

1 Dominance

1.1 Introduction

The concept of dominance appears often in the animal behavior literature. When defined at all its meaning and usage are often inconsistent, making any comparison of results among experiments ambiguous. How we think of dominance necessarily influences findings obtained by observation (Syme 1974). Perhaps because domestic cats are asocial (Chapter 3), their expressions of dominance seem strongly situation-specific (Bernstein 1981, Richards 1974, Tufto *et al.* 1998) rather than manifestations of a societal mandate, making dominance–subordinate relationships less predictive of reproductive success and other fitness measures.

My objectives here are to define and describe dominance behavior and try to evaluate its relevance in the lives of free-ranging cats. Much experimental work on dominance and subordination in laboratory settings has only peripheral application to cats living outdoors. Consequently, I seriously doubt that watching cats crowded together in cages yields anything except measures of aberrant behavior, not at all unusual when circumstances keep animals from dispersing (Spotte 2012: 221–227).

The dominance concept has done little to enlighten our understanding of how free-ranging cats interact, its utility seemingly more applicable to animals demonstrating true sociality. As I hope to make clear, agonistic interactions between free-ranging cats are mostly fleeting, situational, and the consequences seldom permanent because neither participant has much to gain or lose. Baron *et al.* (1957) and Leyhausen (1965) used *relative dominance* when referring to how vigorously an individual dominates subordinates, meaning that some cats are more dominant than others in *relative* terms, perhaps by not allowing subordinates to usurp them even momentarily at the food bowl if a subordinate growls or by refusing to share food. That measurements of relative dominance, situational dominance, or dominance by any category have utility in assessing the interactions of free-ranging cats is doubtful. Food is not highly motivating. Small groups of cats, whether captive (Mugford 1977), feral (Apps 1986b), or stray (Izawa *et al.* 1982), seldom fight over food or anything else, raising the question of whether the “dominance” observed during arena tests and based on food motivation is not mostly an artifact of experimental conditions. As Mugford (1977: 33) wrote of laboratory cats fed *ad libitum*, “Less than 1% of total available time was accounted for by feeding, so it would be difficult for any single dominant animal to retain exclusive possession of the food pan. ...”

1.2 Dominance defined

The most useful definition of any scientific term consists of a simple falsifiable statement devised to reveal some causal effect in nature beyond mere description and data



analysis. Flannelly and Blanchard (1981: 440) made clear that “dominance is not an entity, but an attempt to describe in a single word the complex interactions of neurology and behavior.” This is important to remember and useful conceptually, although difficult to wrestle into falsifiable hypotheses if the only available method of testing involves observation without manipulation of the subjects or conditions.

Any definition necessarily encompasses *agonism* (Drews 1993), which some consider a synonym of aggression, but properly interpreted and applied includes both dominance and submission (Spotte 2012: 40–42). Drews employed the terms dominant and subordinate to indicate relative rank in either a *dyad* (a group of two individuals) or more complex hierarchy (i.e. triad or higher). It follows logically that *dominance behavior* and *submissive behavior* denote specific responses (e.g. striking with a forepaw, sibilance, aggression, fleeing). Thus a subordinate owes its rank – as perceived by us – to behaving submissively when encountering a dominant conspecific.

Gage (1981) proposed studying dominance in either of two ways. One approach starts by proposing a theory that not only identifies the concept but encompasses conditions necessary to realize its application (*functional definition*). This step is followed by derivation of a testable hypothesis derived from theory that includes a definition. Empirical results then force acceptance or rejection of the null hypothesis of no difference along with the definition. The free-ranging cat literature largely ignores functional definitions. However, to qualify as scientific the design of an experiment is obliged to take a functional approach because all testable hypotheses must be grounded in theory. Descriptions not based on this principle leave no means of explaining the observations.

In the second approach (*structural definition*), observable states of dominance are tacitly assumed to exist outside theory, an operational definition is proposed, and tests are conducted to determine whether the term as defined has merit. The most complete structural definition is from Drews (1993: 308), who did not offer a functional counterpart: “*Dominance* [italics added] is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation.” A consistent winner is therefore dominant, the consistent loser subordinate. This winner–loser format describes how agonistic encounters are resolved and assessed observationally by an investigator.

Drews’ definition, along with the majority of others he reviewed, demonstrates that the animal behavior literature (including that portion dealing with free-ranging cats) is almost entirely data-driven, descriptive, and relies on structural definitions. In the absence of hypothesis testing, the causal basis of dyadic asymmetry and dominance hierarchies (see later) can only be inferred. To make inductive inferences is to step outside the boundaries of structurally-based experimentation and attempt to explain function, an impossible undertaking. When induction takes precedence, accounts of structurally based experiments morph into general, or universal, statements (Popper 1968: 27), none of which can ever be valid.

Some combination of signals is necessary before dominance ranks or hierarchies can assemble in sustainable configurations. *Communication* can be defined as “an association between the sender’s signal and the receiver’s behavior as a consequence of the signal” (Spotte 2012: 33). Assuming agonism is a form of communication – that is, measurable in terms of signal and response – then *dominance* considered within communication’s restricted context is one animal’s attempt to influence another’s behavior

(also see Krebs and Dawkins 1984, Maxim 1981, Smuts 1981). My purpose here is to ascertain how this is possible and attempt to assess the different manifestations.

Operationally, the individual signaling first (i.e. the cat attempting to influence how the other responds) can be either the dominant or subordinate member of a dyad. For example, crouching is considered submissive male behavior. If so, a male that crouches on encountering another male signals submission, announcing his subordinate status. The dominant male then has two choices: ignore the signal or respond by signaling his dominance. The latter behavior acknowledges respective status, although in either case the dominant-subordinate relationship likely has been established even between cats meeting for the first time (Cole and Shafer 1966), and any chances of aggression are diminished. The dominant male's first option (passive disregard) is evidence that "Subordination-acknowledging ... is not always prompted by dominance-confirming, and either of them can serve as a signal or response" (Spotte 2012: 41).

