Correlation of dominance as determined by agonistic interactions with feeding order in cats

Rebecca J. Knowles, MS; Terry Marie Curtis, DVM, MS; Sharon L. Crowell-Davis, DVM, PhD

Objective—To determine whether the direction of dominance as determined by agonistic interactions away from food was different from the direction of dominance as determined by access to a resource in cats.

Animals—28 cats.

Procedure—Dyadic relationships and hierarchy formed from observation of agonistic interactions away from food were compared with those formed from interactions at the food bowl. A cat was scored as subordinate to another cat if it lost 3 of 3 interactions or lost ≥ 75% of the interactions when > 3 interactions occurred.

Results—Cats were observed for 449.4 hours. Hierarchy rank determined by agonistic interactions away from food was significantly correlated with rank determined by interactions at the food bowl. In 27 of 31 dyads, the direction of dominance was the same for food bowl and agonistic relationships, which was significant. In post hoc analyses, when considering the relationship between 2 cats, the heavier cat most likely ranked higher in each hierarchy; however, age was not significantly correlated with either hierarchy. On the basis of dyadic information, the older cat in a dyad was more often dominant in agonistic interactions. Males had a higher mean dominance rank than females; however, sex had no effect on rank determined by interactions at the food bowl.

Conclusions and Clinical Relevance—Factors influencing dominant-subordinate relationships are of interest for understanding and treating behavior problems such as aggression and resource control. The outcome of agonistic interactions away from food was related to, but not perfectly correlated with, the outcome of interactions at the food bowl, although winners of those agonistic interactions tended to have control of food. (*Am J Vet Res* 2004;65:1548–1556)

The description of a social hierarchy in chickens and the unidirectional pecking order by Schjelderup-Ebbe[1] spurred research into the existence of similar hierarchies in other animals. The presence, development, maintenance, and function of dominant-subordinate relationships, or the lack thereof, have been described in a variety of species, including horses,[2-4] dolphins,[5] goats,[6] and birds.[7] The greatest abundance of research into social structure, however, may be found in literature on primates (eg, macaques,[8-10] mountain gorillas,[11] capuchin monkeys,[12] baboons,[13] and lemurs).[14] Although in clinical settings, dogs are considered to have dominance hierarchies, empirical studies with cats have not been performed . The relevance of animal social interactions to veterinarians has been previously described.[15-18]

A dominant-subordinate relationship between 2 animals is established through learning their strengths and weaknesses with each other, via playing or fighting, or in early development so that observed behavior becomes the result of past interactions. A relationship exists only if the animals remember the outcome of those previous interactions. For these reasons, an observer can look for less obvious forms of communication, such as avoidance, rather than rely solely on intense, aggressive interactions that may have occurred in the past to determine the direction of a relationship. A subordinate animal, through its own actions of submitting to or ignoring another animal's attention, helps to design the dominance relationship.[19] Therefore, in the social organization of a group of animals, submission may be more important than dominance. Because of this, Rowell[19] adopted the phrase subordinance hierarchy in 1974. Nevertheless, the term dominance hierarchy, which was first used to describe the social organization of a group in which some animals consistently win over or give way to others, has remained the standard, although requiring submission alone to rate an interaction as "lost" became common.[3,4,6,7,9-11,13]

In the study reported here, the definition of dominance is based on Bernstein's[20] qualification that a dominance relationship can be assumed between 2 animals if it can be consistently predicted which of the animals will be submissive to the other prior to an agonistic encounter, because that submission is based on past interactions between those 2 animals. To researchers, knowing social status between animals is useful for making predictions about the outcome of future interactions or agonistic encounters. For veterinary behavior practices, factors influencing dominant-subordinate relationships are of interest for understanding and treating animal behavior problems such as aggression and resource control. One of the presumed functions of dominance is control of access to resources such as food or mates.[10,21]

Other studies[22-25] examining control of access to resources have had problems with methodology or were less applicable to present-day owners of domestic cats. Some of the first studies[22-24] investigating social interactions in cats were performed in a laboratory environment with only a few cats and used the common technique of food competition to measure domi-

Received September 10, 2003.
Accepted March 8, 2004.
From the Department of Anatomy, Radiology, and Behavior, College of Veterinary Medicine, The University of Georgia, Athens, GA 30602.
Address correspondence to Ms. Knowles.

nance. For instance, Cole and Shafer[25] compared dominance relationships in a multiple-cat environment using food competition to examine the group as a whole and when fed in pairs. Different hierarchies were detected in the 2 situations; however, the experimental method used could have caused disruptions in the hierarchies.

Other studies[26-28] have investigated dominance relationships within groups of cats. Dards[29] believed that a social hierarchy existed in a group of male dockyard cats, which was determined by sexual maturity. Results of a study by Natoli and DeVito[28] indicated that there was no correlation between a dominance hierarchy determined by agonistic interactions of 19 male cats and mating success. Van den Bos and de Cock Buning[30] also described a linear hierarchy from agonistic interactions in cats; however, it was determined by only 167 clear win-loss interactions between 10 sexually intact female laboratory cats. In that study, ≤ 3 interactions occurred among the 5 most dominant cats.

To the authors' knowledge, the social hierarchy of cats in an environment similar to that of a large outdoor enclosure of primates[9] has not been described. A large, outdoor, naturalistic but enclosed environment permits easy tracking of animals and observation of conspecific interactions and interactions with the environment in a semi naturalistic setting. Because the extensive home ranges of free-roaming cats make observation of behavior difficult,[5] cats in a residential household with limited outdoor access would provide similar benefits.

A colony of cats in close proximity permits a greater chance for encounters between cats; therefore, the dominance hierarchy should be well established and maintained, and observation of submissive behavior and threats of aggression, in addition to actual acts of aggression, can be used to determine dominance relationships within dyads and develop an analyzable hierarchy. If the dominance hierarchy influences access to resources, including food, then the dominance rank should be positively correlated with rank at the food bowl. The correlation is not expected to be perfect because motivation and social dominance influence which cat obtains a resource.[3,20,31]

The purpose of the study reported here was to determine if the direction of dominance determined by agonistic interactions away from food was different from the direction of dominance determined by access to a resource in cats (ie, do cats that are socially dominant control access to food?). The dyadic information and hierarchy formed from observation of agonistic interactions in a group of cats within a colony away from the food bowl were compared with the dyadic information and hierarchy formed from interactions at the food bowl with an ad libitum food supply. We hypothesized that a dominance hierarchy determined by agonistic interactions away from food would have a positive, but not perfect, correlation with rank at the food bowl and that the direction of individual unambiguous dyads determined by agonistic interactions would be the same as that for dyadic relationships at the food bowl.

