 2 hours per day).

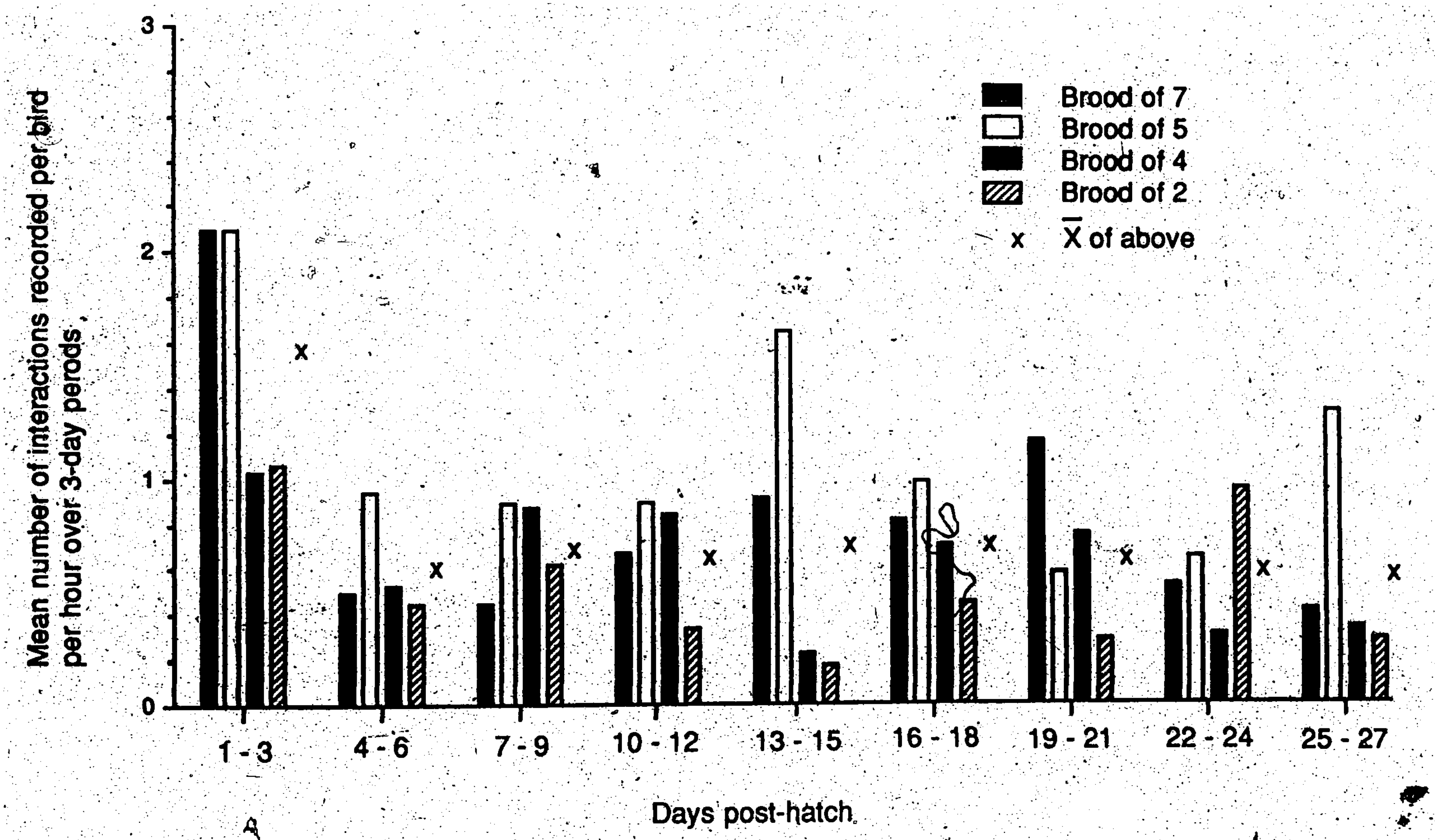

Figure 2. The frequency over time of agonistic interactions among goslings of Canada geese in broods of different size, in 1985 (mean data for replicate groups; each brood observed for 1.5 hours per day).