As mentioned, an agonistic encounter produces a so-called "winner" and "loser," one animal emerging dominant, the other subordinate. A fight might serve to establish a dominant-subordinate relationship initially. However, mutual acknowledgement of status is what sustains the relationship over time, and perpetuation without change is based on recognition and familiarity. Fighting is rare afterward, and a stable relationship from both sides of the agonistic divide has been established. Dominant-subordinate status can be established quickly in dyadic contests. Cole and Shafer (1966) tested eight cats in 10 round-robin trials (28 combinations) and noted that in 82% of dyads the relationship became apparent during the first trial.

Dominance is conceptually fuzzy like "stress" and "species." As Hinde and Datta (1981: 442) emphasized, "If dominance is used to describe the directionality of interactions, it explains that directionality no more than the 'migratory instinct' explains migration." Familiarity makes dominance especially difficult to assess (de Boer 1977b). Landau's (1951: 1) rigorous mathematical analysis led to this conclusion: "The hierarchy is the prevalent structure only if unreasonably small differences in ability are decisive for dominance." Thus, "If all members are of equal ability, so that dominance probability is $1/2$, then any sizable society is much more likely to be near the equality than the hierarchy; and, as the size of the society increases, the probability that it will be near the hierarchy becomes vanishingly small." In Landau's view, what really controls dominance relationships are factors like the histories between individuals.

By age 8 weeks, cats are threatened by an unfamiliar conspecific or even a cut-out cardboard model of one, responding with *piloerection* (hair erect, or "standing on end") and arched back (Kolb and Nonneman 1975). Can two male cats recognize each other as individuals outside the context of dominant-subordinate or is familiarity predicated on signaling alone and subsequently learned through experience? Not presuming to know the answer raises another question: can dominance-submission be separated from learning and take place before mutual recognition has been established? Maybe the subordinate recognizes some feature of the dominant individual associated with a *prior attribute* (also called *supraindividual characteristic*), or individual trait that bestows rank, like greater body mass, a high-quality display, kinship, or a behavioral sign that induces submission without confrontation (Gauthreaux 1981, Winslow 1938). If so, it might predict the outcome of such meetings between strangers, but dominance *per se* would not be involved (Vessey 1981). This is not the case if the subordinate recognizes in the stranger a prior attribute associated with dominance

that had previously consigned it (the subordinate) to its current status. As a result of that encounter the subordinate now defers and assumes the postures of submission (Bernstein 1981). In this hypothetical situation the *attribute* has prompted the dominant-subordinate relationship, not the individuals.

Dominance is presumably about conflict resolution and supposedly functions by dampening aggression (Hinde 1978). The capacity to prevent dominance from escalating into aggression might hold true in nature where subordinates can disperse. Captive animals are denied this option, and a subordinate is unable to escape the dominant's aggression (Spotte 2012: 221–227). Encounters between strangers require that both individuals recognize and correctly interpret certain properties possessed by the other. Encounters between two familiar animals, if unidirectional over time, are founded on learning, memory, and recognition, three factors that reinforce the agonistic status quo, repress aggression, and reduce the possibility of injury to either party. The expression of threat might be even more important than aggression in establishing a dominance relationship between cats (Cole and Shafer 1966).

As mentioned, dominance has been linked to prior attributes and patterned relationships between individuals, two incompatible concepts. The distinction requires understanding that dominance between animals as assessed by humans is a construct, in practical terms a relative measure rather than some inherent property possessed by certain individuals and not others. Dominance as a result of a prior attribute seems unlikely unless the physical feature (e.g. greater body mass) or trait conveyed (e.g. heightened aggression) exists in recognizable form in the absence of submission. Baron *et al.* (1957) found no consistent association between dominance status and prior attributes like differences in sex, body mass, passivity, and problem-solving ability. They wrote (Baron *et al.* 1957: 65): “Descriptive and correlational investigations such as this will not contribute greatly to our understanding of the determinants of social behavior in animals.”

Dominance by definition must be relative, a dominant individual comprising one-half a dyad. It seems doubtful that physical attributes alone are reliable predictors of dominance, despite our sometimes explicit presumptions (e.g. piloerection makes body size appear larger, standing straight gives an appearance of being taller). I offer three reasons. First, examples abound of smaller, weaker individuals dominating stronger, more physically imposing opponents in dyadic situations. Second, because a prior attribute can be associated with putative rank (e.g. body mass, head volume, age in males) as claimed by Bonanni *et al.* (2007) raises the possibility of secondary associations that might be more meaningful (i.e. that one or more of these variables is merely a secondary expression of a behavioral trait and irrelevant in isolation). Third, if dominance can be recognized simply on the basis of prior attributes we should expect rank-order to mirror a continuum of the attributes themselves (e.g. heaviest is dominant followed by next heaviest, and so forth), but direct correlation of such factors is not consistently predictable (Hinde 1978).

Laboratory cats that had been dominant in both dyads and group hierarchies became timid and submissive to their former subordinates after psychological manipulation rendered them neurotic, yet nothing about their physical appearance had changed (Masserman and Siever 1944). In fact, the rank-order could be turned upside-down (*dominance reversal*) and then re-established by psychological manipulation of the test cats while keeping physical prior attributes constant. These last experiments indicate that dominance in cats emerges from a behavioral trait and not a physical attribute.

Dominance has sometimes been defined as “priority of access to resources” (Drews 1993: 299). As Drews made clear, for this to be predictable “implies *a priori* that dominance influences the pattern of access to resources or else that priority of access to resources be part of the definition of dominance.” As a useful measure of behavior it presents two problems. First, if the premise states that dominance directly affects access to resources then measuring its impact based on access to resources involves circular reasoning (Richards 1974, Syme 1974). Second, limiting observations to any specific factor inevitably obscures interpretation: dominance envelopes all instances of conflict resolution, but in this example not every conflict is about resources (Drews 1993, Hand 1986).