Materials and Methods

Cats and research site—The colony was comprised of 28 neutered cats (16 males and 12 females) that were from 3 months to 11 years old at the beginning of the study.[32] Data from the male cat that was 3 months old were excluded from analyses because of the potential for shifting dominance relationships as this cat matured. All other cats were ≥ 1 year old at the beginning of the study. Mean age and weight of male cats was 4.4 years (range, 1.1 to 11 years) and 6.04 kg (range, 3.4 to 8.5 kg), respectively. Mean age and weight of female cats was 4.1 years (range, 1.1 to 8 years) and 4.98 kg (range, 3.2 to 7.0 kg), respectively. Mean time that male and female cats had spent in the colony was 4.1 years (range, 1 to 11 years) and 4.1 years (range, 7 months to 6.8 years), respectively. Familial relationships between these cats includedthe following: 2 pairs of male and female siblings (siblings from 1 of those pairs were separated for 6 months when the cats were < 1 year old) without a related queen, 1 queen with 1 related male kitten, 1 queen with 1 related female and 3 related male kittens, and 1 queen with 1 related female and 2 related male kittens. An additional male kitten was added to the colony at the same time the latter group was introduced and was raised with this group. To the owner's knowledge, the remaining cats were unrelated. The cats had been adopted at various times and from various sources; therefore, the odds of the remaining cats being related were low. All cats were neutered before being introduced to the colony or at 6 months of age and had lived most of their lives in the colony. All cats were quarantined for 2 weeks before being introduced to the colony, and all cats introduced within the last 6 years were tested for FIV and FeLV. The vaccination status of all cats was adequate. All cats were treated monthly with a topical product for control of fleas and ticks.

The colony was located in a residential household in Athens, Ga, and was studied from September 17, 2001 to May 31, 2002. Cats were not familiar with the observers before the study. Cats had access to 2 rooms in the house, the feed room (4.8 × 3 m) and the master bedroom (30 m^2). A cat door in the feed room provided 24-hour access to a porch (40 m^2) and an escape-proof yard enclosed by a fence (approx 953 m^2). The door between the master bedroom and the feed room was always open. A room in the garage (5.7 m^2) containing 4 litter boxes was also always available. The yard had 5 areas with shrubs and trees (approx 102 m^2). Four of the trees had trunks that were ≥ 25 cm in diameter. Those 4 trees and 3 smaller trees were used by cats for climbing, scratching, and shade. In addition, a small winter cat room (36 m^2) was available to cats beginning in late December. This room was closed off from the rest of the house but was accessible from the yard via a step leading to a cat door located 66 cm from the ground. Food was available in this room only at night. Activities in this room were not visible by the observer; therefore, the step access to the cat door was removed during observation periods. Any cats inside could still exit but none were able to enter the winter room. Most of the area in the 2 rooms in the house, the outside porch, and approximately a third of the yard were visible from the feed room.

Cats were fed a high quality, dry adult cat food that was constantly available from a food bowl (approx 35 × 15 cm) on a table (0.88 × 0.76 m) in the feed room. Cats were also fed cat food treats occasionally. The food bowl had an automatic dispenser with a 4.5 kg capacity that was refilled at least 3 times a week, as needed. A few cats caught insects, squirrels, birds, snakes, or opossums, but this was rare.

Study protocol—All cats were habituated to humans. Data collection began after 8 hours of observation on-site to permit cats to habituate to the 2 observers. The observers did not handle the cats before or during the study. After the 8-hour habituation period during which cats learned that the observers would not pet them, all cats typically ignored the observers, or briefly investigated the observers as they entered the observation area, then returned to normal activity.

Data collection was designed to maximize collection of information on agonistic activity and activity at the food bowl (**Figure 1**). On arrival at the study site, the observers made a survey of the area to determine locations of cats. If 1 cat was eating in the feed room and at least 1 other was waiting on that cat, recording of activity at the food bowl began (**Appendix**). Cats had access to all of the areas during observation periods and could enter or leave an area at any time during observation. At the end of every 15 minutes, if 1 or more cats were eating and 1 cat was waiting to eat, recording continued for another 15 minutes.

If no cats were waiting on another cat at the food bowl at the beginning of the observation period or at the end of any 15-minute session in the feed room, recording of all episodes of agonistic interactions began in 1 of the 3 main areas (the bedroom, the porch [including the small yard and litter room], or the yard). These scoring sessions lasted 15 minutes. An assessment of cat distribution was made before each 15-minute agonistic interaction recording session. The most populated area was observed first for a complete 15-minute session, followed by the most populated of the remaining 2 areas for another 15 minutes. This 2-step process was repeated so long as no cats were waiting on other cats at the food bowl. Observations would continue in the same area for a consecutive 15 minutes if only 1 cat was present in each of the other 2 areas. If an equal number of cats were present in the 2 most populated areas, the area with the highest density of active cats was observed. For example, if there were 12 cats in the bedroom and 12 were on the porch, of which 7 in the bedroom were sleeping while only 2 on the porch were sleeping, then the cats on the porch would be observed. Recording of agonistic interactions continued in 15-minute sessions until 1 or more cats were waiting on a cat that was eating in the feed room, at which time the recording of activity at the food bowl resumed. If at the end of any 15-minute session in the feed room no cat was waiting on another cat, 15-minute sessions of agonistic interactions were again recorded on the basis of cat distribution.

