Niche Expansion and the Natural History of Human-Cat Kinship

Jessica W. Lynch and Christopher M. Kelty

Domestic cats (*Felis catus*) have flourished alongside humans for 10,000 years. What accounts for this success? We argue here that cats and humans collaborate in this success because cats are very good at niche expansion across multiple dimensions into new human-facilitated niche space and at niche space saturation across both new and old niche spaces. Cats are neither simply biologically adapted nor simply domesticated by humans but possess their own agency. Cats involve themselves in human projects and benefit from human care and kinship; they develop forms of tolerance and trust but also independence and self-reliance. To demonstrate this thesis about cats, we explore the various dimensions of the cat niche, and in each case we ask, how does that dimension differ between modern cats and their wild ancestors? How have humans collaborated through time with cats to expand the cat niche in multiple dimensions? What have been the cumulative effects or consequences of these expansions? We show that even attempts to control or eradicate cats can play into forms of niche expansion. Our goal is to direct scholarly attention to the relations of participation among humans and other species, beyond the narrow focus on species as more or less isolated and stable bundles of traits and behaviors.

Introduction

Over the past 10,000 years, domestic cats (*Felis catus*) have flourished alongside humans. They live well on every continent on the planet, including even the Kerguelen Islands in Antarctica (Martin et al. 2013). They have been culturally and religiously central across multiple traditions (Engels 1999; Malek 2006; Walker-Meikle 2011; White 2020), and they are today one of two creatures at the center of global pet capitalism worth billions every year (Alexander et al. 2020; Boje and Rosile 2019; DeMello 2021).

What accounts for this success? Answers to this question typically take two forms. First, it can be argued that cats have evolved adaptive traits that have led to this species' success around the globe. Second, it can be argued that the success of cats is due to human domestication or human cultural practices of feeding, transport, care, and control of breeding.

Both explanations miss the mark. The first is confounded by the fact that domestic cats are extremely close in all biological respects to wildcats; modern cats emerged from populations of the African wildcat *Felis lybica* roughly 10,000 years ago (Driscoll et al. 2007, 2009*b*). Yet they have managed to expand their range and success in multiple dimensions, with significant ecological consequences for both existing wildcats and many other species; they have done this repeatedly and in a relatively short period of time, evolutionarily speaking. Other closely related cat species have not had this success.

The second explanation is confounded by the fact that modern cats have a remarkable ability to go back and forth across the feral-tame spectrum, some individuals just as easily living sociably with humans as they do freely without. Humans (as cat owners will attest) do not control cats, and cats are not domesticated in the sense of being dependent on or under the control of humans or directed to specific tasks. And, related to the first point, domestic cats are almost indistinguishable genetically and biologically from wildcats—so much so that the International Union for Conservation of Nature (IUCN) explicitly distinguishes domestic cats as a distinct species because without that recognition there would be no basis for the protection of wildcats (Kitchener et al. 2017; Werdelin et al. 2010; Yamaguchi et al. 2015).

From cats' perspective also, these explanations come up short: the first grants no meaningful agency to cats—only the impersonal luck of genetics and the environment combine to produce a uniquely adapted, highly successful creature. The second grants almost all of the agency to humans—humans make choices, care for cats, enhance their environment, and ultimately breed them under controlled conditions. But cats have more agency, and humans perhaps have less, than traditional theories of evolution or domestication presume. Cats, without a doubt, have become "companion species" (Haraway 2010) possessed of their own capacities, experiences, and choices. But companionship does not just happen: in some nontrivial sense, cats have chosen to associate with humans just as much as humans have chosen to keep cats around.

This paper tells the natural history of that companionship. We focus on the biological and cultural details of the cat-human relation, not simply that of cats or humans on their own: cats have capacities that allow them to take advantage of opportunities that humans provide, both intentionally and unintentionally. The core of our analysis is focused on how cats can saturate, expand, and diversify their niche. Their ability to do this depends on their genetic and biological heritage but also on their kinship with humans. It is this combination that sets them apart from

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the kinds of creatures who simply occupy niches, or from those that we might argue modify their niche to benefit themselves directly, to instead become entities engaged in human-associated niche expansion.

We focus on the concept of the niche because it has been long formalized in biology but traditionally limited to analysis of the lifestyle breadth of nonhuman species in an ecology. We also focus on kinship (in the sense used in cultural anthropology), adopting Sahlins's (2013) definition as "mutuality of being" or participation by entities in one another's existence. The niche directs our attention to the detailed dimensions of cat biology and behavior; kinship directs our attention to how humans and cats dwell together in the world—on ships, on farms, in cities, and in homes—resulting in a millennia-long collaboration.

The niche is, as Hutchinson (1957, 1965) famously formalized it, a multidimensional hypervolume representing all aspects of a species' ability to thrive in an environment. To demonstrate the utility of niche expansion, we look at 10 of these dimensions: geography, habitat, circadian rhythm, lifespan, reproduction, diet, social organization, living quarters, degree of docility, and morphology (summarized in table 1). For each of these dimensions, we ask, how have domestic cats expanded beyond the niche of their wildcat ancestors (as evidenced by their living wild counterparts), how have humans enabled or constrained this expansion through kinship with cats, and what are the consequences for ecological relations in each of these dimensions?

To take just one example, consider the starting point of our own research. We came to these puzzles about the success of the cat through collaborative research into urban cats in Los Angeles and, especially, the controversial practice of "trap-neuter-return" (TNR). Los Angeles has an estimated 400,000 feral cats moving freely across multiple settings, from being solitary wild animals to being housebound companions to living together in human-provisioned feral communities or colonies (City of Los Angeles 2020). TNR is a practice whereby volunteers trap cats, bring them to veterinarians or nonprofit organizations to be spayed or neutered, and then return them to the city to be fed and cared for on the streets—or to fend for themselves.

There is little evidence that TNR works to control cat populations; it may instead exert strong selection pressure to avoid being trapped, since untrapped cats enjoy a dominance advantage and reproductive skew in their favor under these circumstances (Cafazzo, Bonanni, and Natoli 2019; Coe et al. 2021; Crawford, Calver, and Fleming 2019; Gunther, Finkler, and Terkel 2011; Kilgour et al. 2016). The practice is highly controversial since free-roaming cats continue to roam and hunt wildlife, causing more than 43 billion US dollars of economic damage per year around the world (Cuthbert et al. 2021) and killing an estimated 1.3–4 billion birds each year in the United States alone, alarming conservationists and public health experts concerned about zoonotic disease (Loss, Will, and Marra 2013; Loss et al. 2022). By contrast, TNR advocates and shelter workers are troubled by high levels of euthanasia in animal shelters and conservation projects (Sinski 2018; Spehar and Wolf 2018).

Although this paper is not a detailed ethnographic account of these practices, the example illuminates a key dimension of the cat niche and provides one important way that human-cat kinship unfolds. Humans choose to both alter cat biology (sterilization) and to grant the animals autonomy of movement in the city, which can include autonomy of hunting, timing of daily activities, and social relations with other cats. Cats, in turn, must deal with these new facts, we argue, by expanding dimensions of their niche in order to thrive: they can become "hyper-predators" (Longcore, Rich, and Sullivan 2009), they can attract excessive food provisioning (by having multiple "owners" on the street), and they can establish new forms of sociality and dominance (affected both by their new hormonal state and through interactions with human feeders).

TNR also creates novel human-cat kin relations: forms of affective exchange that benefit both parties collectively (whole populations) and individually. Narrowly understood, TNR is a practice of reproductive control designed to address the overpopulation of cats. But it is also a method that allows humans to avoid killing cats, to constrain so-called nuisance behaviors, and, in many cases, to increase the affective exchange by feeding and caring for large numbers of community cats. TNR allows cats to attract additional human care but also allows cats to offer new kinship relations through altered behaviors (i.e., "nuisance" behaviors that some many humans dislike). Overall, the cat niche expands to encompass those cats that both do and do not engage in these kinship opportunities.

Observing TNR thus opened a window into a possible explanation for the success of domestic cats. Cats' reproductive behavior—one dimension of the cat niche—differs from that of wildcat ancestors when some individuals are subjected to widespread sterilization. Seemingly paradoxically, modern cat populations actually thrive under these conditions because the overall size of the cat niche has been expanded in more than one dimension. The vagaries of outdoor urban living can be offset by a concentration of care and feeding resources served by humans, leading to population stability or growth despite targeted sterilization (i.e., continued large and clumped population density despite widespread spaying and neutering). The result is that urban cat populations, even under conditions of attempted human control, thrive and come to represent an ecological threat to other species and ecosystems.

TNR is just one of several examples that illuminate the expansion of the cat niche. At multiple points in recent history, the evolutionary or genetic heritage of wildcats, combined with the help of humans, has allowed a population of cats to expand into new niche space as populations or individuals (see fig. 1). The Neolithic revolution, with its concentration of grains, rodents, and cats in cities, is one key example, as are Western colonization and pet capitalism, which create diverse forms of mutuality of being—cats on ships, cats in barns and ranches as predators of mice and rats, cats in homes as pets, cats as familiars to witches, cats as mousers, or cats as therapy animals—the list is obviously long.

In what follows we explain first why focusing on human-mediated cat niche expansion can enable a new approach to

understanding the natural history of cat-human relations. We then detail the multiple dimensions of the cat niche and cat-human kinship and conclude with reflections on the questions opened up for analysis in both biological and cultural anthropology.

Secrets of the Successful Cat

Background: Niche, Niche Width, and Domestication

To explain the success of cats in the context of anthropology is necessarily to ask about the relations of humans and cats. Most academic work on cats in the disciplines of biology or genetics, while recognizing that they have a long, intimate relation with humans, is nonetheless concerned with cats as a separate species. Conversely, little work in anthropology, whether cultural or biological, has taken cats seriously in understanding human evolution or culture. Ethnoprimatology, however, serves as a model for taking this relation seriously. Recent work in ethnoprimatology (Ellwanger and Lambert 2018; Fuentes and Hockings 2010; Riley 2018; Sponsel 1997) has set the stage for considering biology and cultural dynamics across two or more species as a necessary corrective to the idea that species develop on their own in species-specific evolutionary trajectories. It furthermore opens up ways of looking at situated interactions and forms of kinship (Cormier 2003) that enrich more mechanistic biological models of symbiosis or commensality (Hulme-Beaman et al. 2016; Mathis and Bronstein 2020).

"Multispecies ethnography" (Kirksey and Helmreich 2010; Locke 2018; van Dooren, Kirksey, and Münster 2016) emerged out of this work as a call, primarily for cultural anthropologists, to attend to the role nonhumans generally play in human cultures everywhere, beyond the symbolic or totemic function assigned to them in classic social anthropology (Descola 2013; Kohn 2013). Recent work has extended this approach in new ways, including methods from ethology (Hartigan 2021), new approaches to justice (Chao, Bolender, and Kirksey 2022), and resistance (Beilin and Suryanarayanan 2017; Chao 2021). Additionally, various versions of "ethno-X-ology" have emerged, such as ethnoelephantology (Hussain and Floss 2015; Locke 2017; Remis and Robinson 2020), ethnocanidology (Fijn 2018; Lupo 2019; Musharbash 2017), and ethnoungulatology (Fijn 2011).

Building on both ethnoprimatology and multispecies approaches, archaeologists such as Hussain et al. (2022) have argued for paying much closer attention to the "inescapable and historically significant co-making of hominins and animals" (3) from very early periods to the present. Thus, an ethnofelidology (Hussain and Floss 2015) takes seriously the long-standing interface of the worlds, histories, livelihoods, and biology of multiple taxa (Riley 2018).

However, all of this work stands in the still-significant shadow of debates and discord around the uses of evolutionary theory, biological determinism, and sociobiology in the history of the discipline of anthropology (Fuentes and Kohn 2012; Schultz 2009). Recent work attempting anew an integration of biological and cultural anthropology has developed through the concept of "niche construction." Jablonka and Lamb (2005), a biologist and a historian of science writing together, promoted a "new synthesis" that considers epigenetics, behavior (including niche construction), and language as additional inheritance mechanisms alongside genetic inheritance. A 2016 special issue of *Current Anthropology* proposes alternatives to a strict neo-Darwinian party line, relying heavily on niche construction as a possible way forward (Fuentes and Wiessner 2016).