Prediction is a necessary feature of dominance, but insufficient to define it (Vessey 1981), and description alone is obviously limited by a lack of both predictive and explanatory power, leaving underlying cause, or function, indeterminate. As pointed out by Drews (1993), definitions based on observation instead of theory are closed to empirical investigation, leaving no way of comparing them. Each such asserted definition stands isolated, untestable against any others. Distinctions devoid of theory are relegated to semantics (Gage 1981), and a definition that incorporates presumed synonyms lacks even descriptive value. The literature on free-ranging cats is notable in this respect, commonly identifying dominant males as “aggressive” or “winners.” Making subjective evaluations in ways that dominance equates with aggressiveness and “winning” a dyadic encounter classifies one cat as dominant and the other subordinate (e.g. Bonanni *et al.* 2007, Cafazzo and Natoli 2009, Natoli *et al.* 2001). This method meets a basic statistical definition (Tufto *et al.* 1998: 1489) that “dominance is defined as a parameter characterizing the relationship between two individuals, determining the expected number of successes of the first individual in disputes with the other.” In the end, however, attempts at explanation devolve inevitably into conjecture because cause has been omitted from the statement of hypothesis.

Tufto *et al.* (1998) pointed out that assessing dominance relationships in dyadic terms provides a parameter p_{ij} in which individual i dominates j . Dominance is therefore a parameter describing a relative relationship between two individuals along an infinite series of values spanning 0 and 1. Thus i dominates j if $p_{ij} > 0.5$. If the value of p_{ij} is exactly 0.5 then neither individual in the dyad is dominant, but the requirement is always

$$p_{ij} = 1 - p_{ji} \tag{1.1}$$

It should come as no surprise that the process of devising and then sorting categories of behavior based on description seldom opens an illuminated path to insight. As Drews (1993: 297) wrote, “An asymmetry in the outcome of particular interactions is not a sufficient justification to introduce a dominance concept, either as a descriptive tool or an explanatory mechanism.” This is perhaps even truer in attempts to describe nonlinear hierarchies in which kinship can force intransitivities and context determines the outcome, as when offspring dominate their mothers in some situations but not others (Tufto *et al.* 1998).

Even if predictive value is high, accuracy and precision are not confirmation of a definition but a description of how the animals behaved in those circumstances; that is, a definition can have “heuristic value” without explanation (Drews 1993: 299). Science is the business of testing theories. As emphasized, descriptive studies have limited



scientific utility unless placed firmly within the context of hypotheses. The ultimate objective should be to address how and why animals behave as they do, which renders behavioral description as half-completed and executed in reverse; that is, data are collected before testable hypotheses have been devised. The large number of structural definitions of dominance relative to functional ones, combined with a history of inconsistent results, is evidence of this deficiency.

1.3 Dominance status and dominance hierarchies

According to Drews (1993: 283), “*dominance status*” [italics added] refers to dyads while *dominance rank* [italics added], high or low, refers to position in a hierarchy and, thus, depends on group composition.” From this structural perspective, learning through past encounters, individual recognition, and other important but confounding variables become irrelevant. What the subordinate recognizes is some feature of the dominant individual perhaps associated with a prior attribute. Here clarification is warranted. Note that Drew’s structural definition identifies dominance as *an attribute of the pattern of interactions*, and although the submissive animal recognizes some feature of dominance in its opponent’s signals it is the exchange of signals and responses – characteristics of *pattern* – that determine respective status within the dyad, not a prior attribute of either individual.

A dominance hierarchy that places individuals of a group into ranks of descending dominance can exist between two individuals or among several, but such relationships are always sums of composite interactions occurring *between* two individuals, not *among* three or more. Even in tight settings the process is sequential, although often appearing to be simultaneous. In other words, a cat confronted suddenly by two antagonists must instantaneously assess first one then the other. However, because dominance-submission prompts interaction, results of isolated dyadic measurements are unlikely to be realistic descriptions. In any case, assessments of dominance hierarchies in captive domestic cats have limited application to knowledge of relationships in free-ranging cats because the focus is limited to aggressive encounters. As Kerby and Macdonald (1988: 72) pointed out, “None of these studies shed light on the workings of a hierarchy in the cat’s natural history, and none has reported the subtle behavioural cues one might expect to signal the *status quo*. ...”

The truth of this last statement casts an antinomic shadow. We need to know what mechanisms make dyadic interactions in isolation different from those in groups and elucidate why an animal that seems dominant in one situation is not in another. Perhaps the answer is simple, an inability to evaluate the status of more than one conspecific simultaneously relative to your own, as mentioned in the paragraph above. Consider humans at a cocktail party. What looks superficially like multi-person interactions are actually shifting dyads of focus. One individual speaking while the rest listen is a monologue. Humans behaving socially communicate as dyads using dialogue. The word “dialogue” is a comparatively minor entry in the English lexicon. Cats are no different. After watching kittens, West (1974: 433) wrote, “In play involving three or more individuals the nature of the play patterns allows for only peripheral interaction by the ‘third’ member.”

Experimentally, dominance status of cats is assessed through “tournaments,” the objective being to seek the underlying dominant-subordinate structure within a group. This is evaluated by placing pairs of cats from the same group in an “arena” together for predetermined periods until every individual has been tested against each of the others in round-robin competition. Resultant scores are expected to reveal a pattern. One



troubling aspect is that the results of such tests are artifactual by taking place outside the only context that really matters, which is the group itself. Although individuals presumably interact in dyads, any outside influence has been walled off. Another is the problem of apparent linear rankings sometimes being indistinguishable from randomness (Appleby 1983, but see Jameson *et al.* 1999).

Hierarchies are of two basic kinds, neither especially relevant to the lives of free-ranging cats. A *transitive hierarchy* describes a linear (i.e. straight-line) scale of dominance, or “peck-order,” in which animal A is dominant to animal B, and B is dominant to animal C. Consequently, A is dominant to C. This can be expressed symbolically as $A > B > C$. An *intransitive hierarchy* is similar to the first: $A > B > C$ except that $C > A$, implying a nonlinear looping back of the dominance order. The further an intransitive hierarchy deviates from linearity, the more intransitive it becomes (i.e. the greater the possibility that intransitive loops will increase with the number of criteria). Intransitive relationships are common, surfacing during dyadic encounters when the outcome is determined by two or more factors (Petraitis 1981). Perfectly linear hierarchies occur most often in small groups; that is, groups having <10 members (Chase *et al.* 2002, Drews 1993). The larger the group the more its pattern slides toward intransitivity (Jameson *et al.* 1999).