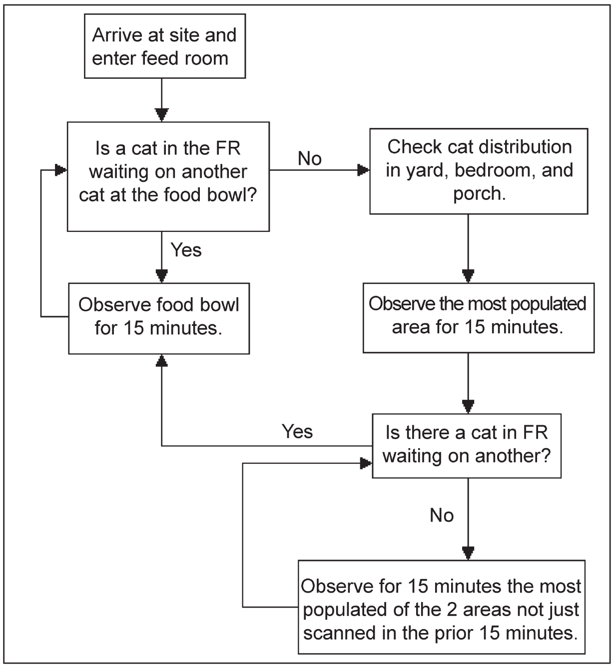

Figure 1—Decision protocol flowchart used for observations of dyadic dominant-subordinate relationships as determined by agonistic interactions away from the food bowl and interactions at the food bowl in a colony of 27 cats. FR = Food room.

Because the colony was in a residential home, the cats were observed Monday through Friday between 7:30 AM and 5:30 PM when the owners were not at home. Video recording of activity at the food bowl was also completed when video equipment became available, from the middle of April to the end of May. Activity of cats was recorded with video equipment whenever the observer left the site for the afternoon or evening; therefore, feeding behavior was observed until 7:30 PM.

Agonistic interactions in which 1 cat clearly lost the interaction were recorded. Likewise, only interactions in which cats were obviously waiting on another cat at the food bowl, as determined by both proximity to and watching of the cat at the food bowl, were recorded as such. Behavior was recorded only in the context of dyadic interactions, except during observations of activity at the food bowl in which interactions involving multiple cats were recorded. Interactions were recorded in which the cat that won the interaction had dominant behavior and the cat that lost the interaction had submissive behavior. However, whereas the loser must have had submissive behavior toward another cat, dominant behaviors from the winner were not required.

Data analyses—A cat was considered subordinate to another cat if it lost 3 out of 3 interactions or lost ≥ 75% of the interactions when > 3 interactions between 2 cats occurred. The dyadic relationship was then included in the analysis of relationships. The same standard was used for interactions at the food bowl. Agonistic interactions occurring at the food bowl were used for the analysis of rank at the food bowl. However, agonistic interactions that occurred in the feed room but not at the food bowl were excluded from agonistic data to eliminate food as the immediate motivator in those interactions. Cats were ranked for each hierarchy by assuming transitivity.[33] If this did not resolve an ambiguous relationship, whether because of a near-equal amount of interactions with wins and losses with another cat or no interactions with another cat, the mean of the positions was obtained and the rank shared. The highest-ranking cat determined by this procedure, hereafter referred to as the initial hierarchy, was assigned the rank of 1 and the lowest ranking cat was assigned the rank of 27.

A few cats did not have sufficient interactions with cats of various hierarchical ranks to permit a determination of rank. For instance, a cat may have had a clear relationship with one of the top-ranked cats and a clear relationship with a low-ranked cat, but not with another cat in the hierarchy. Rank assignments and comparisons between hierarchies were thus simplified by use of the following procedure. Once initial hierarchies were set up as described, each cat had to have an unambiguous relationship with ≥ 3 cats other than the top or bottom ranked cats to be included in the ranking analysis. Top and bottom ranked was defined as the top 4 and bottom 3 cats, respectively, because those relationships were ambiguous. The final hierarchy used for data analysis included only those cats that had ≥ 3 known dyadic relationships with cats ranking in the middle of the hierarchy. This procedure removed 8 cats from the hierarchy analyses but did not alter the hierarchy structure of the remaining 19 cats (11 males and 8 females), but did clarify assignment of rank. Unambiguous dyadic relationships between those 8 cats and other cats were included for analysis of individual dyadic relationships.

There was 1 relationship triangle in the agonistic hierarchy and 5 in the food bowl hierarchy that spanned > 4 cats. To simplify statistical analyses, hierarchy triangles spanning > 4 positions were ignored when assigning ranks for statistical analyses. With this method, there were no triangles in the dominance hierarchy and 1 triangle in the food bowl hierarchy.

Statistical analyses—Commercial computer software[a] was used for statistical analyses. A value of $P < 0.05$ was considered significant. Spearman rank correlation (r) was used to test for correlation between food bowl rank and agonistic interaction rank.

Post hoc tests included binomial distribution to determine if the direction of dominance of unambiguous dyads was the same in agonistic interactions and interactions at the food bowl. Also, after testing the main hypotheses, the effects of age, weight, and sex on rank within each hierarchy and on the individual dyadic relationships were analyzed. Ages and weights of dominant and subordinate cats were compared by use of Wilcoxon signed rank tests (T). These were performed on dyads grouped according to agonistic interaction data away from the food bowl, at the food bowl, and on dyads present in both data sets, without assuming transitivity. A 1-tailed Mann-Whitney U test was used to determine differences in weight, rank determined by agonistic interactions, and rank determined by the food bowl hierarchy between male and female cats. Spearman rank correlation was used to test for correlations between rank determined by food bowl interactions or agonistic interactions and age or weight.

Results

Cats were observed for 449.4 hours, from 10 to 25 h/wk. Data from 98 hours were obtained from recording of concurrent data from another project[32] performed from September 17 to December 18, 2001. From the middle of January to May 31, 2002, 134.4 of the 449.4 hours included activity at the food bowl. Fifty-two hours of video recording in the feed room were obtained. Scanning for agonistic interactions in locations away from the food bowl comprised the remaining 165 hours.

A total of 1,066 agonistic interactions were recorded away from the feed room and 1,459 interactions at the food bowl were recorded. Rank determined on the basis of agonistic interactions was significantly correlated ($r = 0.405$; $P = 0.043$) with rank determined on the basis of food bowl interactions. Hierarchies that included only cats with ≥ 3 unambiguous relationships with cats in the middle of the hierarchies were determined **(Figures 2 and 3)**.

Without assuming transitivity, there were 109 unambiguous dyads determined on the basis of agonistic interactions away from food, and 96 unambiguous dyads determined on the basis of interactions at the food bowl, out of the 350 possible dyads in the 27 cats. Thirty-one dyads had unambiguous dominant-subordinate relationships (ie, they had a ≥ 75% difference in wins and losses from > 3 interactions) in both the feeding and agonistic observation situations. In 27 of these 31 dyads, the direction of dominance was the same for both food bowl and agonistic dyadic relationships, which was significant ($P < 0.001$) as determined by binomial distribution. Four reversals occurred in which the cat that was dominant in one of these situations (either food bowl or agonistic interaction) was submissive in the other situation.