Niche construction itself emerged within biology as an attempt to account for the agency and behavior of animals as more than just a collection of static inherited traits discretely distributed along a strand of DNA, conferring selective advantage in a mostly unchanging environment (Laland, Odling-Smee, and Feldman 2000; Odling-Smee, Laland, and Feldman 1996). Niche construction recognizes that, for instance, beavers transform wetlands and earthworms change the soil chemistry around them, leading to a transformed environment that itself is "inherited" from generation to generation (dubbed "ecological inheritance") to the advantage, usually, of the creatures doing the constructing.

In anthropology the focus of recent work is on the human niche, but it implies that hominins transformed the environment for themselves and in diverse ways; there is also the implication that the environment must also have been transformed for other creatures as well (Fuentes 2016, 2017; Kissel and Fuentes 2018; O'Brien and Laland 2012). Ellwanger and Lambert (2018), as an example, offer a generative model for how to study the impact of human niche construction on nonhuman primates.

A different and long-standing explanation for human impact on or modification of other species is the concept of "domestication." But ideas of domestication have also seen significant alteration in the past 30 years (Larson and Fuller 2014; Scott 2017; Swanson, Lien, and Ween 2018; Zeder 2015). The Neolithic revolution and the advent of agriculture, as Stépanoff and Vigne (2018) point out, used to be the crown jewel in a narrative of humanity's ingenuity, transcendence from nature into culture, and the beginning of civilization (Childe 1937); today, however, it is "the worst mistake in the history of the human race" (Diamond 1987)—one proposed origin of the Anthropocene (Lewis and Maslin 2015).

Many archaeologists now speak instead of "pathways" to domestication (Larson and Fuller 2014; Zeder 2015) and have blurred the lines between hunting and tending, between commensality and companionship, and have raised questions about the presumed role of human intentionality or ingenuity in this process (Cassidy 2007; Swanson, Lien, and Ween 2018). The current approaches suggest that domestication is an ongoing, possibly unending, process that depends on complexes of humans and animals, such as the "the late Neolithic multispecies resettlement camp," as James Scott (2017) dubbed it, or what Stépanoff and Vigne (2018) call "hybrid communities." Zeder (2016) has proposed that domestication, understood this way, could be a "model system" for understanding niche construction processes. Boivin et al. (2016) document that humans can modify environments for almost all other taxa and that "widespread

Table 1. Expanded niche dimensions of *Felis catus*

Niche dimension	Characteristic niche of *Felis lybica*	*Felis catus* niche expansion	Cat capacities: niche complementarity with humans	Consequences of niche expansion	Key case or example (see fig. 1)
1. Docility	Wild; no human contact	Encompasses the feral-docile spectrum; first approached human settlements to attain concentrated prey in granaries; later highly successful as confined pet; survives feral despite human attempts at eradication	Domestication and tameness; small enough to be controlled and contained as captive; maintain wariness and feral capacities in response to human cruelty; through selective breeding individualized and diversified in terms of morphology and personality; purring adaptations to respond to humans; can survive/thrive in hoarding situations with excess care; massive attacks on feral cats push cats to be more wary, completely independent, and avoidant of humans	Human cultural practices around cats, ritual and spirituality: human sacralization (revered in ancient Egypt; demonized in Western European Christianity); coproduction of the divine and demonic; design, extraction of resources, manufacture, marketing, and distribution of pet products, consumption, and waste generation; cats can enjoy more human-ascribed value than wildlife or environment or be targets of eradication, sometimes simultaneously	Ancient Egypt sacralization/medieval demonization, pet capitalism
2. Living quarters	Natural environments	Shift to use of built environments: granaries, barns, ships, houses, shelters, pet stores, cat cafes, veterinary clinics, and hospitals	Initial adaptations to storage areas where rodents concentrated around grain; perceived cuteness/need led to human care and protection; valued by humans for companionship and special privileges; litter box (and cats' ability to use it) as key innovation facilitating shared indoor living with humans	Increasing population size as cats live in both natural and diverse built environments, some specialized for cats (like shelters and vet clinics); individual cats can also circulate across these different types of living quarters in their lifetimes (fig. 2: cat living quarters and transitions)	Neolithic revolution (cats in cities); Western European human expansion via global colonial conquest; pet capitalism (indoor cats)
3. Distribution	Originally Fertile Crescent but widely distributed across Africa, Europe, Middle East, and West and Central Asia (map in fig. 4*A*)	Fertile Crescent to worldwide: most of Europe, Asia, Australia, North and South America, Africa, and islands throughout the world (map in fig. 4*B*)	*Felis lybica* and *Felis silvestris* widespread generalist adaptation, but blocked by mountains, extreme deserts, and ocean; humans facilitated expansion across these barriers, especially with advent of seafaring	Massive population increase due to geographic expansion; hybridization and competition with wild *F. silvestris* and *F. lybica* in many areas	Western European human expansion via global colonial conquest
4. Habitat	Mountain steppe, tropical and subtropical grasslands, savannahs, scrublands, desert	All terrestrial habitats, but anthrodependent in cold climates with harsh winters	*Felis lybica lybica* harsh desert adaptation may have facilitated ability to expand across habitats; complementarity with human habitats (housing, barns, agricultural and urban settings)	Predator in novel environments for naive species not evolved to respond to their characteristics; can persist in new habitats even when adversarial relations with humans or other animals; leads to extermination industry	Neolithic revolution; Western European human expansion via global colonial conquest; Australia cat war
5. Circadian rhythm	Primarily nocturnal/facultatively diurnal	Nocturnal to diurnal, different individuals can be awake anytime in 24-hour cycle	Human-mediated expansion into diurnal waking periods through feeding reinforcement and human time schedules; artificial light, regular feeding, indoor excretion, indoor-outdoor habitat partitioning among cats using built and natural environments	Allows predation to occur throughout the 24-hour cycle by different cats in a given area (indoor cats only allowed out during day; feral cats hunting at night); this leads to expansion of dietary breadth (fig. 5: cat niche expansion)	Rise of pet capitalism; trap-neuter-return (TNR)

6. Ecological role and diet	Predator and obligate carnivore	Predator; scavenger of human foods; directly fed by humans; wider dietary tolerance; hunting as sport possibly becomes more common in context of food abundance	Highly developed olfaction for detecting food; likely had scavenging capacity in ancestral cat; ability to acclimate to close proximity to humans facilitated being fed, but also able to hide and avoid humans and survive on predatory diet with wide diet breadth	Predator, agricultural pest control, garbage scavenger (ecosystem services through waste removal), and meat eater of human-processed cat food; rise in animal husbandry, rendering plants, manufacture of cat food, which benefit cats; continued/increased cat predation to naive native wildlife as key threatening process, despite abundant food	Neolithic revolution, pet capitalism
7. Social organization	Solitary, except for mothers raising kittens	From solitary to large aggregations/colonies or hoarded captive households	Tolerance to humans at centralized food source may also facilitate tolerance for other cats at food source	Increase in social learning, competition, fighting; increase in outdoor colonies when fed by humans; concentration of cats in colonies creates nuisance for humans to be managed, functions to outcompete other native predators in a particular area (hyperpredation); indoor cat hoarding also concentrates cats and care	Neolithic revolution, Ancient Egypt sacralization/medieval demonization, pet capitalism, TNR
8. Morphology	Lightly built grayish-tan tabby with stripes on legs and tail; some diversity in size and robustness across geographic range (fig. 3*A*: wildcats)	Cat fancying and artificial selection in past 200 years has led to ~80 distinct breeds/morphotypes	Cat breeding has limits because of short timespan of practice as well as genetic homogeneity of cat (no extreme body size changes as in dogs); axes of differentiation mostly coat color, head shape, muzzle shape, gracility/robustness, coat length, and tail shape—almost all morphodiversity based on conferring human pleasure rather than functional attributes	Extreme breed variations for elite; most do not translate to long-term feral living (i.e., hairlessness, flat muzzle, long hair not seen often in community or street cats); coat color pattern variation on short-hair cats allows for human individualization and conferring "personhood" to cats, leading to heightened cat care (fig. 6)	Pet capitalism, TNR
9. Lifespan	4–5 years	15–17 years in domestic households	Artificial life extension through human intervention, food service, medical care, reproductive control, developmental advantage, or other aspects of coliving with humans	Longer lifespan could increase fecundity or relative reproductive success; however, has also resulted in the rise of spay/neuter as standard practice and the need for care for older cats to keep them alive	Pet capitalism, TNR, and reproductive control of cats
10. Reproductive capacity	Can reproduce at 4–12 months of age; average 3.7 per litter, seasonal breeder	Polyestrus (multiple litters per year); average 4 per litter; 1–12 kittens per litter; however, also many cats spayed and neutered so live long non-reproductive lives	Feeding and fostering assistance ensures survival of cats that would not survive otherwise; higher kitten survival rates through human intervention and care; more cats per litter from higher and more consistent protein feeding	High reproductive success, more cats than wanted by humans, overpopulation; greater competition should, in the absence of humans, place a check on population growth; emergence of spay/neuter as a standard practice, which also changes cat behavior owing to altering reproductive endocrinology	Pet capitalism, TNR

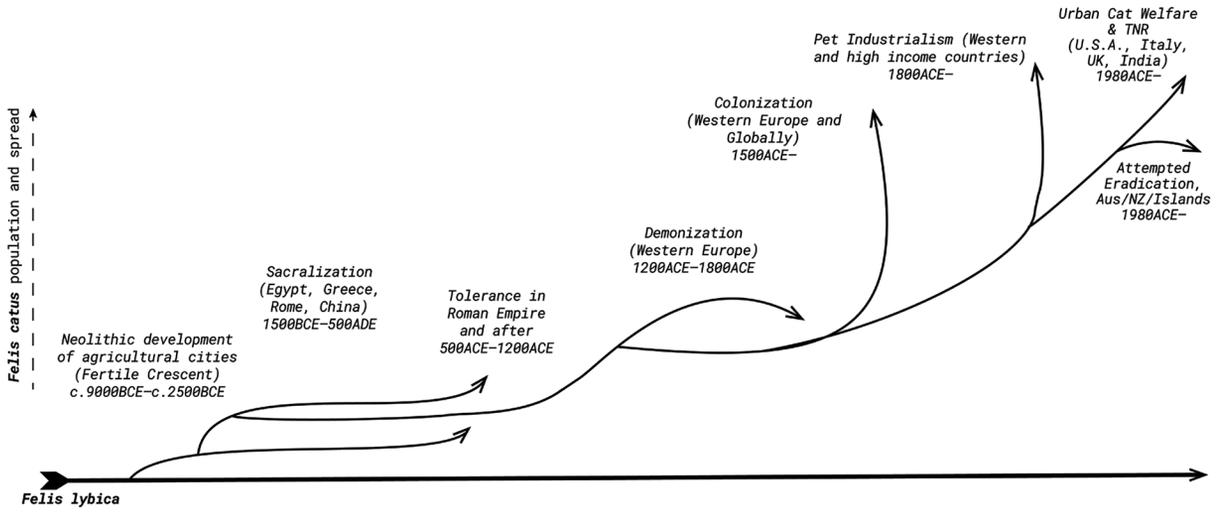

Figure 1. Rough timeline of the rise of *Felis catus*. Cat time, not to scale. Diagram by C. Kelty.

shaping of global biodiversity probably began in the Late Pleistocene or early Holocene" (6393).

Despite the dethroning of human ingenuity in the context of domestication, work in multispecies ethnography maintains a focus on both the witting and the unwitting effects of this anthropogenic power. Tsing, Mathews, and Bubandt (2019), for instance, have proposed that significant ecological modifications they call "modular simplifications" such as plantation farming fail at the goal of controlling nature and instead drive "feral proliferations" of plants and animals, creating a "feral atlas" that reflects the destructive power of colonialism and capitalism at a global scale (Tsing et al. 2020).

Multispecies approaches urge attention to animal experience and interspecies forms of communication, affection, or interaction generally as a counterpoint to human exceptionalism and hubris. Most biological knowledge, however, depends on measuring the observable external physiology, behavior, and interaction of species, which saves biologists the trouble of having to attribute specific internal states or representations to animal minds but sacrifices the ability to make assertions about animal agency or experience as multispecies approaches would like to do. What a multispecies approach gains in relaxing mechanistic assumptions, it loses in biological tractability. Recognizing both of these restrictions is important for proposing new approaches.

To understand why cats have been so successful over 10,000 years requires detailing the specific biological capacities cats possess that allow them to thrive in a variety of contexts and situations alongside humans, at the same time as recognizing that it has been particular humans with particular kinship relations and forms of being in the world who have set the stage for cat success.