Rank based on prior attributes (Section 1.2) is thought to influence rank-order within a linear hierarchy, but these factors alone are not its building blocks (Chase *et al.* 2002). Thus the linear hierarchy of a society can form, disintegrate, form again, and remain consistently linear even if half the members change rank with each iteration (Chase *et al.* 2002). In other words, linearity must be driven by factors and forces other than those easily measured and observed in pairwise contests. This shortcoming, combined with confounding by winner and loser effects (reciprocal reinforcement), bystander effects, the stringent mathematical conditions required to produce linearity if based on prior attributes, and doubtless other factors, call into question the relevance of testing dominance-submission using pairwise interactions and extrapolating the results to the group.

As hinted above, to account for what makes one animal dominant and another subordinate in social species ultimately requires evaluation at the group level. Two hypotheses can be considered. The first is deterministic by stating that an individual's position in a hierarchy is more or less decided in advance by features that enhance its capacity to dominate. This is the *prior attributes hypothesis*, elements of which were described previously, and although it forecasts linear social structures this is not always the result (Chase *et al.* 2002). As noted before (Section 1.2), prior attributes can include behavioral or physical characteristics (e.g. aggressiveness, age, body mass, sex) or a mix of these. If its pertinent elements can be identified and limited, then the individual with the highest prior attributes score presumably emerges dominant over the others. The animal scoring second-highest ranks second, and so forth. Often an animal predicted to be dominant based on a prior attribute (e.g. body mass) turns out to be submissive (Winslow 1938).

The *social dynamics hypothesis* is more stochastic and predicts nonlinear social structures. It states that social interaction among members of the *whole group* and not its paired components drives the formation of hierarchies, and that hierarchical structures emerge from causative factors other than prior attributes (Boyd and Silk 1983, Chase *et al.* 2002). Specific social interactions culminating in intransitive hierarchies possibly include (1) winner and loser effects in which winners or losers of earlier

contests assume a pattern of winning or losing later ones (Chase *et al.* 1994, Hsu and Wolf 1999) and (2) bystander effects during which conspecific bystanders observing individuals interact with others adjust their own behavior (Johnsson and Åkerman 1998, Silk 1999). Seen from this perspective, hierarchies become self-organizing based on group dynamics *within* the social system and not derived entirely from any prior attributes of its individual members (Theraulaz *et al.* 1995).

Each hypotheses has elements of validity, and the two might exert complementary effects (Chase *et al.* 2002). Until recently, support for the social dynamics hypothesis came mostly from models showing that restrictive mathematical conditions are necessary to produce linear hierarchies based solely on prior attributes (Landau 1951). Chase *et al.* (2002: 5748) concluded: “Linear structures should not be assumed to result simply from variation among individuals or from cumulative conflicts among pairs of individuals.” They advocated instead that investigators “look at patterns of interaction across whole groups and understand how these patterns produce hierarchy ladders.”

Stated differently, inherent properties as observed in individuals or dyads are not indicators of social structure and therefore unable to represent it. Going further, they might not even indicate dominance, at least not the transitive kind. Statistical analyses of dyadic interaction are based on paired comparisons. In tests like Appleby’s (1983) the null hypothesis states that from among a group of paired comparisons the chances of any individual winning is random. If the test statistic is then sufficiently large to reject the null the alternative hypothesis simply presumes a transitive underlying structure. Any interpretation that the dominance structure is *actually* transitive falls outside the capability of the analysis and must be incorrect. As Tufto *et al.* (1998: 1489) explained, “rejection of the null hypothesis of randomness implies only that the alternative hypothesis is a better description of the dominance structure among the individuals being studied.”

Winner and loser effects could also be termed *reciprocal reinforcement* because each individual of a pair potentially “trains” the other to perform as dominant or subordinate (Flannelly and Blanchard 1981, Spotte 2012: 54). This situation arises, for example, during paired competition for food under arena conditions. The first to reach the reward and eat it (the “winner”) is scored as dominant, the “loser” as subordinate. Repeated trials usually yield consistent results once the participants become acquainted, and the same is true between evenly matched strangers (Chase *et al.* 1994; Hsu and Wolf 1999; Winslow 1944a, 1944b). Such findings could be artifactual, the animals having learned to solve the problem efficiently (i.e. without strife); that is, outside the assumption of a prior attribute and therefore independently of the experimental design. Instead of revealing true social relationships each animal “trained” the other to retain its respective status, which was then reinforced in subsequent trials. The result is less a hierarchy than the illusion of one. Many times during dyadic interactions competing cats end up sharing the reward more or less equitably or after some harmless nudging and pushing (Winslow 1944b).

The issue is further confused by striking individual differences in any group of cats. Some strive consistently to be more competitive whether they win or lose dyadic contests. Others seem to give up, and still others vary their effort depending on intensity of the competition. Winslow (1944a: 311) wrote, “In general ... the form of social interaction elicited in cats ... depended upon the nature of the social relationship that had existed between the competitors prior to the tests.” This, and the fact that a cat’s performance changes when the competitor is removed (Winslow 1944a, 1944b), indicates to me that dominant-subordinate relationships can be created artificially

simply by placing cats in abnormal situations; that is, conditions of forced interaction. Free-ranging cats ordinarily avoid each other, thereby circumventing conflict and leaving no outward evidence of either dominance or submission.

It seems unlikely that either transitive or intransitive relationships exist as permanent fixtures among free-ranging cats. Laboratory observations to the contrary appear to result from confinement and crowding. The original descriptions of a transitive dominance (i.e. the original “peck-order”) hierarchy were by Schjelderup-Ebbe (1922) in domestic fowl, which unlike cats are unquestionably social. The transitive relationship is therefore one of descending dominance-submission and truly hierarchical. Sustaining such a system requires every individual to recognize, accept, and remember its status. Once in place a transitive relationship is mainly peaceful, the dominant animal seldom fighting to retain its rank. This asymmetric pattern is consistent and unidirectional, and contrary to territoriality (Chapter 2) the direction of agonistic behavior is independent of location (Kaufman 1983).