Of the 1,066 agonistic interactions observed in this group of cats, only 1 involved an actual fight. The encounter occurred between 2 male cats (cat 4 and cat 16) that were similar in age and weight. The encounter involved staring and growling followed by launching at each other, after which each cat cuffed the other repeatedly while sitting upright on their hindquarters; fur from both cats was dislodged.

Post hoc evaluation of supplants at the food bowl exclusively occurred in 16 different dyads (of the 96 unambiguous dyads at the food bowl). Eleven of those dyads performed the supplant down the agonistic hierarchy. Three dyads performed food bowl supplants up the hierarchy, and 2 ambiguous agonistic dyads performed supplants at the food bowl.

In interactions between 2 cats, the older cat was generally dominant to the younger cat, and the heavier cat was dominant to the lighter cat; in interactions between 2 sexes, the male cat was generally dominant

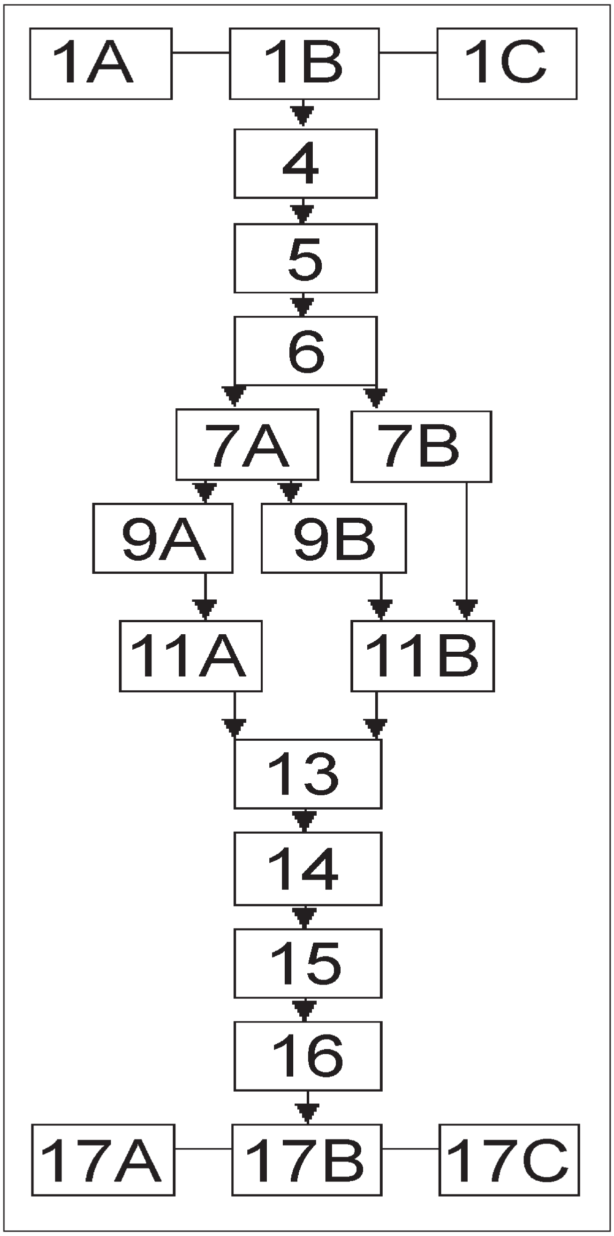

Figure 2—Agonistic interaction hierarchy as determined by dominant-subordinate interactions away from the food bowl in a colony of 27 cats. Cats with the same number but different letters represent different cats with the same rank.

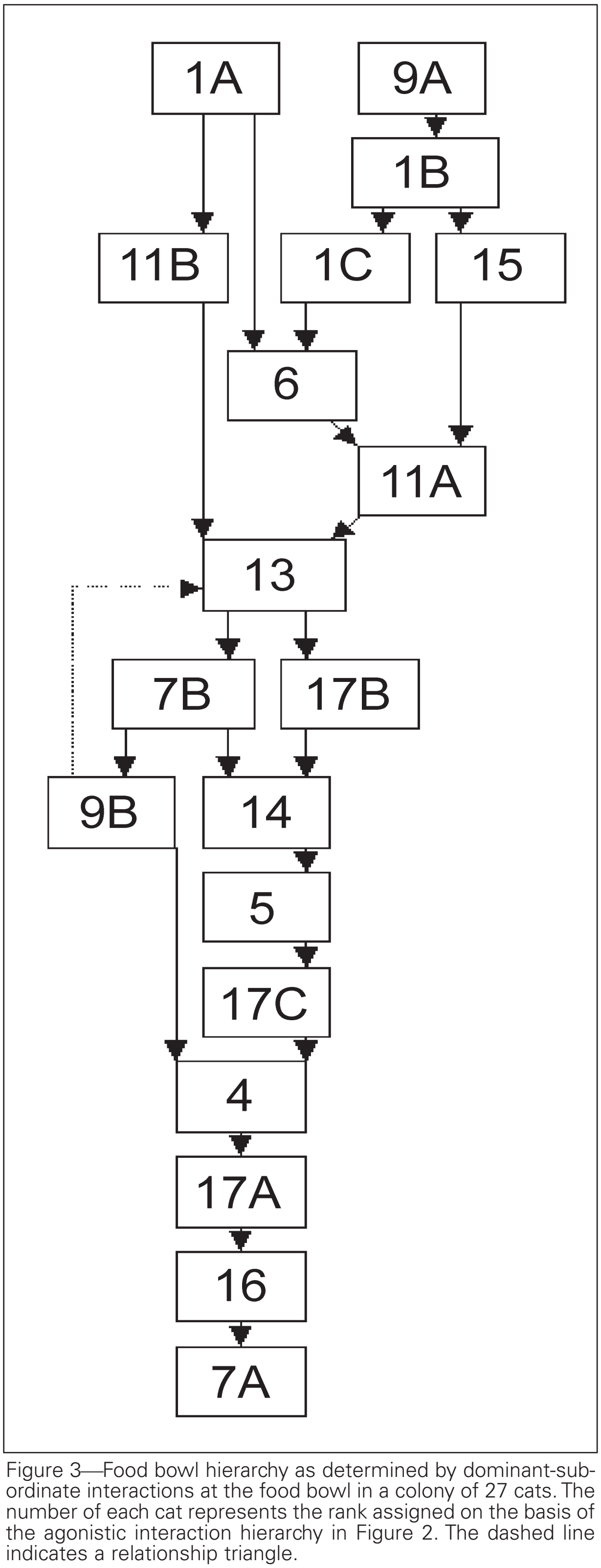

Figure 3—Food bowl hierarchy as determined by dominant-subordinate interactions at the food bowl in a colony of 27 cats. The number of each cat represents the rank assigned on the basis of the agonistic interaction hierarchy in Figure 2. The dashed line indicates a relationship triangle.