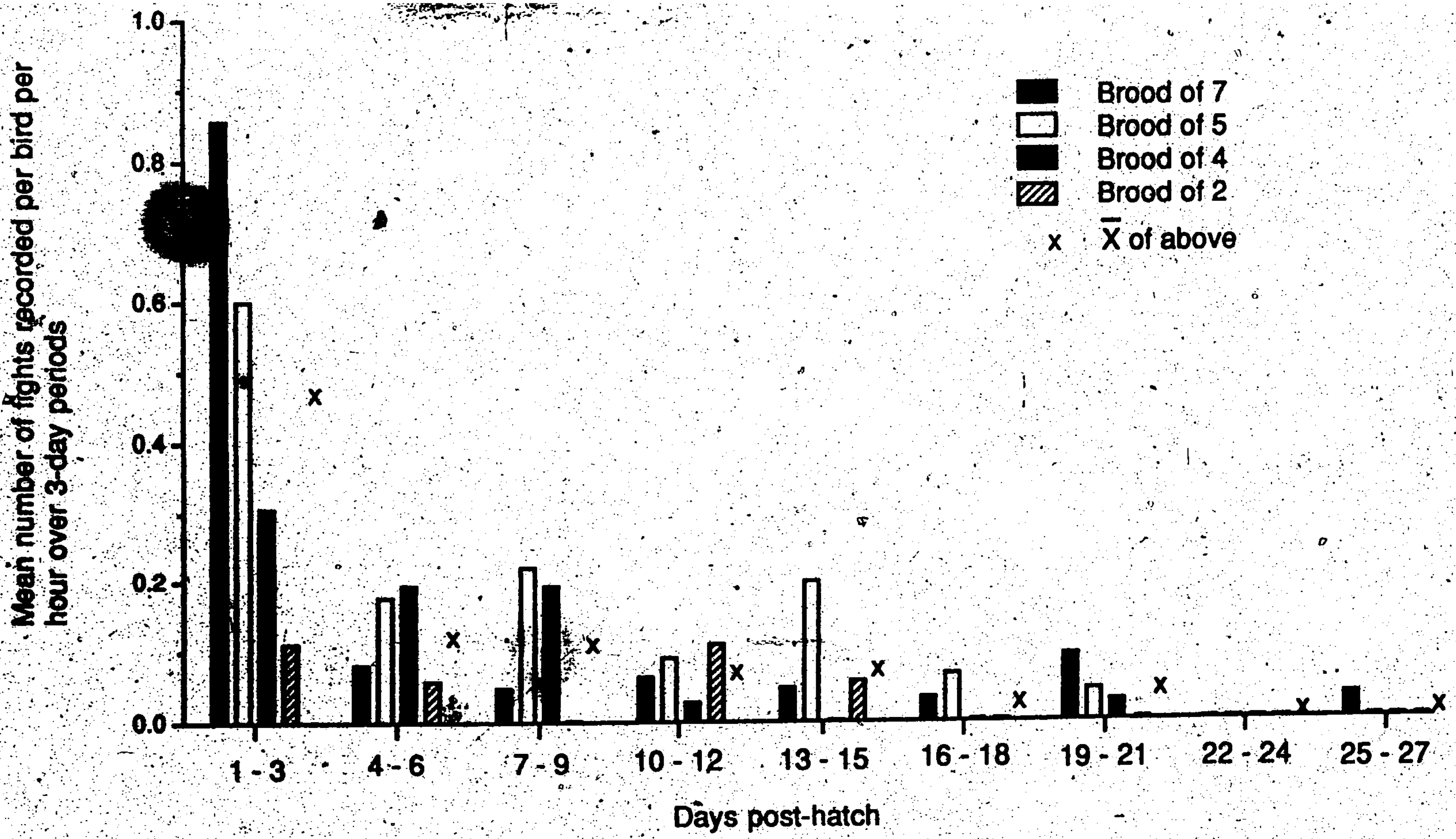

Figure 3. The frequency over time of fights among goslings of Canada geese in broods of different size, in 1985 (mean data for replicate groups; each brood observed for 1.5 hours per day).