Even confining a group of cats in a small space does not predictably induce agonism. Among the most common interactive behaviors is none at all; that is, mutual indifference, each individual spending most of its time alone (Hart 1978, Podberscek *et al.* 1991). Eight adult males (seven castrated) were maintained under laboratory conditions in a cage 2.2 m high \times 1.62 m wide \times 3.9 m long. Three walls had shelves; there were litter boxes on the floor. Of behaviors recorded, agonistic interactions accounted for just 1% and consisted of hissing. When cats played it was usually alone; when grooming, 90% was self-grooming (i.e. licking itself).

Liberg (1980: 347), remarking on Leyhausen’s (1965) comments about social organization of solitary mammals, suggested that territoriality could develop at low population densities, “but at higher densities this might change into a dominance order system.” Say and Pontier (2004) seemed to agree when speculating that urban strays are not territorial. This is certainly true of gray wolves, which form hierarchies in captivity where space is limited but are territorial in the wild (Spotte 2012: 90–107, 221–227). I doubt the existence of a similar pattern in the domestic cats. Location reliably predicts most dominant-subordinate relationships in territorial species, but evidence of territoriality in domestic cats is unconvincing (Chapter 2).

Some investigators have postulated that the population density of free-ranging cats – and consequently social organization – is influenced strongly by the abundance and distribution of food (Macdonald 1983, Liberg and Sandell 1988). I disagree. Evidence seems to show that only the first is true and that cats gathered around waste-disposal sites and feeding stations are aggregations of asocial individuals, not a society as the term is usually understood (Chapter 3). Dominance hierarchies supposedly form in groups of stray cats gathered near clumped food (Dards 1983, Liberg *et al.* 2000, Natoli and De Vito 1991, Say *et al.* 2001). However, clustered resources (e.g. feeding sites, garbage bins, waste-disposal dumps) do not always forecast the competitive interactions that typify social species. Male strays at crowded urban locations, for example, are often more tolerant of each other than feral males at rural areas of low population density (Liberg 1980).

Izawa *et al.* (1982: 377) reported neither avoidance nor agonism among \sim 200 strays around fish-waste dumps at 125-ha Ainoshima Island, Fukuoka Prefecture, Japan, where individuals fed together, and “several cats [as many as 19] often ate the dump of fishery wastes or large fish nose to nose. ...” Page *et al.* (1992) saw no evidence of food competition among strays living at Avonmouth Docks, Bristol, United Kingdom. Garbage was plentiful, supplemented with food set out regularly by employees. Cats

did not crowd the feeding areas, some rarely visiting them at all. Others checked the feeding sites consistently, including some that occupied small home ranges (Chapter 2) centered around them. Denny *et al.* (2002) did not see evidence of male dominance at a waste-disposal site on the central highlands of New South Wales, Australia. Yamane *et al.* (1997) attempted to show that age determined feeding “rank” among male strays, but the data, so far as I could tell, revealed merely a vague outline of pattern, not actual evidence of dominance traceable to underlying cause and effect. Interaction among cats of all ages was peaceful.

Observations of farm cats chasing off the competition might be interpreted as follows, although my comments are speculative. Strange cats are attacked and chased by both resident male and female farm cats (Macdonald and Apps 1978). Females are more tolerant of females of their own group than of females from neighboring farms, with males seemingly tolerant of males from both their farms and others (Turner and Mertens 1986). Farm cats are not always fed consistently, nor does the amount provided always meet their nutritional requirements. The cats might be defending their food supply, which in its meager outlay has become more valuable and easier to protect than the endless pickings at a waste-dump site.

Cats are not overtly competitive. Weaned kittens and adolescents of 4–6 months are generally tolerated by adults and often allowed to feed first (Bonanni *et al.* 2007, Yamane *et al.* 1997). Urban strays apparently did not compete for food with red foxes or stray dogs at Avonmouth Docks (Page *et al.* 1992), and Beck (1971) observed stray cats and dogs, along with rats, foraging peacefully on garbage in a Baltimore alley within centimeters of each other.

If this situation seems confusing, laboratory tests and field observations offer little in the way of clarity. Baron *et al.* (1957: 59) reported “fairly linear” hierarchies emerging from food competition tests among confined cats that knew each other but found no particular association between dominance and aggression. The rankings were roughly consistent whether the number of cats was two, three, or four, but among both captive and free-ranging cats transitivity is generally weak (van den Bos and de Cock Buning 1994, Laundré 1977, Liberg 1980, Natoli *et al.* 2001). Leyhausen (1965) reported a dominance hierarchy at feeding. According to Cole and Shafer (1966) the most food-motivated and aggressive individuals in food competition tests were not necessarily the most dominant during other interactions. Masserman and Siever (1944) concluded that aggression during food competition tests resulted more from frustration at failing to obtain food than a means of obtaining it. Laundré (1977) reported a similar situation and the formation of a female dominance hierarchy among farm cats fed intermittently. Baron *et al.* (1957) did not see an association between dominance and aggression using food competition tests. When the dominant animals of three groups competed among themselves, Baron *et al.* (1957: 64) wrote, “there was no apparent relationship between the status of the leaders as measured by their food-getting success and the aggressivity that they demonstrated while competing together.” Accordingly, these findings “generally confirm the naturalistic impression of the cat as asocial and individualistic in its interactions with other cats.”

1.4 Dominance–submissive behavior

Nearly all the 90 or so visual and tactile behaviors documented for wolves also occur in domestic dogs (Scott 1950: 1013–1015, Table 1, 1967; Scott and Fuller 1965). The cat’s seem impoverished in comparison, including several inconsistently interpreted

elements of dominance-submissive behavior. Slaps and hisses have been classified as low-intensity aggression (Dards 1983) and as submission (de Boer 1977b). Wails, yowls, and piloerection are seen as submissive responses (Dards 1983). Caterwauling has been linked loosely with aggression, although some subordinate cats caterwaul too, and growling can signal either dominance or submissive behavior (de Boer 1977b). Shimizu (2001: 88) described “threatening vocalizations” as “lasting sounds, like a dog howling.” These were emitted by free-ranging, same-sex adults while staring at each other, and were identical to the yowl. However, Shimizu (2001) considered the yowl of adult males to be different from the sound made in the breeding season (Chapter 4). During laboratory tests of dominance an especially aggressive male might briefly mount a less aggressive male competitor (although without intromission), inducing it to become passive (Winslow 1944a). Males mounting each other has also been reported in strays (Yamane 1999).