to the female cat. There was a significant positive correlation ($r = 0.558$; $P = 0.002$) between age and weight. There was no significant ($r = 0.075$; $P = 0.380$) correlation between agonistic rank and age , whereas there was a significant ($r = 0.705$; $P = 0.001$) correlation between agonistic rank and weight. This differs from the nonsignificant correlation between food bowl rank and weight ($r = 0.375$; $P = 0.062$). There was no significant correlation between food bowl rank and age ($r = 0.036$; $P = 0.442$).

Of the 31 dyads with unambiguous relationships in both agonistic interactions and interactions at the food bowl, the older cat within each dyad was not significantly more often dominant to the younger cat than vice versa ($T = –0.348$; $P = 0.728$). However, the dominant cat within a dyad was significantly ($T= –3.163$; $P = 0.002$) more often heavier than the subordinate cat.

Examining the dominance and food bowl dyads separately, the dominant cat in a dyad was more often older than the subordinate cat in the 109 unambiguous dyads away from food ($P = 0.020$) but not in the 96 unambiguous dyads in food bowl interactions ($P = 0.619$). The dominant cat within a dyad was also significantly more often heavier than the subordinate cat in dyad groups away from food ($P < 0.001$) and at the food bowl ($P = 0.002$).

Male cats had a significantly higher mean rank than female cats in the dominance hierarchy determined on the basis of agonistic interactions ($U = 17.5$; $P = 0.026$), but not at the food bowl ($U = 35.0$; $P = 0.492$; **Table 1**). Mean rank of male cats in the agonistic hierarchy was 7.6, and mean rank of female cats was 13.3. At the food bowl, mean rank of male and female cats was 10.8 and 8.8, respectively. There were no significant differences in either weight ($U = 47.5$; $P = 0.107$) or age ($U = 77.5$; $P = 0.548$) between male and female cats.

Table 1—Number (percentage) of male and female cats in unambiguous dyadic dominant-subordinate relationships as determined by agonistic interactions away from the food bowl and interactions at the food bowl in a colony of 27 cats.

Sex Dominant	Subordinate	Agonistic interaction dyads	Food bowl interaction dyads	Dyads in both interactions
Female	Female	16 (14.7)	21 (21.9)	7 (22.6)
Female	Male	9 (8.3)	18 (18.8)	2 (6.5)
Male	Female	41 (37.6)	21 (21.9)	7 (22.6)
Male	Male	43 (39.4)	36 (37.5)	15 (48.4)
Total		**109 (100)**	**96 (100)**	**31 (100)**

Discussion

In the study reported here, the food access hierarchy in a group of 27 cats significantly and positively correlated with the agonistic interaction hierarchy. Similar to results of our study, results of studies by Warren and Maroney[26] and Bernstein[9] indicate that rankings of macaque species also contained triangles. Warren and Maroney[26] reported a significant correlation between the direction of aggression and feeding order. Bernstein[9] reported a significant correlation between the direction of aggression and feeding order and concluded that although feeding order was clearly related to dominance, it was not a direct measure of dominance. Our study examined interactions at the food bowl and rank as determined by those interactions rather than feeding order per se; however, the conclusion remains applicable. Results of the study reported here indicated that the outcome of agonistic interactions away from the food bowl was related to, but did not completely determine the outcome of, interactions at the food bowl.

Supplantation may be of unique interest if it is presumed to be an interaction in which both motivation for a resource and willingness to submit to another cat are playing a part, and it is for this reason that supplants occurring exclusively at the food bowl were examined post hoc. In the study reported here, most cats that performed supplants at the food bowl did so down the hierarchy, although food was available ad libitum. The provision of an ad libitum source of food may be suspected as a cause of some ambiguities by creating a scramble competition feeding strategy. In the study of dominance relationships, food is the resource most often used to increase the frequency of what may ordinarily be rare aggressive interactions. This may alter the direction of an agonistic interaction from what would normally be seen in an unmanipulated situation; however, this is not always the case. For instance, Clutton-Brock et al[34] reported that the provision of food to free-ranging highland ponies had no effect on observations of rank. A clear, but not fully linear, hierarchy determined on the basis of interactions in a field setting was detected in the highland ponies. Increased interaction caused by supplemental food did not alter the hierarchy. Tyler[2] also reported that triangles were detected among 4 horses in a rank order of 19 horses as determined by field and supplemental feeding data.

The problem of ordering animals from agonistic and feeding data is not limited to domestic cats. In the study reported here, 8 cats were removed from the hierarchy analyses because of insufficient data. However, triangles remained in the feeding hierarchy even after those cats were removed. This was not unexpected because, to the authors' knowledge, there is no evidence that cats are aware of any dyadic relationships other than their own. Circular relationships or ties in any size group or species are not unusual, even when studying relationships away from food, which may change motivation, and are supported by results from studies with primates,[10] horses,[35] and birds.[7] The hierarchy developed from a group can depend on the type of observations being performed, whether comparing the agonistic interactions with the direction of other behaviors[10] or comparing agonistic interactions in a field setting with paired feeding trials,[3] which removes the animals from their normal social and environmental context[22,25] and may disrupt triangular relationships.[3,9] The hierarchy resulting from a data set is also affected by the decision protocol used for deciding relationships and ordering animals.