For this purpose, we argue, paying special attention to the niche can help. For the most part, niche construction theories do not explore this side of the concept, which has its own history of disputes and complex theoretical debates. Niche construction is useful for retooling evolutionary theory, but it leaves the concept of the niche relatively untouched.

There is a long history to the concept of the niche (Griesemer 1992; Pocheville 2014), including within "ecological anthropology" from the 1940s onward (Barth 1956; Hardesty 1972; Love 1977). While ecological anthropologists have described the human niche in various ways, including analogically in terms of technological and market forms (such as markets or farming techniques), the focus has not been on describing the coexistence of many different kinds of human and nonhuman species in one ecosystem. At best, domesticated animals have been described as tools that humans use to occupy a niche (e.g., in Barth 1956).

G. Evelyn Hutchinson (1957, 1965) famously formalized the niche as an *n*-dimensional hypervolume or "abstractly inhabited hypervolume." The niche in this sense is not a place or a habitat (Hutchinson referred to real spaces as "biotopes") but an abstract relation between a population (or species) and the "abiotic and biotic conditions where a species can persist" (Wiens 2011:2336). These parameters are conventionally things like food, light, or nesting spots, defined in advance of an inquiry. In practice, most studies have limited themselves to a few dimensions, but theoretically, the niche is a "multidimensional hypervolume, defined by a set of *n* independent variables that represent biologically relevant axes," and this filled hypervolume also represents intraspecific trait variability (Carvalho and Cardoso 2020:1). Most investigators differentiate between the fundamental niche (the abstract multidimensional shape of all conditions and traits) and the "realized niche" of particular populations in a real habitat.

Most uses of the concept of niche in biology and in anthropology have been deflationary: an entity can deplete a niche only through consumption or use of a resource—which is furthermore a way of accounting for how competition develops. The niche was, for Hutchinson, primarily a way to make sense of the principle of competitive exclusion. This is where niche construction offers a counterpoint: it posits that creatures also improve niches

in some way—the metaphor of construction implies an active building, but it can also be simply a feature of inhabiting a place—which renders a niche as sometimes increasing capacities for flourishing rather than simply a resource that can only be depleted, with obvious implications for most evolutionary approaches.

However, the prior question of the "width" of a niche has been the subject of considerable work (Bolnick et al. 2003; Pagani-Núñez et al. 2019; Sjödin, Ripa, and Lundberg 2018). Van Valen (1965) suggested a "niche variation hypothesis" intended to capture how a niche can vary depending on how much individuals and populations themselves vary. For instance, a type of animal with very diverse dietary preferences can occupy a wide dietary dimension of the niche. But a population where different individuals specialize on different food can also have a "wide niche" by virtue of all the members eating different things (Bolnick et al. 2003; Roughgarden 1972). The "total niche width" within a population thus includes both the "between-individual component" (BIC) and the "within-individual component" (WIC).

By focusing on the variability of individuals' and species' capacities, we suggest that it is necessary to understand human-animal relations from the perspective of the complementary and interacting components of the width of their niches. In doing so, we open up the concept of the niche to greater flexibility in response to the work of kinship—mutuality of being or participation—as the total niche width of each niche dimension can vary with the behavior of the entities involved, individually and as populations or cultures.

Human-mediated cat niche expansion throughout the hypervolume. Whereas the narrow biological understanding of niche width tends to assume the absence of humans (or of other environment-modifying creatures or forces), we propose instead that cats, especially the domestic cat *Felis catus*, are exceptional at expanding their niche in participation with human populations and saturating across old and new niche space. They can do this, we suggest, across many, if not all, relevant dimensions of their niche (see table 1). Cats can go back and forth between being feral and tame, they can switch from hunting at night to hunting in the day, and they thrive even in situations where hunted or sterilized by humans. Cats expand and exploit particular new spaces across multiple dimensions of their niches while retaining occupation of the full spectrum of their original niche, through diversification of individual and population-level cat niche space use (Bolnick et al. 2003).

For example, with human-assisted geographic expansion, cats can fill the same niche space over a much wider distribution than their wildcat ancestors. If both cats and humans settle in a place, cats gain access to human resources (shelter, food, care), allowing them to expand the breadth of their niche in multiple dimensions within a given location. Once established, cats may then occupy the original wildcat niche as well as the new human-facilitated space within the niche simultaneously in the same location. This niche saturation across the old and new niche space by different populations of cats or different individuals within a cat population, spanning the spectrum of old and new possibilities for lifestyle, allows for overall higher population density and environmental impact. Niche space saturation also acts as a buffer for cats against population decline as a result of human-mediated niche contraction because individual cats can move across the niche space in multiple dimensions.

Cats' capacity for niche expansion is a complement to human forms of niche construction, forming a dance that differentiates cat-human relations from many other possible kinds of multispecies relations. What is the mechanism in the natural history of cat-human relations that allows for niche expansion?

First, it is clear that both habitat modification and cat modification by humans are essential drivers for cat niche expansion. There is little evidence that cats modify their own environment in any significant way, but it is clear that in various times and places, humans do modify their habitats with unintentional or incidental benefit to cats (i.e., agriculture concentrates rodents or urbanization opens up built environments that cats capitalize on). There are also diverse examples of intentional cat modification (artificial selection, hormonal manipulation, human contact with kittens resulting in differences in their development, degrees of captive control), and each of these inputs expands cat niche space in different dimensions.

Second, cats have the developmental flexibility to span broad space within many dimensions of their niche, most importantly along the axis of docile to feral. Cats can be free living and solitary, free living in colonies, solitary in close human contact, and so on, allowing them to occupy different positions within the niche space for a given dimension. Strong individual variation and specialization (the BIC of niche space) means that interindividual differences within populations may be the most important driver for niche space expansion, as different individuals acquire different resource acquisition regimes or behavioral strategies (Bolnick et al. 2003; Costa et al. 2008). This allows for the overall increase in carrying capacity for cats in a given location because different individual cats specialize in different foods, are awake at different times, and live in different parts of the landscape and built environment, in part based on their different relationships with humans.

This flexibility also suggests that capacity for or performance of individual and social learning—both from humans and from other cats—may also vary with populations and by individual. Social learning among cats is poorly studied, and what is known to date primarily revolves around learning how to obtain food, most commonly from one's mother (Adler 1955; Winslow 1944), probably through stimulus enhancement (Zentall 2006). Cats are notoriously difficult to work with in experiments because they quickly lose interest (Grimm 2019), but there is some recent work showing that a cat (named Ebisu) could at least "copy" humans by learning to produce a limited number of familiar actions on command (Fugazza et al. 2020) and that cats can learn their own names (Saito et al. 2019) and their friend cats' names (Takagi et al. 2022). Social learning about food may be enhanced when cats are made more social with each other through human manipulation (feeding, captivity). It is also possible that the

concept of "social niche construction" in nonhuman animals may be relevant to cats: in some social species, an individual's behavior can influence group social dynamics and thus selection acting on that sociality (Mielke et al. 2021). This may be especially true when cats are concentrated in groups through human care and feeding. However, we do not propose social learning as an overarching mechanism through which cats expand their niche space; rather, facultative development and individual learning seem to be more important.

Third, cats also exhibit strong cross-populational variation. After expansion into a new geographic space, entire cat populations may specialize on a new range of prey items—for example, in Australia cats as a whole have largely specialized on diverse marsupial prey species, none of which are encountered in the ancestral wildcat ecosystems. Both individual learning (neophilia or willingness to try new foods) and social learning (e.g., mother cats teaching kittens which prey to pursue) could play a part in this expansion of dietary niche.

Cat niche expansion, as we describe it, thus includes intraspecific variation (including within a particular cat across time, across individual cats in a given population, and across cat populations). But it also includes forces that modulate the width of niche dimensions from outside, such as human food provision and care (expansion), and attempts at eradication or sterilization (contraction). Some cats also develop kin relations with humans (tolerance of humans and human fostering) and even with each other mediated by human actions (social vs. solitary) that aid in this expansion.

Current biological approaches to understanding the nongenetic components of different species' outcomes include intraspecific social learning and the identification of specific innovations that form "cultural" traits (e.g., sensu Whiten 2021) transmitted from generation to generation or across populations. However, in cats, individual learning and contingent developmental trajectories toward tameness and social tolerance based on early environmental exposure may be enough to explain much of their success, in tandem with their ability to induce human affective kinship.

Cat-human kinship. The kinship relation of specific cat and human populations is a long-standing form of affiliation that must be, in part, responsible for their success. The arguments for domestication are weak, in part because cats maintain the facultative capacity to live with humans or go feral, suggesting that genetic traits and biology have not undergone domestication in quite the same way as other animals. Nonetheless, cats have spent millennia in association with humans, their divine role attested in classical Egypt, Greece, and Rome (Donalson 1999; Engels 1999; Malek 2006), and their demonization in the medieval and early modern period (Darnton 2009; Sandall 2018; Walker-Meikle 2012). They have accompanied humans as part of Western European colonization (Mukharji 2017) to become one of two creatures central to pet keeping and the cultivation of human character (Grier 2006; Ritvo 1987; Serpell 1996; Tague 2015).

Multispecies kinship, however, cannot simply be social relations built on top of biology—rather, all kinship is a form of relating, with implications for biology (Sahlins 2013). Kinship, as cultural anthropologists have elaborated it, consists of forms of relatedness that can also determine choices about food, affiliation, group belonging, and biological reproduction rather than simply the reverse. To be kin, for the cultural anthropologist, does not presuppose or require genetic relatedness or even the capacity for biological reproduction, but it nonetheless can have (among other things) a determining effect on human reproduction and choices about reproduction or care.

Recent multispecies approaches assign kin relations primarily to relations between humans and other animals. A now-classic example would be the work of Cormier (2003) on human-monkey relations among the Guajá (or Awá, as they call themselves). But it is also characteristic of Haraway's (2010) analysis of human-dog relations and other recent work (e.g., Govindrajan 2018). Although the literature in multispecies ethnography uses the term "kin" or "kinship" in this sense, it is not the originator of this idea. Theories of kin relations as mutuality of being with humans and other than humans are well attested in diverse indigenous traditions, articulated long before current academic attention. To take one example, Kyle Whyte (2018, 2021) uses the term "collective continuance" as a label capturing some of the relations of responsibility and care that make up a kinship relation among particular peoples and with animals and landscapes as well. Interestingly, cat-human kinship relations, specifically *F. catus*, also complicate these theories because modern cats are cocolonizers with Western Europeans in the recent history of the planet (see also the case of cattle in the Americas; Ficek 2019). Relations with other kinds of cats, including big cats, vary in such forms of kinship (Benson 1972; Hussain and Floss 2015; Mathur 2021), including many forms of inequality given various human efforts to exert power over cats' reproductive, spatial, or bodily autonomy.

It may be possible, or necessary, to describe some aspects of animal behavior and relations between species in terms of kinship as well as in terms of animal cultures or forms of social learning (Whiten 2021). Individual variation in a population could be understood not only as a random distribution of different traits but also as learned and taught behaviors specific to a human-animal assemblage—with implications for the size of a given niche.

For instance, as we discuss here with cats, learning where to find food, what to hunt, and how to relate to other cats can vary dramatically in an urban cat population because some cats are raised in homes and then go feral, some feral cats are fostered and sterilized and then returned to the landscape, and some cats go from being born feral to living in homes or shelters or living individually (see fig. 2). Basic ethnographic observation of the complexity of these relations in the urban cat population confirms that intraspecific variation is an important component of niche width. This variation includes not only a diversity of traits across individuals (BIC) and the plasticity of cats as individuals (WIC) but also the diversity of kin relations with humans and other cats that develop, especially in dense urban contexts with institutionalized forms that cats depend on, avoid, or exploit.