As defined by Fox (1975: 413), “A *display* [italics added] is a composite of different units or actions (e.g. tail and ear positions and movement, angle of body, crouch, forward lean, back arch, etc.)” Visual signaling between individuals is apparently less important to cats than to social monkeys. Young stump-tail macaques (*Macaca speciosa*) blinded shortly after birth were harassed by sighted conspecifics. The cause was “lack of comprehension of visual signals” (Hyvärinen *et al.* 1981: 4), requiring them to be separated from the sighted group. In contrast, Crémieux *et al.* (1986: 231) reported that “The social behaviour of the blind cats with the other blind and control [sighted] cats was almost normal.” Although the experimental cats were tested as adults they had been purposely blinded as kittens and were oblivious to visual signals. The importance of visual signaling needs to be assessed. Whether the absence of signals like tail-up (see later) go unnoticed when tail-less cats fail to provide them is unknown. The only conclusively demonstrated use a cat has for its tail is maintenance of balance (Walker *et al.* 1998). *In the following descriptions, hyphenated terms in italics refer to distinctive signals in a kind of shorthand used elsewhere in the text.* On meeting, two males might sniff noses (*nose-sniff*) before displaying signs of agonism, but this behavior declines with increased familiarity (de Boer 1977b). Aggression among cats that know each other is minimal: 14 instances in ~1200 interactions seen in four barn cats comprising an adult male and three adult females (Macdonald and Apps 1978). According to Dards (1983), greeting behavior between cats of either sex consists of any or all of three components: (1) raising the tail vertically (*tail-up*), (2) nose-sniff, and (3) rubbing heads (*head-rub*). In tail-up the tail, normally carried at an angle of ~45 degrees below horizontal, is lifted to horizontal or higher (sometimes to 90 degrees with a slight curl at the tip) when encountering another cat. Before or after nose-sniff another part of the body, particularly the perianal region might be sniffed (*perianal-sniff*). A head-rub (Fig. 1.1) might extend from the other cat’s head laterally along its body. Females are about twice as likely to greet males than to be greeted by them in return, and greetings initiated by females are often more intense (Dards 1983). The male’s response is likely to be less intense, if he responds at all.

Male–male interaction is generally splenetic, ranging along an ascending continuum from mutual avoidance to tolerance to aggression (Dards 1983). Rarely is it openly friendly. Even if neither male runs away, agonistic encounters are usually restricted to transient displays of agonism, vocalizing, or mutual disregard. What the vocalizing component signifies is uncertain. Bonanni *et al.* (2007: 1371) included in dominance

Fig. 1.1 Head-rub.
Source: © Ruzanna
Arutyunyan |
Dreamstime.com.



behavior “ritualized vocal duels and real duels” without defining either term. Several observers have described the cat’s agonistic behaviors (Bonanni *et al.* 2007, Dards 1983, de Boer 1977b). In assuming a posture of dominance a male stands straight (*stand-straight*), supposedly for the function of appearing taller. The pupils of his eyes constrict (*pupils-small*). He moves with exaggerated slowness, *stiff-legged*, hindquarters seemingly higher than the shoulders. Cole and Shafer (1966: 49) called this “strutting behavior.” The tail is arched near its base (*arch-tail*), body hair in some degree of pilo-erection, tail hair usually moreso. He emits low wails escalating into yowls (*yowls*), lashes his tail from side to side (*tail-lash*), holds his head high (*head-high*) with chin pointed down (*chin-down*) and jaw chomping rhythmically (*chomp*). Alternatively, he makes licking motions (*lick-lips*) or smacks his lips (*smack-lips*). He might also strike at his opponent with a paw (*paw-strike*). Sometimes cats sit and assume agonistic poses while displaying some of these signs (Fig. 1.2).

A male displaying submissive behavior half-sits (*half-sit*) or crouches (*crouch*), sometimes with chest and abdomen pressed to the ground (*ventrum-pressed*). He might lick-lips or smack-lips, lie down, even roll onto his back, occasionally paw-striking (*paw-strike*) or hissing (*hiss*) at the other cat, although dominant cats also hiss during agonistic encounters. The head is pulled back and kept low (*head-low*), the ears flat to the sides (*ears-flat*) or laid back or folded (*ears-folded*) against the head (Fig. 1.3). From any of these postures he might yowl or spit (*spit*) at his aggressor.

If a fight breaks out it happens suddenly (de Boer 1977b). The two antagonists grip each other face to face and scratch with all four legs. Usually the dominant then leaves while the subordinate remains in a defensive posture (e.g. crouch). Afterward, and sometimes when fighting has not occurred, both cats sit facing each other, alternately opening and closing their eyes slowly (*blink*).

According to de Boer (1977b), behaviors that seem associated with either aspect of agonism – that is, dominance or submission – can include exploration (*explore*) and sniffing of the area (*sniff*), spraying urine (*spray*), rubbing against objects (*object-rub*, Fig. 1.4), grooming themselves (*self-lick*), sitting (*sit*), assuming a Sphinx-like posture

Fig. 1.2 Agonistic encounter between two strays on an urban street. Source: © Andris Daugovich | Dreamstime.com.



Fig. 1.3 A cat displaying simultaneous agonistic expressions, hiss and ears-flat. Source: © Georgiy Pashin | Dreamstime.com.



(*sphinx*) while blinking, and sitting opposite the opponent while looking askance (*look-away*).