A nonlinear hierarchy was constructed on the basis of agonistic interactions within this group of 27 cats. The hierarchy included outcomes of interactions in which the losing cat reacted solely to the presence of the winning cat (27% of the interactions). Increasing the number of observations may have clarified many of the ambiguities in our study. A review of dates of interactions revealed that the ambiguities did not appear to be caused by a changing of dominance relationships or outcomes of interactions at the food bowl with time. That is, within the food bowl interactions, neither cat in a dyad waited on the other cat more toward the end of the study than at the beginning of the study. The same was true of ambiguous dyads in the agonistic hierarchy. A few dyads had numerous interactions with no clear dominant cat by the end of the study (eg, cat 4 won 14 times over cat 16, whereas cat 16 won 12 times over cat 4).

In a laboratory setting, repeated pairings of previously unacquainted cats have unsurprisingly caused gradually fewer agonistic interactions,[36] similar to results of a study by Warren and Maroney[26] in which confrontation and avoidance between less familiar macaques were initially obvious. Barry and Crowell-Davis[37] reported that pairs of cats that had lived together longer than other pairs of cats aggressed against each other less. Fewer agonistic interactions would be required to maintain relationships once they are established if both animals continue to respond appropriately to each other's signals. It is for this reason that the subordinate plays a large role in maintaining its position relative to the dominant,[19] through avoidance or preemptive defensive postures.

For example, of the 1,066 agonistic interactions observed in this group of cats, there was only one observed prolonged encounter between 2 cats. The high level of ritualized submissive and dominance signals, paired with an almost total absence of actual fighting, would be expected in a stable social group of cats that remember the outcome of their past interactions. Results of a study by Natoli et al[27] on agonistic interactions in a group of farm cats indicated that dominance rank determined by submissive behaviors was more reliable than that determined by aggressive behaviors.

However, there were multiple instances when one of the most dominant male cats (cat 1A) regularly deviated from his path of travel to chase, cuff, or supplant the oldest male cat or the heaviest male cat , who were ranked fifth and seventh, respectively, in the initial agonistic hierarchy comprising all 27 cats. The oldest male cat was excluded from the final agonistic hierarchy because there was not enough information for placement of this cat in the hierarchy determined by food bowl interactions. Cat 1A was dominant to both of the other cats at the food bowl. Preemptive, small-magnitude, high-frequency actions may be a method of maintaining relationships with individuals that may have threatened cat 1A's position, thereby avoiding confrontations of higher magnitude, such as the encounter between cat 4 and cat 16. In contrast, few agonistic interactions or interactions at the food bowl occurred between cat 1A and the 2 other highest-ranking cats as determined by agonistic interactions.

Within dyads with unambiguous relationships determined by agonistic interactions, the rare periodic reversals of interaction outcomes at the food bowl could be explained by a variety of factors includingthe following: a high-ranking cat with low food motivation, perhaps because that cat had just eaten recently; a low-ranking cat's relaxed posture that does not stimulate aggression; and a relationship firmly established in the past such that, because a subordinate cat never routinely challenged the dominant cat in the dyad, 1 incursion did not require immediate reinforcement by the dominant cat of the usual relationship direction through agonistic behavior to elicit a submissive response from the subordinate cat.

In post hoc analyses, although age and weight were positively correlated, the correlations between rank and age versus rank and weight were different. The heavier cats in this colony tended to rank higher in the agonistic interaction hierarchy than the lighter cats. This was not the case in the food bowl hierarchy. When considering individual dyads, the heavier cat within a dyad was more often dominant to the lighter cat in both agonistic interactions and at the food bowl. Weight had a greater influence than age in the dominance hierarchy and when examining individual dyads; the only time age was significant was when the older cat in a dyad was dominant in agonistic interactions. Results of a study[30] in a group of sexually intact female laboratory cats indicated that there was no correlation between rank determined by agonistic encounters and weight, although higher-ranking cats tended to gain more weight. Results of 1 study[38] indicate that the most successful sexually intact males of a colony had a higher mean weight than the less successful males, although they were not always the most successful when visiting an outside colony. However, results of another study[39] indicate that there was no association between body weight or age and copulatory success.

Results of 1 study[40] indicate that in interactions between 2 cats, the younger cat deferred to the older cat at the food bowl more often than chance would predict, although an outlier bias may have been present in that study. In our study, age was not associated with food bowl rank, indicating that the youngest cats did not receive preferential treatment from adult cats and may indicate that relationships with adult cats were already being established.

In the present study, male cats had significantly higher mean rank than female cats in the agonistic interaction hierarchy. In individual dyads, male cats were generally dominant to female cats, but this did not always occur. Results of other studies[27,41,42] indicate that female cats were dominant to 1 or more male cats. In environments in which food is scarce and female cats expend energy nursing, sexually intact male cats may weigh more and be more capable of ranking higher than sexually intact female cats. However, that rank may be determined by weight rather than sex. Male cats may have a higher mean rank than female cats even in this neutered colony because of prenatal and early juvenile effects of testosterone, which is preparatory for adult behavior in dogs.[43] If such an effect occurs in cats, it may indicate that neutered males are more likely to pursue an agonistic interaction further than a neutered female, who may avoid escalation of an interaction by becoming subordinate. The prenatal and early juvenile effects of testosterone on development of adult behavior in cats are not yet known.

The influence of sex on the agonistic but not the food bowl hierarchy in this colony of neutered cats may be a result of different social behavior. Male and female cats approach the opposite sex more frequently than the same sex,[b] although they are not significantly more often preferred associates.[c] Increased association would make agonistic interactions more likely than in cats that avoid one another. If preferred association played a role, it would not impart agonistic immunity, and may actually increase aggressive frequency,[c] similar to other species. Pereira and McGlynn[44] reported that male lemurs had both affiliation and aggression toward preferred female lemurs, and Ellard and Crowell-Davis[3] reported that mares aggressed most often towards their preferred associates that were also closer to them in rank. Therefore, cats that associate more often with one another will have more opportunities for observable dominant-subordinate behavior, thus also more opportunities to reinforce the relationship, yet they may wait on or tolerate one another without interaction where there is an ad libitum food source.

In the study reported here, the effect of preferred associates may have been observed at the food bowl. Some cats appeared to eat only with or after certain other cats, which may have been better understood by an evaluation of preferred associates[32,c] during eating. Another difficulty at the food bowl was determining the difference between motivation and ability, because 1 or 2 cats appeared to have trouble getting onto the table containing the food bowl. Additionally, a few cats would pace around the food room continually watching the cat that was eating, but then leave and return several minutes later after the cat that had been eating had left. Those cats were not considered to have been waiting on the cat that was eating because there was no objective connection between the departure of the cat that was eating and the return of the cat that was pacing, and the addition of such data may have helped to clarify relationships at the food bowl. A few cats would eat small amounts of food frequently, whereas other cats ate substantial amounts of food less frequently. These issues require further investigation.