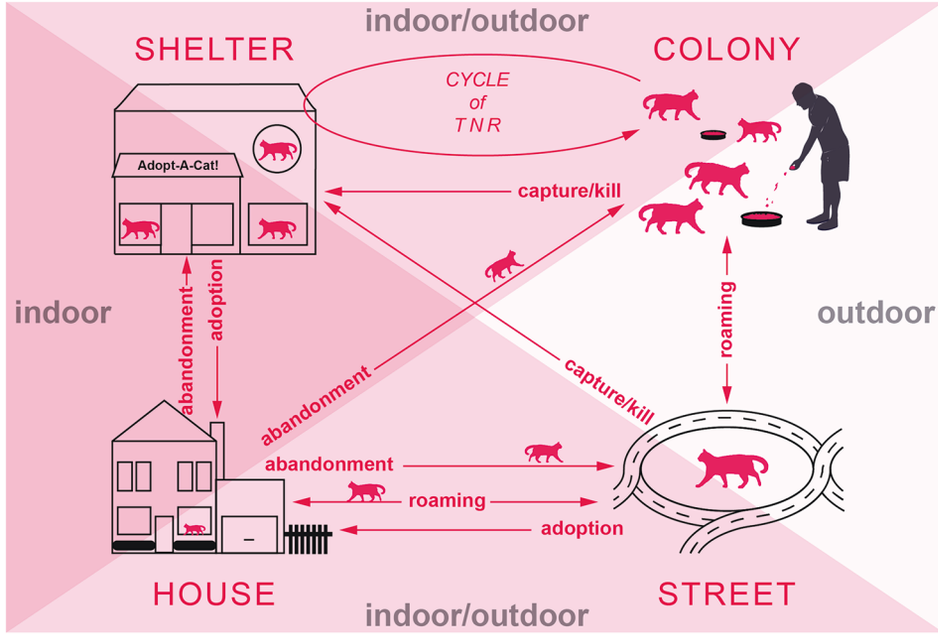

Figure 2. Human-mediated urban cat niches (owned/indoor and indoor-outdoor, street, colony, shelter) and cat independent or human-mediated mobility across these niches, demonstrating the proportion of indoor and outdoor space use and movement. Figure design by A. Gadani, based on figures by the authors. TNR = trap-neuter-return.

In proposing niche expansion as a participation among cats and humans, we ask how niche space altered or opened up by one species is exploited and saturated by another. The question of intention wrapped in the concept of domestication is thus reconfigured as one of collaboration, participation, or mutuality among different entities, with both biological and cultural (or perhaps ethical) implications. Ingold (2022) has recently questioned the centrality of the idea of "inheritance" in favor of thinking more phenomenologically about an "intergenerational life process unfolding in a matrix of relations that overflows the emergent boundaries between organisms and their environments" (S32), including how entities dwell in landscapes that provide different affordances. Such an approach may help explain the continuity of particular long-standing forms of human-cat kinship that has developed over millennia—from the Fertile Crescent to the Mediterranean to Western Europe to cities around the world today.

What it suggests is perhaps that the cat *F. catus* is not just a different species (if it is that) but has become something else—a kin cat—a metapopulation of cats that through the successful use of its biological capacities in a context where "intergenerational life processes in a matrix of relations" has linked them with caring humans, allowing them to flourish beyond the wildest dreams of the wildcat.

Curious Cat: Facultative Docility and Niche Complementarity with Humans

The domestication process has led to cat populations within which individuals span the feral-tame spectrum, owing to the facultative developmental nature of docility in cats and in which individuals may live in the wild, in built environments, or both (see table 1, rows 1 and 2). Like all domestic animals, modern cats and their ancestors had to be tolerant of humans at the very least, if not risking sociability with humans. Cat domestication occurred later (~10,000 BP) than other animals like dogs, and the consensus is that cats began to associate with humans largely when agricultural cultivation started to centralize prey like mice and rats, possibly also sparrows, around Neolithic cities in the Fertile Crescent (Driscoll et al. 2007, 2009*a*, 2009*b*; Ottoni et al. 2017).

Contemporary domestic cats lack clear genomic evidence for behavioral and morphological differences from wildcats, except for tameness or docility (Montague et al. 2014), also described as a lack of fearful or aggressive response to human caretakers (Wilkins, Wrangham, and Fitch 2014). As a result, domestication of cats has been partial at best, despite their obvious centrality as one of the two main companion animals of humans worldwide. Driscoll, Macdonald, and O'Brien (2009) emphasize that wildcats were "improbable candidates for domestication" (9974) and even modern domestic cats do not perform directed tasks.

Montague et al. (2014) also point specifically to cats' wild ancestors as being extremely poor candidates for domestication because they are solitary, nocturnal, and carnivorous. Throughout their history of human companionship, cats have remained only semidomesticated: they have retained, or regularly renewed, the capacity to "go feral," to live on their own both in cities and far from them without the help of humans, yet they have equally retained the capacity to return to the warmth of the human hearth. This facultative docility—the ability to become feral or tame depending on the developmental environment—is a key to

cats' success in the face of rapidly changing human cultural practices in treatment of cats as companions or pests.

Cats' utility as mousers and ratters has always been debatable (ancient Greeks used local polecats and ferrets instead, and modern rat terriers are far more efficient and trainable; Campbell 2014:171–173; Driscoll et al. 2009*a*, 2009*b*; Parsons et al. 2018). Nonetheless Montague et al. (2014) argue that having cats around for rodent control during the onset of human agricultural production and grain storage was an ongoing sustained benefit to humans. This preadaptation to commensality alone may have been most of the story of semidomestication of cats: if any domestication has occurred, it has been along a commensal pathway (Larson and Fuller 2014), not by artificial selection (Turner and Bateson 2014), before the past 150 years.

Cats' tolerance of humans is complemented by humans' attraction to and fascination with cats. Many human groups find cats cute and charismatic or at least do not systematically kill or hunt them in all places. It is a complex historical story (Barak 2014; Darnton 2009; Engels 1999; Malek 2006; Walker-Meikle 2011) with some biological elements (Bennett, Gourkow, and Mills 2017).

Domestic cats do show some signs of domestication syndrome—that suite of morphological and behavioral changes claimed to result from artificial selection for tamer individuals (Lesch et al. 2022; Wilkins, Wrangham, and Fitch 2014). Human cultural preference for neoteny is sometimes proposed as a selective mechanism through which cats have become so cute, but house cats in juvenile or adult form do not possess greater neoteny than other closely related small cat species, such as the sand cat (for visual comparison, see fig. 3). Cat evolution into diverse small, cute forms from bigger, scary forms long predates the evolution of modern humans. The small leopard cat and wildcat lineages had already diverged 6 million years ago (Werdelin et al. 2010), and the jungle cat–wildcat group (depicted in fig. 3) had diverged by 4 million years ago (Li et al. 2015). Small body size likely was an adaptation to catch small-bodied prey, and many "cute" traits that attract humans to cats and kittens are hunting adaptations for a small predator: large forward-facing eyes for

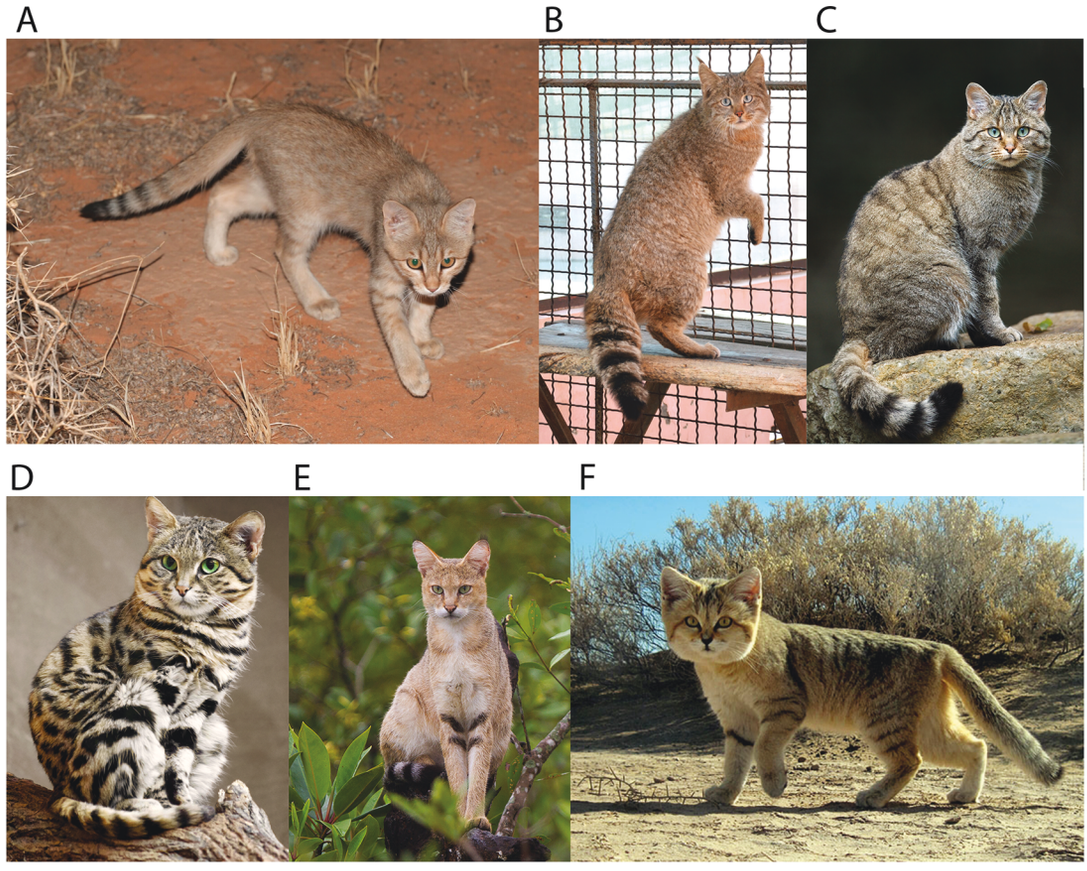

Figure 3. Preadaptation for extreme cuteness: cute wildcats and relatives depicted here had already begun to diversify at 4 million years ago, well before the evolution of *Homo sapiens* (Li et. al. 2015). *A*, African wildcat (https://www.inaturalist.org/photos/451562704; photo by Marius Burger; license: public domain). *B*, Chinese mountain cat (Chinese mountain cat [*Felis bieti*] in XiNing Wild Zoo by 西宁野生动物园; license: CC BY-SA 3.0). *C*, European wildcat (attribution: Lviatour; license: CC BY-SA 3.0). *D*, Black spotted cat (by Patrick Ch. Apfeld, derivative editing by Poke2001, own work; license: CC BY 3.0). *E*, Jungle cat (https://commons.wikimedia.org/wiki/File:Jungle_Cat_on_tree_at_Sundarban,_West_Bengal,_India.jpg; attribution: Soumyajit Nandy; license: CC BY-SA 4.0). *F*, Sand cat (https://commons.wikimedia.org/wiki/File:Persian_sand_CAT.jpg; attribution: Payman sazesh; license: CC BY-SA 3.0). Photos from Wikimedia Commons.

nocturnal prey detection, wide ears for locating rodents, soft footsteps for stealth, long tail for balance in trees, and warm fur for insulation. However, some adaptations by domestic cats set them apart from wildcats in that they use behavior to signal information to their human companions; notably, domestic cats have evolved two different kinds of purrs, one for pleasure (common among different cat species) and one that is more of an insistent cry for food, directed toward human caregivers (McComb et al. 2009). This shows that kinship with humans can be a force driving cat behavioral and vocal change.

Evidence for intraspecific variability of cats might be inferred from the large range of names humans use for cats: tame, wild, stray, owned, house, shelter, homeless, feral, domestic, adopted, fostered, working, barn, outdoor, indoor, indoor-outdoor, community, and colony. These different names reflect the fact that cats easily move between different locations: cats can be unowned and solitary or can join colonies; they can be fed by humans or hunt and forage for prey. In colder climates they are anthrodependent, requiring the built environment provided by humans to stay warm through the winter (Hulme-Beaman et al. 2016), but in hot cities like Los Angeles, cats thrive independently yearround.

In figure 2 we diagram some of this complexity for urban cat populations, demonstrating how they can saturate geographical niche space in cities. Because of their ability to move across living quarters, cats can saturate niche space across built and natural environments; some sorting and natural selection occurs because some cats escape, some can avoid the traps, some live long captive lives of sterile comfort, and others live short harsh lives before being trapped and euthanized.

Cat development plays a key role in docility. Most cat caregivers talk about the first four to five weeks as a crucial period for taming a cat but also agree that cats can later go feral. Slater et al. (2013) describe a "socialization spectrum" to determine whether a cat is feral—because in some places (like California), this veterinary determination can affect whether it is euthanized. Cats' early development window of habituation to humans provides individual flexibility to become more wild or docile depending on early environmental cues. For cats, that means that local urban populations usually saturate the spectrum of wild to docile adult phenotypes.

Captain Cat: Global Habitat and Geographic Niche Expansion

Cats were domesticated in the Fertile Crescent, but their wildcat ancestors were already widely distributed across Africa, Asia, and Europe; movement with humans has led to a near-worldwide distribution (see table 1, rows 3 and 4). Perhaps the most obvious aspect of the success of the cat is that it is now everywhere and especially everywhere humans live.