Sometimes elements of dominance and submission are mixed (Dards 1983). A submissive cat might stand up instead of crouching, although with its back arched (*arch-back*). It might also display piloerection and lift a forepaw partly off the ground as if preparing to slap. The combination of arch-back, piloerection, *arch-tail*, and the neck flexed (*neck-flex*) is the embodiment of the cartoon Halloween cat, which I shall call *halloween* (Fig. 1.5). It can be expressed with or without a forepaw raised (*forepaw-raised*) or stepping sideways (*side-step*). Males sometimes stand before each other with heads averted (*head-avert*), or one of the two might head-avert with chin-down and chomp. Encounters ordinarily end not in a fight but with one or the

Fig. 1.4 Cats rub against objects for unknown reasons, but deposition of scent (i.e. “marking”) is probably not among them (Chapter 2). The so-called cheek glands of cats have never been described. Perioral glands on the lips could potentially deposit scents, but their function in this regard is unconfirmed. Source: © Astrid228 | Dreamstime.com.



Fig. 1.5 Kitten displaying arch-back, neck-flex, piloerection, and side-step, in combination called halloween. Source: © Tatyana Chernyak | Dreamstime.com.



other retreating, often walking away slowly and stiff-legged. The departing individual might be the aggressor (Konecny 1987a), in which case evaluating which of them “won” the putative contest is unclear.

1.5 Dominance in free-ranging cats

Probably all dyadic interactions are potentially contentious, but as mentioned at the start, dominance in asocial species is likely to be situation-specific. Here are seven examples. (1) Bonanni *et al.* (2007) reported directional dominance relations based on correlation of aggressive and submissive behavior from observations of 13 cats (males and females); both sexes displayed aggressive behavior more or less equally. (2) Adult female cats are sometimes aggressive toward strange females and young males (Macdonald *et al.* 1987). (3) Females with kittens often attack males (Natoli 1985a). (4) Castration can cause diminished dominance behavior and increased submissive behavior (de Boer 1977b). (5) In a group of Roman strays the females were consistently more aggressive than males when near food, often dominating them, although the males seemed otherwise dominant (Bonanni *et al.* 2007). (6) Among female farm cats, most agonism was seen at feeding sites, not over food specifically but as a result of crowding the location in expectation of being fed (Panaman 1981). (7) Baron *et al.* (1957) found that feeding a “dominant” cat prior to a food-competition test sometimes caused it to lose status.

I question whether dominance assessment in free-ranging cats is worthwhile. Experiments using dyadic outcomes to establish rank-order (e.g. Bonanni *et al.* 2007, Natoli 1985b) incorporate an unknown factor, the presumption of evolutionary relevance. Unless hypothesis-based, such endeavors yield results amenable only to conjecture, leaving even the matter of sociality unaddressed. For example, if devising rank-orders is intended to reflect kinship bias in females, does high rank offer privileged access to resources like food and shelter? If so, does rank-order demonstrably affect fitness? The fact that female cats sometimes live in “kinship groups” does not necessarily ameliorate conflict. Inherited relationships failed to bestow detectable privileges on subordinate females among rural Swedish house cats, some of which succumbed to conspecific pressure (including aggression) and dispersed to nearby houses that had no cats (Liberg 1980). Neither was kinship bias evident during competitive feeding experiments in laboratory cats (Masserman and Siever 1944). Before kinship is presumed to affect dominant-subordinate relationships or relationships of any sort in free-ranging cats, its possible effects must be separated from familiarity and the two variables tested and evaluated independently.

Stating that directionality observed between familiar individuals reflects dominance status and then claiming that mutual history is the proximate cause of their respective ranks is tautologous, and tautological statements are not empirical (Popper 1968: 85). Actually, learning by both dyadic members is the proximate cause of such dominance relationships, its existence shown by consistent directionality of the asymmetry (Bernstein 1981).

Prior attributes do not reliably determine dominance even in barnyard fowl that form clearly transitive hierarchies (Schjelderup-Ebbe 1935), and the same is true in the less structured hierarchies of both captive and free-ranging cats (Baron *et al.* 1957, Panaman 1981, Winslow 1938). Cole and Shafer (1966: 48) thought that “it is recognition of the overt behaviors which serves as the important cue for the development of

dominance-subordination relationships." Agonistic behaviors (e.g. aggression, submission) were on display more often during arena situations than when cats were tested in pairs, suggesting social stimulation. Cole and Shafer (1966) mentioned how cats in dyadic food competition trials displayed declining interest once the dominance relationship had been established.

Many investigators seem to view dominance and dominance hierarchies as ends in themselves or treat them as intervening variables mediating other behaviors (Hinde 1978, Hinde and Datta 1981). To Seyfarth (1981: 448) they are "simply shorthand, descriptive terms used by observers to describe what they have seen. ..." Dominance hierarchies are sometimes taken for granted and presumed to exist even when no evidence has been presented (e.g. Macdonald and Apps 1978). To accept the existence of dominance relationships does not require acceptance of dominance hierarchies too, especially transitive ones; their causes might be completely different (Bernstein 1981). Deviation from linearity is common in most species (Hinde 1978).

Are hierarchies even relevant in behavioral assessments? Certainly not without evidence obtained using streamlined definitions and testable hypotheses. Baron *et al.* (1957: 65) wrote, "Systematic manipulation of experimental variables such as motivation and social learning of individual subjects holds greater promise for comparative studies of behavior. ..." And Bernstein (1981: 428) warned, "Shotgun correlational techniques and closely reasoned logical arguments of what *should be* [italics added] the case ... will not prove that agonistic dominance ranks are a factor in social organization." Moreover, in abbreviated dominance hierarchies (e.g. only two ranks, high and low), identifying rank-order adds nothing beyond what we already know. This is apparently the situation in cats when females and males, and just females, are kept together in small groups: one or more individuals appear dominant and the rest seem to rank lower with nothing separating them in terms of status (Baron *et al.* 1957, Laundré 1977, Panaman 1981, Rosenblatt and Schneirla 1962, Winslow 1938).