[a]SPSS, version 10, SPSS Inc, Chicago, Ill.

[b]Sung W. *Effect of gender on initiation of proximity in free-ranging cats* (*Felis catus*). MS thesis, Department of Veterinary Anatomy, Radiology, and Behavior, The University of Georgia, Athens, Ga, 1998.

[c]Wolfe R. *The social organization of the free ranging domestic cat* (*Felis catus*). PhD dissertation, Department of Veterinary Anatomy, Radiology, and Behavior, The University of Georgia, Athens, Ga, 2000.

References

1. Schjelderup-Ebbe T. Beitrage zur sozialpsychologie des haushuhns. *Z Psychol* 1922;88:225-252.
2. Tyler, SJ. The behaviour and social organization of the New Forest ponies. *Anim Behav Monographs* 1972;5:85-196.
3. Ellard M, Crowell-Davis SL. Evaluating equine dominance in draft mares. *Appl Anim Behav Sci* 1989;24:55-75.
4. Weeks JW, Crowell-Davis SL, Caudle AB, et al. Aggression and social spacing in light horse (*Equus caballus*) mares and foals. *Appl Anim Behav Sci* 2000;68:319-337.
5. Samuels S, Gifford T. A quantitative assessment of dominance among bottlenose dolphins. *Mar Mamm Sci* 1997;13: 70-99.
6. Barroso FG, Alados CL, Boza J. Social hierarchy in the domestic goat: effect on food habits and reproduction. *Appl Anim Behav Sci* 2000;69:35-53.
7. Seibert LM, Crowell-Davis SL. Gender effects on aggression,

dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (*Nymphicus hollandicus*). *Appl Anim Behav Sci* 2001;71:155–170.
8. Rowell TE. Hierarchy in the organization of a captive baboon group. *Anim Behav* 1966;14:430–433.
9. Bernstein IS. Stability of the status hierarchy in a pigtail monkey group (*Macaca nemestrina*). *Anim Behav* 1969;17:452–458.
10. Bernstein IS, Cooper MA. Dominance in Assamese macaques. *Am J Primatol* 1999;48:283–289.
11. Watts DP. Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). *Behav Ecol Sociobiol* 1994;34:347–358.
12. Di Bitetti MS, Janson CH. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Anim Behav* 2001;62:47–56.
13. Leinfelder I, de Vries H, Deleu R, et al. Rank and grooming reciprocity among females in a mixed-sex group of captive Hamadryas baboons. *Am J Primatol* 2001;55:25–42.
14. Radespiel U, Zimmermann E. Female dominance in captive gray mouse lemurs (*Microcebus murinus*). *Am J Primatol* 2001; 54:181–192.
15. Dodman NH, Shuster L, eds. *Psychopharmacology of animal behavior disorders*. Malden, Mass: Blackwell Science, 1998.
16. Houpt KA. *Domestic animal behavior for veterinarians and animal scientists*. 3rd ed. Ames, Iowa: Iowa State University Press, 1998.
17. Serpell J. *The domestic dog: its evolution, behaviour and interactions with people*. Cambridge, UK: Cambridge University Press, 1995.
18. Turner DC, Bateson P, eds. *The domestic cat: the biology of its behaviour*. 2nd ed. Cambridge, UK: Cambridge University Press, 2000.
19. Rowell TE. The concept of social dominance. *Behav Biol* 1974;11:131–154.
20. Bernstein IS. Dominance: the baby and the bathwater. *Behav Brain Sci* 1981;4:419–457.
21. DeVore I. *Primate behavior: field studies of monkeys and apes*. New York: Holt, Rinehart and Winston,1965.
22. Baron A, Stewart CN, Warren JM. Patterns of social interaction in cats (*Felis domestica*). *Behaviour* 1957;11:56–66.
23. Winslow CN. The social behavior of cats II: competitive, aggressive, and food-sharing behavior when both competitors have access to the goal. *J Comp Psychol* 1944;37:315–326.
24. Winslow CN. The social behavior of cats I: competitive and aggressive behavior in an experimental runway situation. *J Comp Psychol* 1944;37:297–313.
25. Cole DD, Shafer JN. A study of social dominance in cats. *Behaviour* 1966;27:39–53.
26. Warren JM, Maroney RJ. Competitive social interaction between monkeys. *J Soc Psychol* 1958;48:223–233.
27. Natoli E, Baggio A, Pontier D. Male and female agonistic and affiliative relationships in a social group of farm cats (*Felis catus* L.). *Behav Processes* 2001;53:137–143.
28. Natoli E, De Vito E. Agonistic behaviour, dominance rank and copulatory success in a large multi-male feral cat colony (*Felis catus* L.) in central Rome. *Anim Behav* 1991;42:227–241.
29. Dards JL. The behaviour of dockyard cats: interactions of adult males. *Appl Anim Ethol* 1983;10:133–153.
30. van den Bos R, de Cock Buning T. Social behaviour of domestic cats (*Felis lybica* f. *catus* L.): a study of dominance in a group of female laboratory cats. *Ethology* 1994;98:14–37.
31. Syme GJ. Competitive orders as measures of social dominance. *Anim Behav* 1974;22:931–940.
32. Curtis TM, Knowles RJ, Crowell-Davis SL. Influence of familiarity and relatedness on proximity and allogrooming in domestic cats (*Felis catus*). *Am J Vet Res* 2003;64:1151–1154.
33. Shein MW, Forhman MH. Social dominance relationships in a herd of dairy cattle. *Anim Behav* 1955;3:45–55.
34. Clutton-Brock TH, Greenwood PJ, Powell RP. Ranks and relationships in Highland ponies and cows. *Z Tierpsychol* 1976;41:202–216.
35. Araba BD, Crowell-Davis SL. Dominance relationships and aggression of foals (*Equus caballus*). *Appl Anim Behav Sci* 1994;41:1–25.
36. de Boer JN. Dominance relations in pairs of domestic cats. *Behav Processes* 1977;2:227–242.
37. Barry KJ, Crowell-Davis SL. Gender differences in the social behavior of the neutered indoor-only domestic cat. *Appl Anim Behav Sci* 1999;64:193–211.
38. Yamane A, Doi T, Ono T. Mating behaviors, courtship rank and mating success of male and feral cat (*Felis catus*). *J Ethol* 1996;14:35–44.
39. Ishida Y, Yahara T, Kasuya E, et al. Female control of paternity during copulation: inbreeding avoidance in feral cats. *Behaviour* 2001; 138:235–250.
40. Yamane A, Emoto J, Ota N. Factors affecting feeding order and social tolerance to kittens in the group-living feral cat (*Felis catus*). *Appl Anim Behav Sci* 1997;52:119–127.
41. Laundré J. The daytime behaviour of domestic cats in a free-roaming population. *Anim Behav* 1977;25:990–998.
42. Panaman R. Behaviour and ecology of free-ranging female farm cats (*Felis catus* L.). *Z Tierpsychol* 1981;56:59–73.
43. Ranson E, Beach FA. Effects of testosterone on ontogeny of urinary behavior in male and female dogs. *Horm Behav* 1985;19:36–51.
44. Pereira ME, McGlynn CA. Special relationships instead of female dominance for redfronted lemurs, *Eulemur fulvus rufus*. *Am J Primatol* 1997;43:239–258.