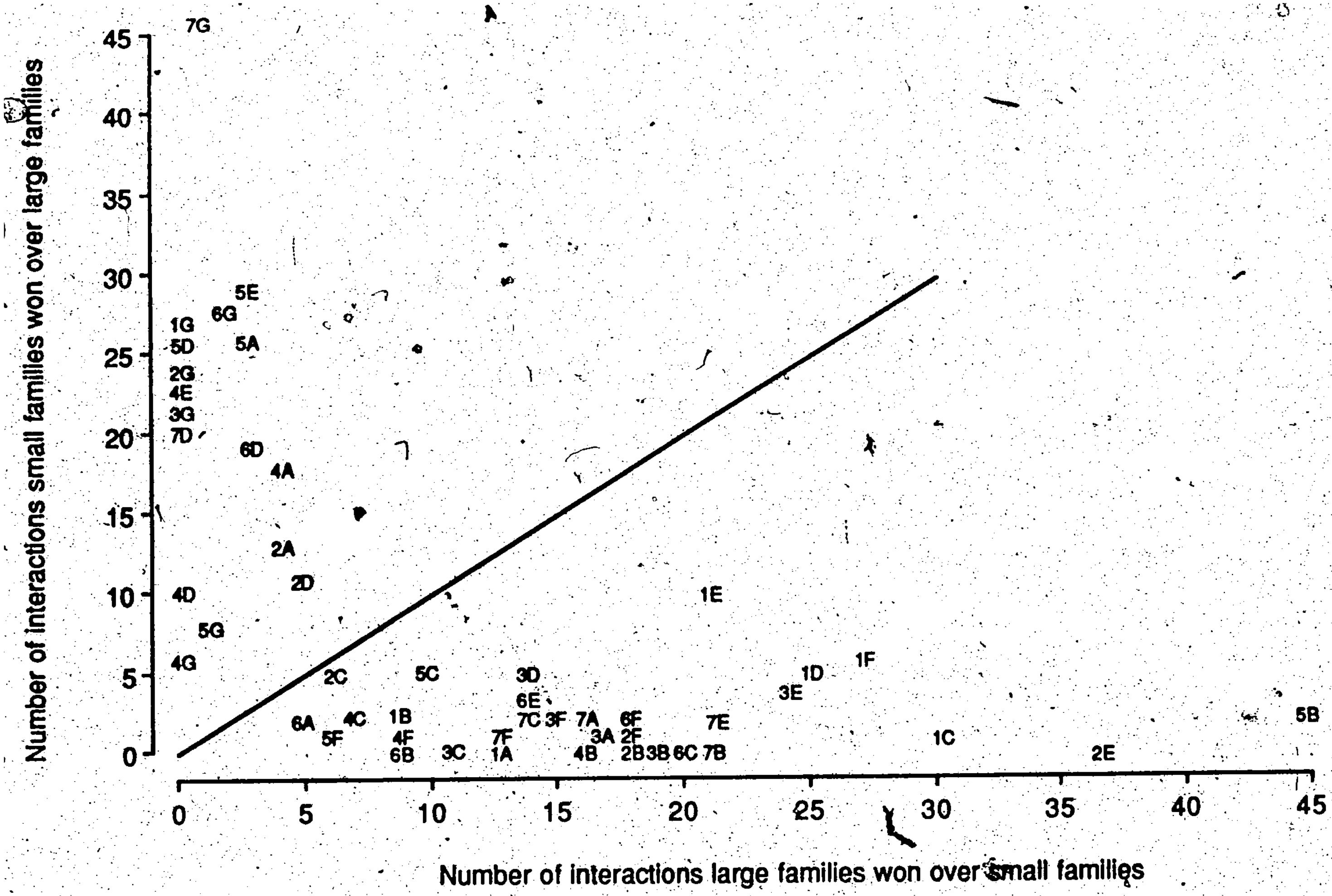

Figure 4. Record of outcomes of agonistic interactions between seven large Canada goose families (four or five goslings) and seven small families (one or two goslings). Each code number represents a large family, and each code letter represents a small family (data for all possible dyads of Phase 1, 1985 - see text).

