FREE-RANGING

CATS

Behavior, Ecology, Management

Stephen Spotte

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To Puddy, Tigger, Miss Sniff, Wilkins, Beavis, and Jinx

You enriched my life

Contents

Preface

The dog is humankind's obsequious, slavering companion ever sensitive to its master's moods and desires. The cat is ambiguous, irresolute, indifferent to its owner, if indeed any human who co-habits with a cat can be called that. Many of my cats have been memorable, perhaps none moreso than Miss Sniff, who adopted me when I lived on a Connecticut farm. It happened like this. One night in late autumn I heard a noise outside and opened the door. In walked an ugly, leggy, calico cat. She had the triangular head and blank stare of a praying mantis, and her nose was in the air mimicking a sort of feline royalty. With startling arrogance she jumped onto the couch and made one end of it hers. And so I named her Miss Sniff.

For months my barn had been plagued by rats. Their excavations were everywhere, around the perimeter of the building and even deep into the clay floors of the horse stalls. Nothing I tried could eradicate them. They ignored traps, snickered at poisoned grain, shouldered aside the barn cats and ate the food from their bowl. Some, bored with the furtive life, lounged brazenly outside their burrows in full sunlight.

That first night I fed Miss Sniff and eased her out the door. She greeted me the next morning with a freshly killed rat, a large shaggy beast of frightening proportions. Female cats without kittens to raise often bring their prey home, laying it out in a convenient place and giving little churring calls to their humans. Paul Leyhausen (1979: 88−89) wrote: "The important thing for the cat is … not the praise but the fact that the human serving as 'deputy kitten' actually goes to the prey it has brought home, just as a kitten thus coaxed does." I have no idea if Leyhausen's interpretation is true, but I nonetheless congratulated Miss Sniff, gave her a pat, and every morning thereafter she presented me with a dead rat. Within a few weeks she had caught them all. In retrospect I realize how mere praise was a paltry reward, and to express proper gratitude I should have sat down on the porch steps and eaten the rats in front of her. At least one or two simply to be polite.

The common cat is the most widespread terrestrial carnivoran on Earth, occupying locations from 55°N to 52°S and climatic zones ranging from subantarctic islands to deserts and equatorial rainforests (Konecny 1987a). This is possible because few carnivorans except possibly the red fox (*Vulpes vulpes*) can match its ecological flexibility and the capacity to find food and reproduce almost anywhere. As further evidence of protean adaptability, the cat has become the most common mammalian pet with an estimated 142 million having owners worldwide (Turner and Bateson 2000). Domestic cats are now the most popular house pet in the United States (Adkins 1997). According to the Pet Food Institute (2012) the estimated number of pet cats in the United States is >84 million, well in excess of the number of pet dogs (>75 million). Castillo and

Clarke (2003) set the total number of US cats at 100 million, including those without owners.

At the same time, free-ranging cats – many of them house pets – exact a devastating toll on wildlife around the world. May (1988) estimated that there were ~6 million free-ranging house cats in Britain. Although well fed, they killed an average of 14 prey items each per day, which extrapolates to ~100 million birds and small mammals annually. In the final chapter I present evidence that killing unowned cats is the only sensible method of controlling their depredation on wildlife. Eradication programs are unpopular with those bent on saving cats at all costs. However, the pressure placed on wild creatures should be alleviated whenever possible, and subtracting alien predators from terrestrial ecosystems is one way of reducing the carnage.

The underlying thesis throughout is that effective management of free-ranging cats is best achieved if based on understanding their behavior, biology, and ecology. In this respect I take issue with experts who claim cats to be social, occupy rank-order positions in dominance hierarchies, disperse under pressure from inbreeding avoidance, are territorial, have a polygynous mating system, and live in functioning kinship groups in which cooperation is common. The data do not support any of these positions, and failure to discard them stands in the way of real progress toward our understanding of why cats behave as they do. More important, casual disregard of the cat's reproductive biology and unusual nutritional requirements has hampered the search for novel methods of population control, limiting current choices to biological agents (e.g. feline panleucopenia virus) and nonselective poisons, augmented by trapping and shooting.