Appendix appears on the next page

Appendix

Ethogram: agonistic interactions and activity at the food bowl

Actions and visual signals of the subordinate cat. The following behaviors are classified as submissive. The cat with the signs of submissive behavior (cat B) is considered as the loser of that single agonistic interaction. Cat A is considered as the winner of that single interaction. All of the following behaviors were recorded only in the context of dyadic interactions.

Walk around—Cat B comes to within 0.5 m of cat A, but deviates from its original course after looking at cat A, with the consequence that cat A maintains a position it was holding prior to the activity of cat B. Cat B resumes its straight course once around cat A.

Wait on—Cat B and cat A are walking toward the same location, from either the same or different directions. Cat B looks at cat A and stops walking so that cat A can pass first, then cat B continues.

Avoid—Cat B comes to within 1 m of cat A but no closer than 5 cm, looks at cat A with tail held $< 90^{\circ}$ perpendicular to body, and then changes its course 90° to 180°. To be sure of an avoid behavior, changes $< 90^{\circ}$ were not scored. The ears are often but not always rotated.

Retreat—Whenever cat B immediately moves away from cat A, which has moved to within 1 m of cat B without having actually supplanted cat B.

Submit—Cat B has signs of submissive behaviors immediately after cat A approaches or has signs of dominant behaviors, but cat B does not move from the position it held prior to the activity of cat A.

Flinch—Cat B tenses immediately subsequent to a sign of dominant behavior being directed to it by cat A. Cat B's reaction may also include blinking once with a quick rotation of the ears back.

Hunch—The head is drawn toward the shoulders and lowered; the forelimbs flex slightly.

Crouch—With at least 3 paws on the ground, the shoulder, cubital, hip, stifle, and hock joints flex. An extreme crouch is when the belly is in contact with the ground.

Roll (submissive)—Cat B places one side of the body in contact with the ground, including the shoulder and hip with part of the belly exposed, when approached by cat A. Rolls are only classified as submissive if the approaching cat has signs of dominant behaviors prior to the rolling or the rolling cat has other signs of submissive behaviors such as putting the ears back.

Ears side—Ears held flat at the side of the head, except immediately prior to or during a cat fight, when both cats may have ears to the side.

Ears back—Ears held flat to the rear of the head, except immediately prior to or during a cat fight, when both cats may have ears back.

Tail tucked—Tail curled cranioventrally and lying against the lateral side of a hind limb.

Avoid eye contact—After observing that cat A is looking at it, cat B redirects its gaze away from cat A but not toward cat B's own direction of travel if moving. Cat B may slow its prior pace, and an ear may be rotated toward cat A.

Actions and visual signals of the dominant cat. The following behaviors are classified as dominant. The cat with signs of dominant behavior (cat A) is considered as the winner of that single agonistic interaction. Cat B is considered as the loser of that single interaction. All of the following behaviors were recorded only in the context of dyadic interactions.

Block—Cat A walks in front of cat B's direction of movement and holds position so that it is necessary for cat B to deviate from its path to progress.

Supplant—Cat A approaches cat B; cat B leaves, and some part of cat A's body occupies some of the space just vacated by cat B.

Feint—Rapid movement by cat A cat towards cat B of < 3 strides that is immediately followed by submissive signals from cat B (see visual signals of the subordinate cat).

Chase—Cat A takes at least 3 rapid strides towards cat B. Cat B runs away with ears or tail down (to distinguish from possible play).

Upright—With at least 3 paws on the ground, a standing posture is maintained or adopted by cat A that includes further or extreme extension of the forelimbs or extreme extension of the hind limbs.

Ears up rotated —Ears up but stiffly upright and turned so that the apertures are directed laterally rather than rostrally.

Tail arch-base—Tail is curved at the base with the remainder of the tail drooping. The fur may be piloerected.

Stare—Fixed stare, > 3 seconds and not easily distracted by other activity around it; often directed at the other cat's eyes and maintained even when the other cat makes eye contact.

Mount—Cat A bites the nape of cat B and positions itself on top of cat B so that its thorax and abdomen are in contact with the lumbar area of cat B.

Additional behaviors observed in the feed room

Watches—Idle observation, distinguished by eye and head movements to track what is being watched.

Wait on—Cat B sits or lies on the table, chair, or floor of the feed room and watches cat A eat; followed by eating or jumping onto the food table and eating within 2 minutes after cat A leaves or ceases to eat. Cat B may also pace rather than sit or lie down, so long as it is watching cat A on the food table and has watched cat A for ≥ 3 seconds.

Intervening wait on—Cat B and cat C are both waiting on cat A in the feed room. Cat A leaves, and cat B gets up to eat. When cat B leaves, cat C gets up to eat. Cat C is considered to have waited on cats A and B.

Retreat from food bowl—After jumping on the table or chair, cat B sees cat A on the table and leaves, with or without action from cat A.

Supplant—Cat A displaces cat B, which was eating, and takes the position at the food bowl. Cat A must eat. Cat B must have signs of submissive postures or leave immediately while still chewing.