Domestic cats are one of the world's most populous mammals, estimated at 600 million (Baker et al. 2010). The apparent skew of high domestic cat density in Europe and areas that Western Europeans colonized (North America, Australia; fig. 4*B*) may be both real and a result of bias based on who has access to and uses the iNaturalist/Global Biodiversity Information Facility (GBIF) network to record species sightings. Domestic cats are often described as having a worldwide distribution, but this claim is poorly documented; figure 4 shows that tropical forests, extreme deserts, mountains, and colder climates at high latitudes are much less hospitable for cats.

Domestic cats (*F. catus*) around the world descend from the Near Eastern subspecies of African wildcats (*Felis lybica lybica*) in the Neolithic Fertile Crescent, probably originating from multiple lineages spanning the southern Levant through Syria to southern Anatolia (Driscoll et al. 2009*a*, 2009*b*; Ottoni et al. 2017). Early evidence for intentional cat taming also goes back to 9500 BP in Crete (Vigne et al. 2004). Why *F. lybica lybica*, and not other regional populations of wildcat, eventually became humans' companion likely has to do not only with biology but also with the serendipity of the location around cities and agriculture. But wildcats were already an extremely successful group spread throughout Asia, Europe, and Africa (see historic and current distribution of wildcats *F. lybica* and *F. silvestris* in fig. 4*A*) before the domestication events leading to the cat lineage.

The desert adaptation of *F. lybica lybica* may have given it the advantage of hardiness to survive across different habitat types. Mitochondrial DNA evidence suggests that cat self-domestication in towns with granaries happened repeatedly within the wide range of wildcats themselves, and sympatric populations of domesticated cats and wildcats were selectively mating within their own populations in many areas within the Fertile Crescent (Driscoll et al. 2009*a*, 2009*b*). At present it is hard to find wildcat populations without evidence for hybridization with domestic cats (Driscoll et al. 2007; Nowell and Jackson 1996; Werdelin et al. 2010).

Evidence for successful direct human-mediated niche expansions by other cat species is thin. Vigne et al. (2016) describes domestication of the leopard cat *Prionailurus bengalensis* in 5500–4900 BP, but all contemporary cats in China are descended from *F. lybica*—likely from a much later introduction (Yu et al. 2021). A juvenile bobcat *Lynx rufus* was found buried with grave goods in an Illinois Hopewellian mortuary pit (ca. 25–79 CE), suggesting cat-adjacent practices in precolonial North America (Perri, Martin, and Farnsworth 2015). Cameron-Beaumont, Lowe, and Bradshaw (2002) found that multiple species of small felids, but not all, were "pre-adapted" for domestication in that those kept in zoos showed affiliative behavior toward humans. Clearly, the particular human-adjacent capacities of *F. lybica* have distinguished it from all other felines as a sustained human companion, although how this kinship differs from other times and places of cat-human relation remains an open question.

Beginning in the ancient world and accelerating with Western European colonization, cats have accompanied traveling humans, especially on ships. Diodorus reports that cats who found their way to Greece or Rome from Egypt (where they were considered sacred) were repatriated on ships. Madagascar's forest cats were brought there on Arabian ships (Sauther et al. 2020). Cats arrived in Japan from China at about 550 CE, brought on ships to protect sacred texts from mice (Tadaaki 2003).

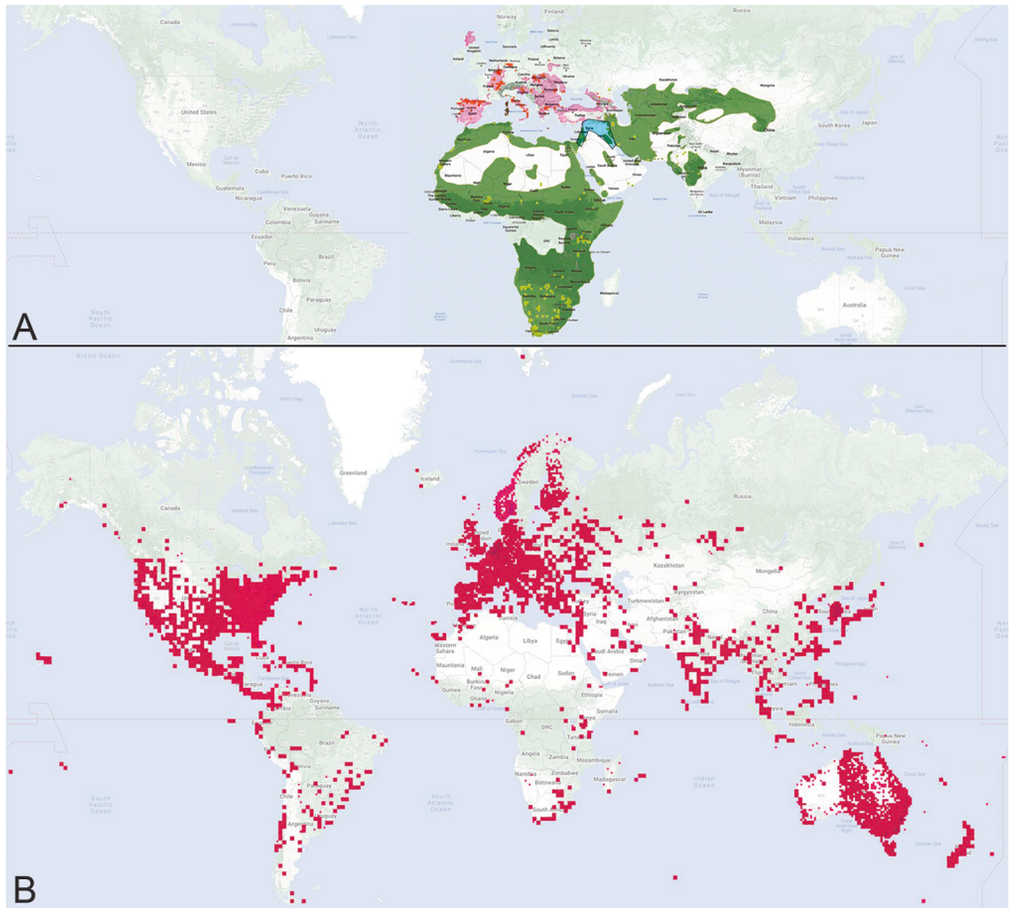

Figure 4. Geographic distributions of domesticated cat and allied species. These images were created by Jessica Lynch using data from Global Biodiversity Information Facility (GBIF) and iNaturalist. *A, Felis silvestris* (European wildcat) historic distribution shown in pink, current sightings (iNaturalist) indicated with red squares. *Felis lybica* (African wildcat) historic distribution shown in dark green, current sightings (iNaturalist) indicated with light green squares. Blue outlined area depicts Fertile Crescent, where *Felis catus* arose ~10,000 years ago through domestication. Data source: *Felis silvestris* Schreber, 1777, and *Felis lybica* Forster, 1780, in GBIF Secretariat (2023). *B, Felis catus* (domestic cat) current sightings (iNaturalist [small red squares] and GBIF [large red squares]). Note the domestic cat's expansion to East Asia, Southeast Asia, Australia, Aotearoa New Zealand, Northern Europe, North and South America, and many small islands worldwide, in addition to occupation of much of the historic ranges of *F. lybica* and *F. silvestris*. Data source: *Felis catus* Linnaeus, 1758, in GBIF Secretariat (2023).

Sculptures of cats on ships and in harbors stretching back to the fourteenth century suggest that cats were common crew members (Sandall 2018). Cats as shipboard pest control officers is attested in maritime law: if a shipment of goods was damaged by rats, the guilt of captains hung on whether a cat was aboard ship or acquired en route (Rocco 2007). Cats also disembarked with sailors around the world, and some missed the departure window. Evidence from New Zealand suggests that cats accompanied Captain Cook and subsequent explorers and were present in significant numbers by the late eighteenth century (King 2019).

The consequences are evident on land masses everywhere on Earth (see *F. catus* distribution in fig. 4) but perhaps most starkly in Australia and New Zealand, where cats have become devastating predators of the island's diverse fauna, especially birds and small marsupials (Gotsis 2014; Koch et al. 2015). The spread of cats and humans has also devastated other wildcat species globally. Interestingly, the decision to separate *F. catus* as a different species from *F. lybica* and *F. silvestris* is more political than biological. Although they are nearly identical and the domesticated cat has only very recently diverged from the wildcat, the 2015 IUCN Red List assessment justifies the separation as "of the highest operational importance because the current legislation intended to protect the Wildcat is framed in terms that can be effective only if the Wildcat is recognized as a separate species" (Werdelin et al. 2010:1). As generalist small mammal predators, therefore, cats with the help of humans have taken maximum advantage of both the native range of wildcats and expanded into a new geographical range and new biomes with naive prey.

24-Hour All-You-Can-Eat Cat: Hunting, Social Organization, Diet, and Activity

Wildcats are primarily nocturnal predators that hunt small prey; domestic cats do all that but also scavenge, eat human-prepared

food, and can stay up all day. Wildcats are solitary, and so are domestic cats, except when humans gather them into captive spaces or outdoor colonies with concentrated feeding opportunities (see table 1, rows 5–7). Cats hunt and eat meat. Cat genomes are enhanced with auditory and vision adaptations for catching prey, and cats have an extremely agile body, claws for climbing trees and swatting prey, and teeth finely adapted for carnivory (Beadle 1979; Montague et al. 2014). Wildcats are solitary hunters that stalk their prey silently, and domestic cats' utility as human commensals has been as hunters of small rodent prey. Cats living with humans over the millenia have clearly adapted from surviving mostly on rodents to eating more human-sourced and served foods. Humans have limited power to control or change the predatory drive by satiating hunger (Adamec 1976), but the role of human emotion and the desire to feed cats clearly has a significant effect on cats' health and flourishing.

Cat diet breadth and hunting behaviors are especially good examples of our claim about niche expansion through human collaboration (see fig. 5). Two aspects of cat diet are especially important: what cats can and do eat (and the role individual specialization in hunting plays in that) and when cats eat and therefore also when and what they hunt for. Human-mediated niche expansion has changed cat diet breadth (especially when cats are fed by humans), hunting behavior (what cats kill vs. what they eat), social organization (how feeding can concentrate cats into colonies), and circadian rhythms (regularization of daytime feeding owing to human schedules).

Cats playing with toys display the same behaviors as when catching prey: crouching, approaching slowly, a brief tense pause, then a pounce and strike. Manipulating a prey item, or playing with it before the kill, is thought to be how cats assess its dangerousness and the risk of injury (International Cat Care n.d.). Kittens learn to hunt better when exposed to prey items consistently in the presence of the mother; in other words, mother cats may teach kittens how to deal with prey (Hoppitt et al. 2008; Thornton and Raihani 2008). Thus human-reared kittens may be affected in terms of hunting abilities, and this could also in part explain why different domestic cats specialize on different prey types.

Contemporary cat diet breadth is wider than expected for a hypercarnivore, especially in urban environments. For instance, in rural Sweden, cats ate rabbits, voles, and mice (Liberg 1984; Piontek et al. 2020). In Pennsylvania, nonfield cats' stomachs were full of "all varieties of table scraps, milk, offal, string, paper and other refuse ingested as food" (Eberhard 1954:285), and field cats' stomachs were mostly full of rodents, birds, rabbits, shrews, and moles, with table foods and garbage a substantial 30% of stomach contents (Coman and Brunner 1972). In Baltimore, 6% of urban "alley" cat scats contained rats and 7% contained insects, but most scat content was cat hairballs and garbage, suggesting that most urban cats made their living scavenging from garbage cans or begging from humans (Fitzgerald and Karl 1979; Jackson 1951).

Individual cats may specialize in different prey items, even in the same locality. Dickman and Newsome (2015) studied within- and between-individual variation in prey and showed through owner surveys that owned cats killed and returned to their owners up to 58 animals per year; those that returned 10 or more kills to their owner varied significantly in prey specialization. This example of niche saturation through individual cat specialization in prey choice allows higher cat carrying capacity because of cats' diverse feeding preferences.