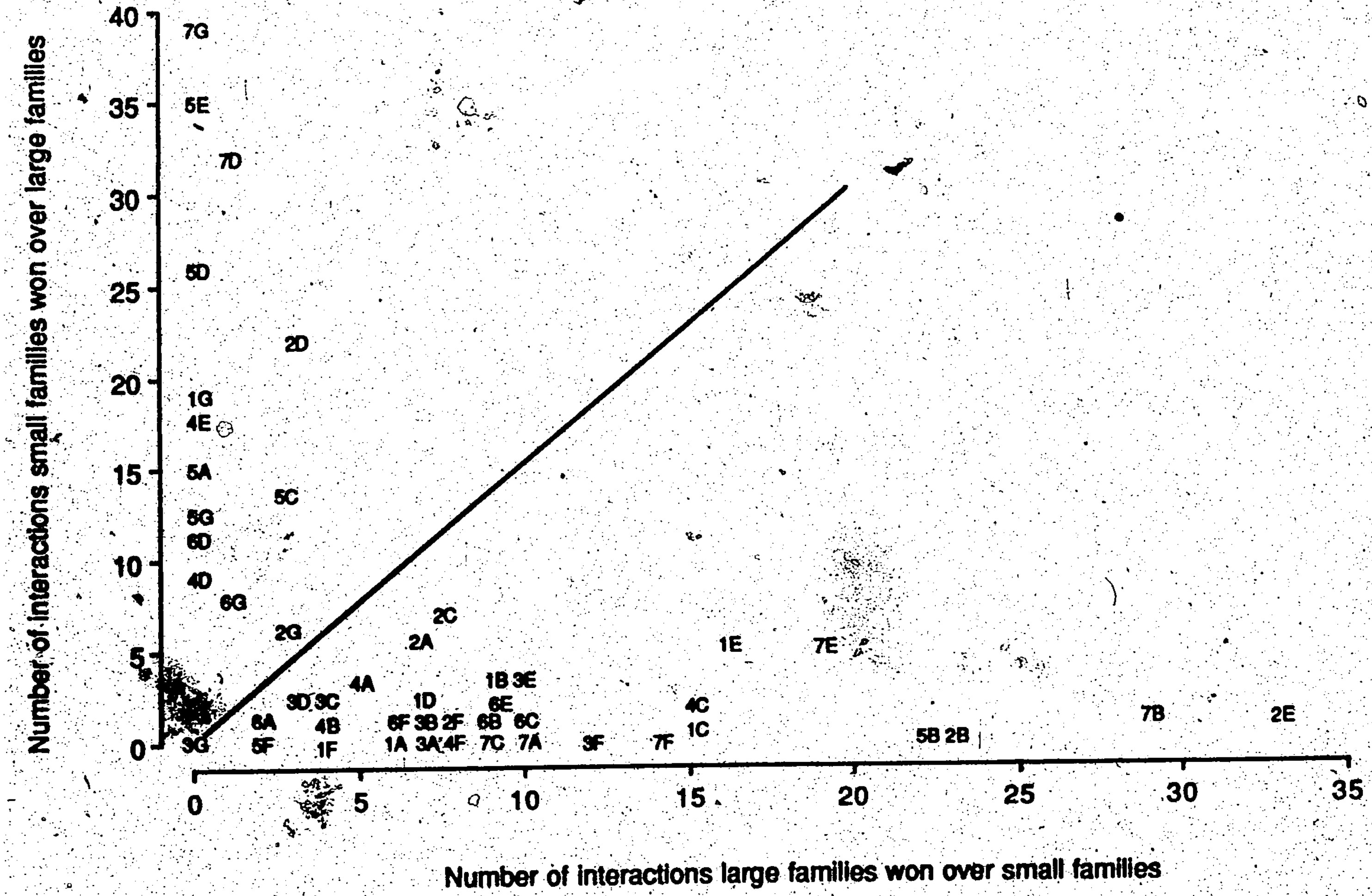

Figure 5. Record of outcomes of agonistic interactions between seven large Canada goose families (four or five goslings) and seven small families (one or two goslings). Each code number represents a large family, and each code letter represents a small family (data for all possible dyads of Phase 2, 1985 - see text).

