FREE-RANGING CATS

Behavior, Ecology, Management

Stephen Spotte

WILEY Blackwell

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Cover image: Two Stray Cats on Garbage Bins. © Vicspacewalker | Dreamstime.com

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To Puddy, Tigger, Miss Sniff, Wilkins, Beavis, and Jinx
You enriched my life

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.

Stephen Spotte
Longboat Key, Florida

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

Chapter 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 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 ½, 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