The ancestral wildcat dietary niche, confined to the night and thus to certain types of prey, has expanded in modern cats. Cats have effectively become 24-hour predators, saturating a wide diet breadth niche space owing to multiple different dietary specializations, living quarters, and activity patterns (see fig. 5). Community or street cats might hunt primarily at night for rodents or other nocturnal creatures, while indoor-outdoor cats or cats in colonies might hunt for birds during the day. With widespread pet keeping, some cats remain permanently inside homes, now facultatively diurnal, following the rhythms

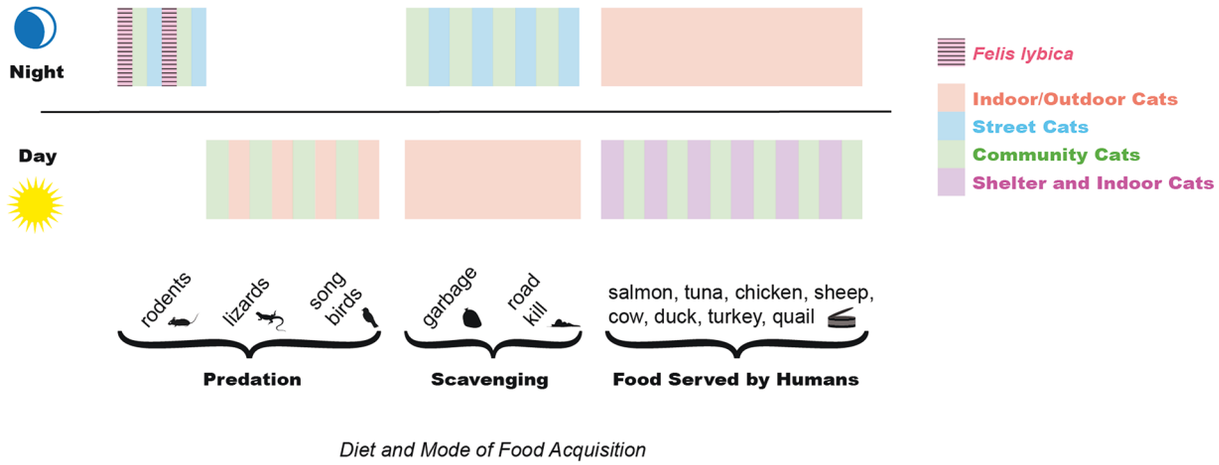

Figure 5. Domestic cat niche expansion and niche space saturation for diet and activity pattern. Figure design by A. Gadani, based on figures by the authors.

of human life, eating human-processed food prepared for them at regular times.

Cats also eat a large range of other animals, from human prepared chicken or fish to commercial cat food (Alexander et al. 2020; Grier 2006). As such, cats' diets have expanded to include cows, pigs, sheep, and turkey—animals too large to otherwise be considered cat prey. This expands the cat's impact on human economy through the building, production, and maintenance of farms, factories, trucks, and stores for cats' benefit.

Humans who feed community cats also overfeed given this ready availability. Natoli et al. (2006) documented extreme overprovisioning of food by humans in three large cat colonies in Rome. Longcore, Rich, and Sullivan (2009) suggest that concentrating through provisioning leads to cat population densities of up to 10–100 times the amount of similar-sized native predators (Nowell and Jackson 1996), and single cat feeders can regularly service up to 100 cats across multiple different colonies (Finkler and Terkel 2011).

Longcore, Rich, and Sullivan (2009) argue that concentrating cats through feeding and consequently assisting their reproduction may together create "hyperpredators" in the city—a concern all the greater when such colonies border on ecologically sensitive habitats. Concentrating food transforms the behavioral ecology of the cats, attracts other species, and creates new kinds of interspecific aggression: in Los Angeles human-subsidized colonies attract new prey (rats), new predators (coyotes), and new competitors (raccoons and opossums).

Pet Cat: The Rise of Cat Breeds and the Cat as Individual

Wildcats have a basic gray-brown tabby coat, but cat fancying has produced a diversity of cat types that have spread across the landscape, allowing us as humans to recognize cats as individuals instead of species, thus increasing their value and received care (see table 1, row 8). While the pet as a concept stretches back to the ancient world (Campbell 2014; Malek 2006; Tuan 2003), it is only in the nineteenth century that widespread practices of pet owning, pet sale, and pet breeding emerged, alongside the growth of a human middle-class population (Tague 2015), changes in culture (Grier 2006), and concomitant rise of industrialized breeding of livestock (Ritvo 1989).

The combination of geographic expansion, genetic drift, and artificial selection through modern pet breeding has led to widescale diversification of morphology of cats. Modern cat variation can be separated into 40–71 recognized cat breeds (Alhaddad, Abdi, and Lyons 2021).

The significant morphological and genetic differences seen today among many Western cat breeds are all less than 200 years old and come as the result of the arrival of "pet industrialism." The morphological variation developed to please rich owners of indoor cats has traveled with cats out onto the street and seems to be an important factor in humans' perception of cats as individuals instead of as interchangeable members of a species (fig. 6). Finkler and Terkel (2011) mention that highly attached colony caretakers in Israel have names for each cat, make physical contact with cats while feeding them, and may even give each cat its own bowl. Humans' preference for "rare variants" may also drive continued cat morphodiversification through increased care toward cats that look different (whether in colonies or at shelters for adoption). Humans value cats above wild animals because they see them as individuals, and care is spread across cats with different phenotypes because of humans' varied preferences. The individualized appearance of cats also helps them to fit into human families with kinship roles.

Grumpy (Old) Cat: Reproduction, Nurture, and Longevity

Wildcats live for about four to five years, but domesticated cats living in human households can live 15 or more years, through food service, medical care, and protection from predators or competitors (see table 1, row 9). Cats have evolved to be fast reproducers. Reproductively active by 4–12 months of age (Ogan and Jurek 1997), even though they do not reach full size until 18 months or two years, they can produce multiple litters per year, coming into heat again about eight weeks after the birth of a litter. Domestic cat litter size averages about four kittens but can range up to 12, with a record 19 reported (Ruiz-Olmo et al. 2018). Cats live much faster than humans—the first year of cat life equals 16 human years—and cats at age 2 are equivalent to humans at age 23 (Cambridge 2017). In most biological systems, a fast reproduction strategy is coupled with high mortality (Promislow and Harvey 1990). Cat litters tend to experience some early loss of life even when raised in a human home. But cat mortality would be much higher if it were not for the lavish care, high-protein diet, and shelter that humans provide them. Ogan and Jurek (1997) estimate longevity of free-ranging cats at four to five years, while indoor cats have a tripled longevity of 15–17 years, pointing to the strong human influence on cat survivorship.

Keeping cats alive longer is related to humans' emotional experience of compassion for cats. Perhaps as a result of the demographic transition in humans, some cats (and dogs) are now also seen as deserving of long, healthy lives, supported by human care and compassion (Grier 2006). Pet practices of the past century have entailed caring for cat health and well-being as they age, visible in both the extended longevity of cats and the increased prevalence of later-onset diseases like diabetes and chronic kidney disease (Greene et al. 2014; O'Neill et al. 2014). Cats live longer with concomitant ecological effects, and aging brings behavioral and cognitive changes that could shift these cats' position within the cat niche space (Bellows et al. 2016).

The Sterile Cat Niche?

Cats are rapid reproducers, and when some individuals in the population are sterilized, the others that elude reproductive control can dominate the sterilized and continue to reproduce at a rapid rate (see table 1, row 10). The success of cats has created its own problems: there are just too many of them. As a result, one now standard pet-keeping practice is to spay or neuter cats. This

Figure 6. Diverse community cats in Valparaiso, Chile, far from the Fertile Crescent origins or cat fancying in Europe. Cats reap the benefit of lavish human care, in part as a result of being individually recognized because of their unique and varied coat patterns. Photos by Jessica Lynch.

practice has extended to include TNR programs in cities around the world. Millions of cats are sterilized every year. Spay and neuter efforts encourage or require pet owners to do so, and "no kill movements" support the spread of these practices, since they seem to trade euthanasia for population control via sterilization.

Yet cat populations are robust and increasing globally. This is an apparent puzzle. Absent humans, increased cat population density should lead to a check or "ceiling" on population growth, as it does with any species in an environment. The theory of the niche predicts exactly this: with limited parameters in a particular place, a creature will find its niche to the exclusion of other competitors, or it will have to compete for the same resources. But in the case of domestic cats, this prediction does not come true because of the ways cats can take advantage of niche expansion and the assistance of humans in that process.

Sterilization may shrink the breadth of one dimension of the cat niche, on the theory that it will be a limiting one. But because cat-human relations expand one or more dimensions of the cat niche, even as they contract another, it can lead to an overall larger niche volume that can be realized by cats. TNR is a good example of this process of niche expansion through human kinship with cats.

Cats' lives, like humans, are organized at least partially around sexual behavior and concomitant forms of communication. Intact male cats wander across large ranges to pursue females and attempt to have sex with them, and intact female cats often present themselves to a number of different males in a given heat (Hart and Eckstein 1997). Cats yowl with sexual desire and then have raucous sex with more yowling. Males engage each other in dominance jockeying with loud duets and physical fights. Aggression is expressed by striking with paws, biting, baring of canines, and chasing, while submission includes crouching with flattened ears, retreating, and hissing (Cafazzo, Bonanni, and Natoli 2019).

Urine and spraying are also essential to cat social life. Male cats mark territory with urine as a warning to other males. Social, sexual, and territorial information is shared by scent. Cats rely on pheromone detection for sociochemical communication—even to the point of a trade-off toward decreased ability to smell prey compared with dogs (Montague et al. 2014).

From the cat's perspective all these behaviors are a normal part of life. But for humans, they are often problematic "nuisance behaviors." As such, the practice of spaying or neutering cats has a double benefit for humans: it is promoted as an attempt to control cat reproduction but also acts as a way to make cats more docile, less wide ranging, and more well behaved.

Spaying or neutering is almost always done by gonadectomy—removing the testes or ovaries. Cats can also be vasectomized or hysterectomized, like humans, which stops their reproductive output but keeps their hormones intact and their behaviors the same. Modeling the effects of trap-hysterectomize/vasectomize-return (THVR) versus TNR showed that THVR

could be significantly more effective at decreasing cat population size (McCarthy, Levine, and Reed 2013). However, most TNR programs prefer simple spay or neuter. It is easier, quicker, and effectively reduces the "nuisance behaviors" of the cats so that they are less troublesome when returned to the street. In fact, for cats, as seen for rescue dogs, reduction of nuisance behaviors may be a life-or-death matter, with euthanasia the outcome for the captured but nonconforming (Porter 2018).

Cats with their hormones altered now face a very different life. Neutering might "drastically reduce the capacity of domestic cats to protect their territory from trespassing conspecifics" (Cafazzo, Bonanni, and Natoli 2019:13; Gunther et al. 2016). It can affect the hierarchy within colonies, which in turn can affect access to food resources—even those provided by humans (Finkler, Gunther, and Terkel 2011; Levy, Gale, and Gale 2003). Neutered cats may become victims in fights with intact cats (Hart and Cooper 1984).

A study of unowned, free-roaming cats showed that after an entire colony was neutered, cats were less active, stopped spraying, and reduced territorial aggression, and some males acted affiliatively toward one another (sniffing noses, body rubbing) as never before (Cafazzo, Bonanni, and Natoli 2019). Another study showed that it is exactly the colonies that have had all members undergo TNR, paradoxically, that grow at a faster rate—precisely because intact males preferentially enter these groups, where they can dominate others (Gunther, Finkler, and Terkel 2011).

Cat biology is thus significantly altered by sterilization practices, but cat health and longevity might also be affected in other ways. Under most TNR projects, cats are allowed back on the landscape to places where they are well cared for and well fed by humans; many TNR programs vaccinate and delouse cats, and in some ways the whole process includes elements of fostering or, at least, sustained human contact. In short, it is a process of kinship making with these cats, even though they will not be pets per se, and one that involves making cats behaviorally more compatible with humans through sterilization, as well as the creation of new forms of cat life in both ad hoc urban colonies and structured community cat programs.

All this looks like a perverse version of domestication. Instead of controlled breeding for the production and enhancement of particular traits, it increases the quality of individual cats' somatic life while constraining their ability to produce offspring or genes in future generations.

Rather than domestication—cats bred and killed under the control of humans—for those cats that humans are able to catch and alter, TNR proposes the best of both worlds (from a human perspective): a long life but one without noisy, smelly reproduction. Such a vision, if it could catch all cats and be carried to its conclusion, would spell extinction for cats eventually. But even with "successful" programs, the decrease in population numbers is marginal to insignificant.