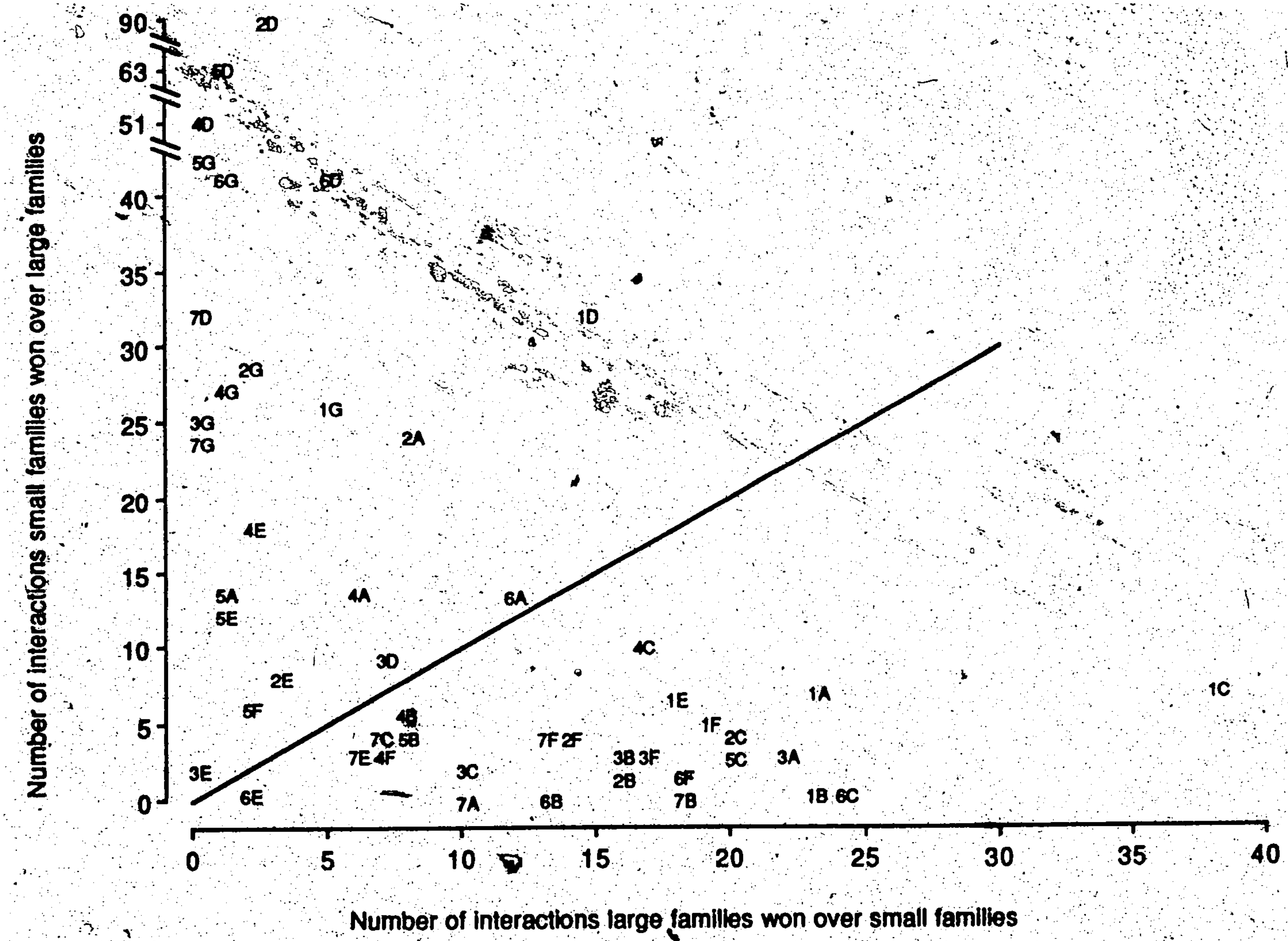

Figure 6. Record of outcomes of agonistic interactions between seven large Canada goose families (four or five goslings) and seven small families (one or two goslings). Each code number represents a large family, and each code letter represents a small family (data for all possible dyads of Phase 3, 1985 - see text).