We should take a closer look at the domestic cat for other reasons too. The family Felidae is thought to contain ~40 species (Wildt *et al*. (1998: 505, Table 1), and all except the domestic cat are under threat of extinction (Bristol-Gould and Woodruff 2006, França and Godinho 2003, Goodrowe *et al*. 1989, Neubauer *et al*. 2004, Nowell and Jackson 1996, Pukazhenthi *et al*. 2001). The ordinary cat has therefore become a model for conserving other felids through study of its reproductive and sensory biology, genetics, behavior, use of habitat, and nutritional needs.

Cat biology is highly context-dependent. Laboratory studies have taught us much, and knowledge of free-ranging cats is paltry in comparison. My discussion focuses on the latter, but where lacunas exist I fill them with what we know from cats kept in confinement and presume that the differences are not too great. This is a reasonable approach, at least from a physiological standpoint. Cat genetics are well conserved (Plantinga *et al*. 2011), meaning the metabolic adaptations of cats are not likely to vary whether they occupy a laboratory cage, alley, or sofa cushion. Endocrine factors driving reproduction, for example, are difficult to monitor except in a lab, but differences compared with free-ranging cats are matters of degree, not kind.

I consider free-ranging cats classifiable into three categories: feral, stray, and house. *Feral cats* survive and reproduce without human assistance and often despite human interference (Berkeley 1982). *Stray cats* occupy urban, suburban, and rural areas where humans assist indirectly by making garbage available to scavenge and by offering shelter underneath houses and in abandoned buildings. Garbage represents a concentrated food source and also attracts rodents and birds, still other sources of food. Although strays are sometimes fed by sympathetic people, they are less likely to be offered shelter and veterinary care. *Free-ranging house cats* are those allowed outdoors unsupervised by their owners, who provide consistent shelter, food, and usually veterinary care.

Never take for granted a cat's understated ability to influence our own behavior. During an election year a while back in the village of Talkeetna, Alaska, the populace grew unhappy with its mayoral candidates. Someone started a write-in campaign for a yellow tabby named Stubbs, who hung out in the General Store. Stubbs won, and is now the mayor. Like politicians everywhere he spends much of his time asleep on the job, refusing to let the responsibilities of elected office become a distraction.

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For cats, indeed, are for cats. And should you wish to learn about cats, only a cat can tell you.

Sōseki Natsume, *I Am a Cat*

Abbreviations and symbols

$\bar{x}$	mean
μmol	micromole
a	scaling constant (power law)
ATP	adenosine triphosphate
BCFA	branch-chained fatty acid
BMR	basal metabolic rate
BSA	body surface area
cd	candela
CL	corpus (corpora) lutea
CM	center of mass
CSF	contrast sensitivity function
d	day(s)
dB	decibel(s)
DHA	docosahexaenoic acid
DM	dry matter
DMI	density-mediated interaction
E	energy
EAA	essential amino acid
EFA	essential fatty acid
EPA	eicosapentaenoic acid
EUNL	endogenous urinary nitrogen loss
FC	food consumption
FPL	feline panleucopenia
FUNL	fasting urinary nitrogen loss
g	gram(s)
GnRH	gonadotropin-releasing hormone
ha	hectare(s)
k	scaling exponent (power law)
kcal	kilocalorie(s)
kg	kilogram(s)
kHz	kilohertz
kJ	kilojoule(s)
L	liter(s)
LH	luteinizing hormone
M	body mass
MAF	minimum auditory field
mg	milligram(s)
min	minute(s)
mmol	millimole(s)
ms	millisecond(s)
MUP	major urinary protein
NFE	nitrogen-free extract
ONL	obligatory nitrogen loss
PAPP	*p*-aminopropiophenone
PUFA	polyunsaturated fatty acid
RDH	resource dispersion hypothesis
s	second(s)
SCFA	short-chained fatty acid
SD (or σ)	standard deviation of the mean
SEM	standard error of the mean
TMI	trait-mediated interaction
TRSN	tecto-reticulo-spinal tract
TS	total solids
UV	ultraviolet
VNO	vomeronasal organ
VR	vomeronasal receptor
W	watt(s)
y	year(s)

About the companion website

This book is accompanied by a companion website:

www.wiley.com/go/spotte/cats

The website includes:
- Powerpoints of all figures from the book for downloading
- PDFs of tables from the book and online appendices

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 "Subordinance-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 inter-actions, 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 "trialogue" 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