Cats' fecundity is a powerful resisting force to human control, which makes cats different from even some other domesticated species like cattle. Furthermore, the necessity of trapping cats in order to neuter them introduces a strong selection pressure in favor of cats good at evading traps, leading to populations of fecund, trap-wary animals that can continue to breed. Thus, the human-mediated expansion of niche dimensions represented by spay-neuter, and especially TNR practices, provides a new opportunity for both cat niche expansion and cat evolution.

Given the centrality of individual variation to the cat niche, cats' ability to thrive at the populational level despite various forms of human control on individuals suggests that cats in groups can simultaneously inhabit reproductively silenced and reproductively "feral" niche space, have new relationships with one another within this space based on reproductive and hormonal status, and together can capitalize on the food, care, and support of humans for their somatic and reproductive flourishing. If the niche, understood as a hypervolume, includes all these modified dimensions—a smaller capacity for reproduction but many other larger aspects—then it is quite possible that on balance, TNR enlarges cat niche space rather than contracting it or maybe even produces a new dimension: the sterile cat niche.

And as if to highlight the famous "nine lives" of a cat, sterilization is not the only threat cats are navigating. In some places, cats are recognized as a grave threat to wild animals. In Australia, feral cats have been targeted as invasive species: an industry of Curiosity and Eradicat poison pellet production and distribution is aimed at erasing feral cats from the natural landscape (Bunyak 2019; Gotsis 2014), where cats have already been a major driver in the extinction of 13 mammal and four bird species. The expanded use of chemical birth control methods, as well as new tools such as gene drives, has been proposed to control cats (Alliance for Contraception in Cats and Dogs 2009; Kachel 2018); the feline leukemia virus was introduced on Marion Island in the Indian Ocean as a method to attempt to eradicate cats (Denny and Dickman 2010).

A complementary attempt to control cats is the miles and miles of exclusion fences in Australia to keep cats out of various key habitats for endangered marsupial species (Long and Robley 2004). Other mechanisms used in Australia for cat control include shooting and trapping (Denny and Dickman 2010). However, as Gotsis (2014) points out, despite cats' ravaging of the Australian ecosystem, with another 80 native Australian species currently at heightened risk for extinction in large part as a result of cat predation, they are also "wonderful companions for an estimated 23% of Australian households" (1).

What is true for sterilization efforts might also be true for eradication efforts. While eradication targets certain populations through poison, exclusion, or other means, other nearby populations grow in size and health. Well-cared-for community and pet cats can intensify human-cat kinship even as that kinship can be severed through conservation efforts.

In Australia and New Zealand, cats are considered invasive animals (i.e., there are no wildcats already there). But the cats being targeted are those most like wildcats—solitary, nocturnal hunters living among rich landscapes of small-bodied prey and, although demonstrably capable of it, sustaining fewer kinship relations with humans. As a result, eradicating wild-like cat populations, which makes conservation sense, nonetheless leaves

behind populations with expanded niches, higher intraspecific diversity, and greater success as a coinhabitant of these places.

Conclusion

In the preceding pages we have documented ways that cats can saturate and expand dimensions of their niche, even including when targeted with sterilization and eradication. They do this not simply by being well adapted in an evolutionary sense and not simply as a result of human intentions to domesticate them.

Rather, specific populations of cats—starting in the time and place of the Fertile Crescent—successfully established an "intergenerational . . . matrix of relationships" (Ingold 2022) with humans that allowed for the modification and expansion of their niche. By exploring various dimensions of the cat niche (table 1), we have been able to show how modern cats differ from their ancestors and how that difference is part of a human-cat kinship that has allowed them to expand the niche of their ancestors. We have explained how human niche modification works together with the cat's flexible biological capacities and its intraspecific variation within populations to achieve the expansion of the cat niche and saturation across old and new niche spaces.

Why focus on the niche? One advantage is that it opens up a different way to think about structural ecological questions of anthropogenic power and influence over the planet. Rather than privileging human dominance, exceptionalism, or outright evil—all of which certainly play key cultural roles—it focuses attention instead on the way human-animal kinship relations of various sorts have structured the ecologies of the Earth—including going back tens of thousands of years (Hussain and Floss 2015; Hussain, Weiss, and Nielsen 2022).

The concept of the niche, and its formalization, was originally an answer to the question: Why are there so many kinds of animals? Biodiversity is and remains a remarkable fact, but for the current era, a slightly different question might be more apposite: Why are there so many extinctions for some entities and so much success for others? It is a basic assumption of the idea of the niche that the normal state of the ecology is the production of maximum diversity. The idea of the "Anthropocene" hypothesizes that humans are a pathological disruption of that normally unchecked production of diversity. While this is undoubtedly possible (loss of biodiversity through monocropping, fossil fuel extraction, overfishing, and much more), there is also the possibility that ecologies at a biogeographic level have more, rather than less, complex structures as a result of collaborations among species. No doubt, humans are the most significant partners in the current era of these forms of relating—not simply through attempted large-scale control of animals but also through the emergence of mutual kinship relations with animals, like cats, who can exploit that compatibility to their own advantage. But it is conceivable that other kinds of multispecies collaborations have existed, beyond acknowledged forms of mutualism or symbiosis.

A range of other animals could be understood in similar terms, but the approach of niche expansion demands a careful focus on the specific nature of the mutual project as much as it does a focus on the capacities of the species. Dogs are an obvious case for comparison, and while they similarly show an ability to expand into new niches, those niches are different from cat niches because dogs need different things, eat and hunt differently, and behave differently than cats—but nonetheless, they have learned to participate in the expansion of human dominance to their extraordinary benefit. Even ungulates, such as cows, goats, and pigs, who often serve as the most classic examples of intentional domestication, are no doubt niche expanders taking advantage of human forms of property, settlement, industrialization, and medicine (Blanchette 2020; Ficek 2019; Fijn 2011). The point is to direct attention to the relations of participation and to look beyond the focus on species as more or less isolated and stable bundles of traits and behaviors.

We have attempted here to show the process by which one population of small-bodied, ultra-cute, carnivorous, nocturnal wildcats, *Felis lybica*, became the master of the human hearth that it is today. Cat evolutionary heritage disposed it to association with humans, at those serendipitous moments when humans opened up the hearth and city gate, streets, and homes to them, and cats risked tolerance in exchange for much more. This heritage includes the developmental flexibility some cats have to be fostered and cared for—a practice that brings pleasure and joy to many humans as well. But it also includes other dimensions of the cat niche, like its ability to span the spectrum of domestic and wild living.

Cats, with our help, have developed a surprisingly expansive niche space across multiple dimensions and are at liberty to move around within this space to evade human control or to develop deeper forms of kinship. Human attempts to control cats—sterilization, eradication, pet keeping—are going to be only as effective as human attempts to control humans, which is to say that the ethical and political questions at stake are different from simply questions of animal rights or suffering. At one and the same time, they encourage reflection on human responsibility for the success of cats and also on whether cats share in this responsibility, including the effects cats are having on the environment and biodiversity.

Could humans have become what they are today without cats? What part of "being human" is attributable to our mutual being with cats—in addition to all the other collaborations such as lactose tolerance as a result of collaboration with ungulates or territorial and hunting success as a result of collaboration with dogs, to say nothing yet of the countervailing participation with rats or mosquitoes?

To decenter the idea of human control over domestication, and to acknowledge the ability and agency of animals to take advantage of possibilities for flourishing, appears to distribute the responsibility for certain actions to nonhumans as well. For instance, could it make sense to say that cats, cattle, and pigs are complicit in the colonization of the Americas, in more than a mechanical sense? Animals clearly benefit from kinship with

humans: the political relation that cats cultivate with humans buffers them against risks that other animals face—from the risks of predation to the risk of extinction—even if it introduces them to new ones as well (e.g., cars and human cruelty). Such a perspective could also demote the sole responsibility attributed to humans, on both moral and biological grounds: why have humans become such good niche expanders with cats, dogs, and cattle, while orangutans and gorillas have not? Is it sufficient to write this off to luck, or do we need a better theory of mutuality, participation, or coconquest carried out among a relatively small collective of species that is, for the time being, disproportionately making the Earth what it is?

Comments

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On Knowing One's Nichemates

Aotearoa New Zealand has a complicated relationship with cats. The country has among the world's highest rates of cat ownership, but cats also pose an acute ecological problem as predators of Aotearoa's relatively defenseless native birds, lizards, and invertebrates. Cats interact with other species here in sometimes counterintuitive ways: they took part in multiple extinctions on Te Hauturu o Toi (Little Barrier Island) from the 1800s, but when removed in the 1980s, native birds' fledging success worsened, and researchers discovered that the cats had inadvertently been protecting nests from rats (King 2019). It took the additional removal of rats to see benefits for the birds—a reminder of the intersecting assemblages cats participate in. Several decades later, the local cultural status of the cat is shifting as a national orientation toward pest control refigures them as predators first and foremost—a framing that, while not wrong, is partial. There is talk of introducing doglike regulation for pet cats (registration, nighttime containment). And while trap-neuter-return has been practiced for some time, now conservation workers have in some places folded feral cats into lethal control. In other words, Aotearoa is an excellent test case for Lynch and Kelty's arguments, not least because of how humans are changing the terms of their participation with cats.

How have domestic cats become so ubiquitous, seemingly on their own terms? And to the extent that in one small country like Aotearoa, they can be simultaneously cherished pets and lethally targeted pests? Attending closely to how cats live, the authors suggest that it is cats' ability not only to engage in niche construction but also to participate with humans to stretch and overflow those niches. Conceptualized as hypervolume, the niche folds space and time, affordances and capacities, together into sites of multidirectional influence. Here, cats act on their (social and natural) worlds. People are powerful but not determinatively so, and the environment is a collective achievement. It is not the actors themselves that are foregrounded but how they hold one another in relation. I found it particularly pleasing to see the sensibilities of biological anthropology and multispecies theory converge in this piece, the latter's attention to complex nonhuman worlds complementing the former's respect for specificity and variation.

Seen as situated and relational, the cat becomes almost insensible in species terms—as the authors note, the taxonomic distinction between domestic and wildcats primarily reflects conservation priorities. In practice, *Felis catus* materializes as multiple and shifting at every level. A single cat might become more or less feral or tame at different points in its life, according to circumstance and perhaps even preference. Other animals, of course, do the same: boars, for example (Arregui 2023), but also, arguably, people. It seems reasonable to consider feline docility as a function of how feral (as distinct from cruel) they regard the human(s) in front of them to be. In Aotearoa, Laura McLauchlan (2024) writes, demonizing representations of cats as killers in need of control met with intense pushback from cat lovers, ultimately tempering the moral and affective registers that pest control was promoted in. And perhaps, McLauchlan suggests, that tempering instigated a real ethical reckoning with the myriad attachments people have with more-than-human others. So cats tame people, individually and collectively as well.

In closing, the authors pose the knotty perennial question of whether we should step from recognizing animal agency to attributing responsibility. To what ends? In Aotearoa, pests have readily been scapegoated as the agents of biodiversity decline, permitting violent forms of "control" and a strategic ignorance of welfare. Meanwhile, conflating conservation with pest control distracts from other environmental harms: intensive agriculture, habitat destruction, mining. Other species might participate, but it is largely human efforts to build and sell things that propel such interventions. Here, I find helpful Giraud's (2021:39) provocation that we consider "how to conceive of and negotiate relationships between life-forms that are actively harmful for at least one of the parties involved." This is not responsibility for responsibility's sake but rather in the service of multispecies justice (Chao, Bolender, and Kirksey 2022). Seen thus, the cat in Aotearoa is indeed harmful to native species but in ways that will shift across variously populated urban, rural, and bush settings and will intersect variably with other species' antics. Andrea Petitt's (2023) similarly instructive writing on multispecies intersectionality draws attention to how power is distributed within as well as between human and nonhuman populations.

I hope some of the proposed niche dimensions will be elaborated in future work. For example, the expanded lifespan of the pet cat is explained here largely in terms of human compassion and demographics, but I would argue that it also reflects changes in how we know the animal. The rise of animal welfare science through the latter twentieth century, for example, has configured "the animal" as an experiencing agent that can have better or worse well-being and that should be treated accordingly. The

authors also suggest that morphological variation allowed people to individuate and extend personhood to their cats. However, people who live or work closely with many kinds of animals come to regard them as individuals, name them, give them social roles, and even police against getting too attached to them (Arregui 2023; Candea 2010; Sharp 2019; Svendsen and Koch 2013). That lab rats and meerkats have not established quite the same global presence as the cat lends support to the argument that it is precisely cats' ability to traverse multidimensional niche space that has enabled their spread.