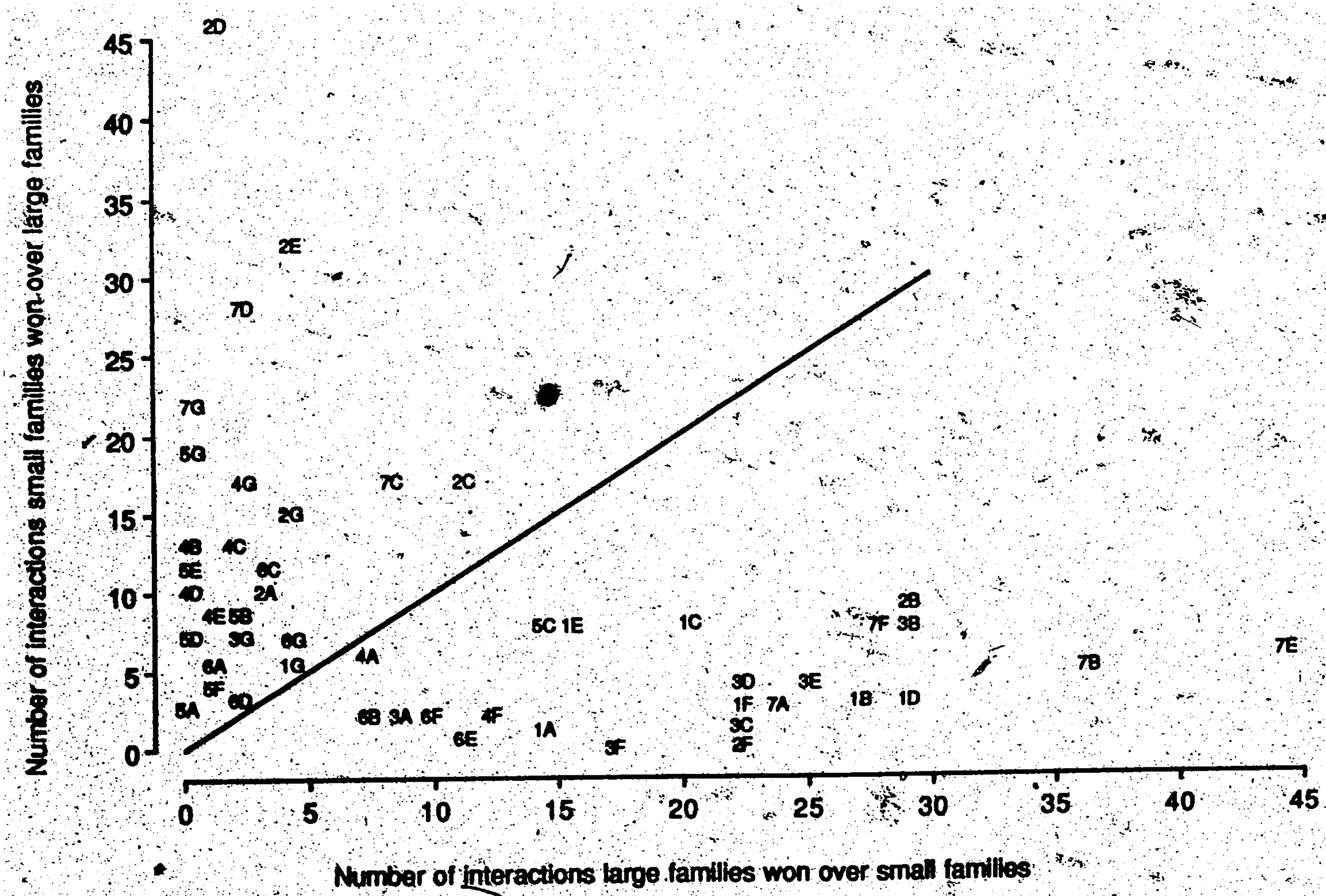

Figure 7. Record of outcomes of agonistic interactions between seven large Canada goose families (four or five goslings) and seven small families (one or two goslings). Each code number represents a large family, and each code letter represents a small family (data for all possible dyads of Phase 4, 1985 - see text).

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