Rosenblatt and Schneirla (1962: 453) speculated that "Dominance relations in the cat appear to be more a matter of indifference of one animal towards another, in which the more active animal appears to be the more dominant, than the end-result of a series of encounters in which mutual relationships are worked out among the individual animals." Such casual disregard of conspecifics is inconsistent with the behavior of truly social species even in confinement. Spotted hyenas (*Crocuta crocuta*) captured as infants were taken to California and reared in separate peer groups. Captivity denied them sustained maternal influence, the opportunity to hunt, and presented other unnatural conditions (e.g. no chance to acquire skills by learning from older, experienced conspecifics). Nonetheless, they arranged themselves into a natural hyenid system characterized by powerful social facilitation (e.g. group eating and drinking, group defecation and scent-marking, group greetings), a complex array of social signals, female dominance, matrilineal organization, inherited social status, and dominance hierarchies in which males were subordinate (Glickman *et al.* 1997). Such complex and coordinated interactions are not required of asocial species like the domestic cat (Chapter 3).

It seems reasonable to ask whether dominance is best measured in terms of arena tests involving competition if such tests are not controlled for the effects of facilitation. Winslow (1944a: 297) defined *competition* in laboratory settings to be situations "in which winners and losers are selected on the basis of their speed or strength in executing the experimental task, with the consequence that winners receive the reward and

losers are denied it.” He defined *social facilitation* as “situations in which an increment in the activity results simply from the presence of other individuals. ...” According to Ward (2012: 223), facilitation occurs “where individuals are more likely to express a given behaviour, or express it a greater rate, in the presence of conspecifics.” Therefore, in dyadic contests is the first animal to the food truly dominant or does the other animal’s mere presence facilitate a faster response by the so-called winner? In sorting this out we might conclude that “dominant” and “subordinate” have little meaning when cats are tested in arenas, and that “social facilitation” implies some standard of interaction rarely encountered in a species that behaves as tolerantly asocial most of the time.

Leyhausen (1965, 1973) doubted that cats form rigid dominance hierarchies, yet believed that dominance status becomes established among free-ranging cats. He noted how familiar males often entered each other’s spaces peacefully. This could be expected only if the occupied areas represent home ranges but not territories, which by definition are *defended* spaces (Chapter 2). As to interactions between strange males, Leyhausen (1973: 127) wrote, “Adult tomcats meeting for the first time are liable to engage in fierce fighting regardless of the season.” In his opinion, fights between males are never territorial disputes because they take place on neutral ground. This seems to me an impossibility because any location occupied by a cat obviously comprises part of its home range even if only temporarily, and although a home range is not defended it is anything but neutral. The presumed hierarchies formed as a result of these dyadic encounters are, in Leyhausen’s opinion, “absolute” and represent fixed dominance status. Afterward, certain “rules of the road” dampen future aggression. As an example, Leyhausen (1973: 125–126) wrote, “If the inferior [subordinate] cat has already entered a commonly used passage before the superior cat arrives on the scene, the latter will sit down and wait until the road is clear; if it does not, its superiority may be challenged successfully.” No empirical evidence was presented to bolster any of these claims.

Relationships in presumed cat hierarchies can fail to show transitivity in other ways. In a hierarchy comprising eight laboratory cats, two individuals accounted for 59 aggressive events, 51 attributable to one cat, eight to the other (Cole and Shafer 1966). The incidents seemed unrelated to dominance rank (the investigators ranked these animals third and fourth).

The putative transitive hierarchies in stray males reported by Natoli (1985b), having been based on paired comparisons, were probably invalid. According to Richards (1974), if a species is thought to be truly social, constructing transitive hierarchies based on dyadic interactions is inappropriate. She listed three criteria for evaluating dominance–submission. First, because accurate assessment of social ranks requires a high frequency of social interactions the species studied must be clearly social. This makes the domestic cat a questionable candidate (Chapter 3). Second, in laboratory settings captivity precludes escape, and observations made of captive groups can yield an artificially inflated number of “social” encounters, particularly of the agonistic kind. Third, the group studied must be stable, its membership unchanged over a long period.

Testing an asocial species as if it were social can yield puzzling and inconsistent results. Cole and Shafer (1966) assessed dominance in eight laboratory cats (males and females) using food competition. The subjects were tested in all dyadic combinations and then as a group in a room familiar to them. Hierarchies from the two experimental configurations were different. In fact, the cat that emerged as dominant

from extensive round-robin dyadic competitions ranked lowest when all cats were in the room together. This individual, which had been eager and motivated in paired comparisons, was “aloof and relatively placid in his behavior” in a group setting (Cole and Shafer 1966: 47). In the end the study failed to show “whether a cat is dominant because of his ability to make the required response in a competitive situation or whether the efficiency of making the response is dependent on his position in the dominance hierarchy.”

Dominance hierarchies for both male and female cats have been reported in urban strays (Bonanni *et al.* 2007, Devillard *et al.* 2003, Natoli and De Vito 1991, Say *et al.* 2001), and male strays supposedly live in established linear dominance hierarchies (Dards 1983, Natoli and De Vito 1991). These conclusions are doubtful. Such rankings depend on the number of individuals that can be defeated by the cat designated as “dominant” in dyadic contests, which does not correlate exactly with the number of times the dominant actually achieves a victory or with the number of wins minus the number of losses (Bernstein 1981). In addition, expected success becomes increasingly inconsistent with declining rank-order even if transitive hierarchies are considered to exist. In a group of free-ranging cats, some might not interact with others or be absent during observation periods. As a result, frequency tables in which encounters are recorded then contain missing values, making statistical assessments of transitivity difficult or impossible (Bonanni *et al.* 2007, Jameson *et al.* 1999).

The importance of familiarity is hard to understate, and perhaps we should be as wary of ranking cats as trying to herd them. Mutual recognition might be the foundation of their associations. Prior interaction in some fishes can predict the results of dominance encounters (Chase *et al.* 1994). A fish that wins is likely to win again if a second opponent is presented shortly thereafter, and this “winner effect” diminishes over time, noticeably so after 1 h. How long the memory of an encounter lasts in cats is unknown, but evidently quite a while. Of a group of four laboratory cats, Masserman and Siever (1944: 9) wrote: “Once established, the dominance hierarchy in feeding responses was found to persist in all possible combinations ... even after weeks of rest from experimentation.”