Ultimately, what is at stake here is how we know our animal others and which ways of knowing we allow to guide our conduct in shared worlds. Recognizing human-cat relations as a kind of participatory world making, and considering what this might mean in both multispecies and evolutionary terms, is an exciting development. Ethnoprimatology has for some time now been a trading zone between multispecies and evolutionary theory. This article is a welcome move to test the wider applicability of that work and to take seriously the resources of our field.

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Niche Construction and Biophilic Values in Multispecies Anthropology

Biology has been undergoing major extensions of its main models over the past 40 years. At all levels of analysis, from Mendelian-Darwinian genetics to epigenetics (Jablonka 2013), homeostasis to allostasis (McEwen and Wingfield 2003), typical behavioral patterns to plasticity (Uller et al. 2024), to debates on the importance of protecting single large or several small forest fragments (Fahrig 2020), the concepts have expanded, in the sense that they do not replace but enlarge the previous ones. With these conceptual expansions, new biological phenomena are being understood, offering greater power to humans to interfere with nature, for better or for worse.

In this article, Lynch and Kelty, coleaders of the Labyrinth Project at the University of California, Los Angeles, Institute for Society and Genetics, present an elegant example of this new reading: from niche selection to niche construction, adaptation taken as a process rather than only a product (Laland et al. 2007). Using domestic cats as a case study, the authors sharply summarize in table 1 how the *Felis catus* niche expanded from *Felis lybica* and *Felis silvestris* because of the complementarities of cats and humans to coconstruct a niche. Expanding on niche characteristics already present in its wild counterparts, such as a generalist predation diet allowing the occurrence in diverse habitats—from mountain steppes and deserts to tropical grasslands across Africa, Europe, and Asia—the domestic cat expanded its niche to live in built environments, widening its dietary tolerance scavenging on human foods and spreading its distribution all over the globe. Departing from a traditional view of cat domestication due to human intent and benefit and cats as passive, lucky entities, the authors frame the process of coexistence as starting from cats' agency of constructing their own niche through developmental changes on risk-taking behavior, tolerance to human proximity, and diet widening. Humans on the other hand had preadaptations to be attracted to neotenic traits such as the enlarged eyes and rounded faces of cats and benefited from the fact that cats ate rats attracted to granaries and barns. This kinship between humans and cats was incorporated into ritual and spirituality in different human cultures across space and time, varying from sacralization to demonization. That is, as cats adjusted their behavior to humans and humans adjusted theirs, niche was expanded; in evolutionary terms, this coexistence increased the fitness success of both species.

In recent times, another complementarity of traits has allowed for a new expansion in the cat-human niche sympatry. The order Primates is the most social within mammals. Moreover, humans are cooperative breeders (Burkart, Hrdy, and Van Schaik 2009), that is, because of an enlarged brain size at birth and a restricted birth canal owing to bipedalism, human babies are born highly altricial, incapable of self-locomotion at birth, with newborn survivorship dependent on multiple caretakers. This need for allocare added to our apelike cognitive apparatus traits observed in other cooperative breeder primates (e.g., marmosets), such as the helping impulse and spontaneous prosociality. Apart from this collective helm, life in urban centers is increasingly individualized and detached from the wilderness. Wildcats are solitary and nocturnal, but domestic cats are becoming facultatively social and diurnal, tolerating the presence of conspecifics and humans when food is not a constraint, as in shelters; cats are even developing specific vocalizations used to communicate with humans. The sit-and-wait foraging strategy is a preadaptation that possibly allows cats to stay quiet for long periods in small households while being able to join intense bursts of play with humans or kids. This tolerance to humans on the cat side, and high social and helping impulse on the human side, matched for living in small familiar households in urban centers. Again, this has consequences, with the cat pet industry expanding and interspecific kinship families being established.

By taking a multispecies anthropological approach, the article debates the efficacy of the trap-neuter-return strategy for urban cat population control and opens a dialogue with the one-health approach to control zoonoses: anthropological studies on human life coexistence patterns will inform and enrich educational projects and management decisions.

However, I could not end my comment on this article without detaching the link between multispecies anthropology, niche construction, and the biophilia hypothesis. Taking apart old criticisms regarding its use as a naturalistic fallacy to legitimize a particular sociobiological view of human nature, the biophilia hypothesis poses that there is an "innate tendency to focus on life and lifelike processes" (McVay 1993:11); however, "it is not a single instinct, but a complex of learning rules" (Wilson

1993:36). These learning rules have no direction: you can love or hate living things, but it is just easier to learn and feel emotions toward life than toward nonliving things, such as rocks or water pools. "What may be an innate tendency to affiliate with animals recognizes the power of cultural categorization which can change any animal's status from kin to vermin—or more recently, from kin to thing" (Katcher and Wilkins 1993:194). Across history, of the nine typologies of biophilic values, cat-human relations fulfill all, with a humanistic value prevailing in recent decades. This value has welfare, economic, environmental, and evolutionary impacts.

Which type of values do we have in a multispecies coconstructed niche? Which type shall we nurture? From individual to multilevel selection (Nowak 2006), from tragedy to governing commons (Ostrom 2009), concepts about life and humans have extended. The more we observe, the more we see the interdependence between the self and the life within and outside ourselves and the greater our responsibility as individuals and as societies. The next extension is clear: "Agape enlarges eros" (Orr 1993).

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Expanding Our View of Human–Other Animal Relations Can Have Positive Conservation Implications

Humans and other animals often engage in complex interactions, affecting one another and coconstructing dynamic niches. Lynch and Kelty provide an intriguing and well-considered approach to understanding the relations between humans and cats and the bidirectional effects and niche expansion that these relationships produce. However, most scientists examining human–other animal interfaces, especially conservationists, often assume relations are conflictual or exploitative, rarely including the frame of mutuality and often underplaying the rich and interconnected lives of sympatric species. Here we offer an extension of Lynch and Kelty's argument to broader human–other animal interface studies with an emphasis on its relevance for conservation research.

As Lynch and Kelty document, the rubric of "domestication" constrains analyses of the animals whose lives are deeply entangled with humans. Moving beyond "domestication," "pet," and "feral" and more fully into the arena of mutualism, or at least an understanding of all parties of an interface as active participants, as Lynch and Kelty do, is beneficial. For many species classically termed "domesticates," and many others termed "synanthropes,"[1] interfaces with humans have existed over generations, often having evolutionarily relevant impacts. Humans and many other animals in such relationships develop a deeper understanding of each other's behavior and bodies and often engage in a diversity of communication and even collaboration as they navigate their mutual ecologies.

At these interfaces, the human–other animal relationships cocreate behaviors that have the potential to become social traditions and even cultures (Hansen and Fuentes, forthcoming; Sueur and Huffman 2024). When such cultures become embedded in populations and endure, they may be important for the survival and welfare of the involved participants (Whitehead et al. 2004). Lynch and Kelty build a robust case for the study of cats in this context, and our work complements theirs with a "nondomesticate," the macaque monkey. Both macaques and cats are synanthropes that can utilize human resources and who are innovative and able to engage in complex social interactions and ecological relations with humans. This web of relations with humans enables both cats and macaques to alter their niches, expanding dietary, behavioral, and ecological possibilities with effects on shared ecosystems that can be positive and negative. These relations facilitate the emergence of population-specific behaviors in both humans and the other animal species in the relationship, such as the dietary and behavioral variation across cat populations and the behavioral and ecological (and cultural) innovation documented in multiple macaques and across a range of other animals (Hansen and Fuentes, forthcoming; Sueur and Huffman 2024; Whitehead 2010).

Interactions between different species can enable indirect social learning, where different species learn from each other (e.g., guide dogs and humans; Guillo and Claidière 2020). Usually when discussing the transmission of behaviors, most scholars focus on intraspecific actions, but the cases where interspecific social learning is examined offer support for the bidirectionality and mutual aspects of engagement by all species in human–other animal relationships. The view that humans and other species not only cohabit but also communicate, conflict, collaborate, learn from each other, and coconstruct niches and cultures is an important frame for future research and, given the current biodiversity crisis, especially in conservation work. We suggest that an understanding of the related and intertwined lives of sympatric species can offer more coherent and effective solutions to managing and sustaining biodiversity in many cases. "Coexistence" is a buzzword for many in the biodiversity conservation landscape, yet the perception of coexistence as static and often conflictual is too common. Lack of recognition of the processes of niche construction, including expansion and reduction, hinders a deeper understanding of the potential ranges, structures, and outcomes of interspecific relations. Other animals often depend on humans as ecosystem and niche engineers, and humans are also often affected by the ecological roles of animals, including their emotional and cultural connections with them (Barua et al. 2021).

There is much in Lynch and Kelty's framing that can be deployed in conservation approaches. For example, they argue for the inclusion of individual variation when discussing niche

1. "Synanthropy" refers to "undomesticated" species (plant or animal) capable of living closely alongside and potentially benefiting from humans and anthropogenic environments.

expansion in these interfaces. This recognizes not only animal personality but also agency. This perspective has particularly serious implications for management and conservation strategies, as the recognition of both species' and population-wide patterns and individual or local group variation in all species involved is necessary for effective modeling of relations and ecologies. Focusing on details of the relations at individual, group, and population levels can illustrate both short-term impacts and longer-term niche construction effects. It is increasingly apparent that in assessing the ability of animals and humans to coexist, and the possibilities for sustainable relations, we need to understand not just the overt competition for resources or other modes of conflict but also the social and ecological niches impacted by emotions, agency, personalities, evolutionary dynamics, physiological needs, and more. The relationships between humans and domesticates and synanthropes are important foci for deepening our understanding of how cocreated ecologies, behavioral patterns, and potential cultures function (e.g., Govindrajan 2018; IUCN 2023). Such perspectives may be central to facilitating expanded sustainability across at least some ecosystems and relations and could enable us to appreciate the myriad relations that the expansion of the human niche has enabled, which may be beneficial for biodiversity and a locus to learn from in conservation efforts.

Lynch and Kelty correctly argue for an expansion of our way of considering human–other animal interactions, looking at long-term effects of relations. Their case study of the cat is crucial and pertinent to the anthropological, animal behavior, and conservation literatures and makes one take the countless memes of cats contemplating world domination a little more seriously.

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Cats are everywhere. What accounts for their success? In their highly engaging article, Lynch and Kelty challenge well-worn explanations of domestic cats' high population levels and geographic breadth—namely, the evolution of certain adaptive traits or the unidirectional domestication of cats by humans—and instead propose that it is cats' agency in cultivating kin ties with humans that has "allow[ed] them to flourish beyond the wildest dreams of the wildcat." Cats are longtime human companions, but, as the authors rightly remind us, "companionship does not just happen"; rather, it is sought out, shaped, and maintained for various purposes by all parties involved. Cats are agents in cultivating kin relations with humans, and it is this animal agency and relationality—missing from most accounts of cats' natural history—that the authors highlight here.

At the center of Lynch and Kelty's intervention is the concept of the niche and, in particular, niche expansion—best understood as a kind of "collaboration, participation, or mutuality among different entities." Cats are excellent niche expanders, not in spite of efforts by humans to exert control—like trap-neuter-return or cat culling—but oftentimes because of them. Humans do not often see it this way; we are confident in our abilities to mold cats to our liking, often in the name of care: we lock them inside our houses, feed them a monotonous diet of highly processed food, require certain behaviors and restrict others, and, through acts that are meant to alleviate suffering but oftentimes create it, surgically modify their bodies. In the name of responsible pet ownership and, indeed, kinship, I too have done all of these things for the three "kin cats" I live with. As the authors point out, these are acts that reveal the close kinship we have developed with cats over millennia—and they with us. They are also acts that, among others, have helped cats expand their niches globally.

With this in mind, Lynch and Kelty argue that "animals clearly benefit from kinship with humans" and that this in part explains why animals who seek out or at least tolerate human kin relations are those who are most successful in multiple domains. I wonder, though, about this language of success, or the language of flourishing, a word the authors also use. "Success" is a common way to indicate high population levels, geographic breadth, and rapid niche expansion, but this word also has certain implications for those who (with agency) choose not to participate in kin making with humans. When we talk about success, what do we mean? Are animals who are decidedly not populous or widely dispersed—who may be endangered or already extinct—failing in some way? What exactly does it mean to flourish in this Anthropocenic world, which for many has already been dystopian and unsuccessful for quite some time? I bring up these questions because the authors, too, are interested in adding nuance and flexibility to terms (like "niche") commonly used to explain biological or natural processes. Success, then, may also be a framework we can rework to think through how we got here, as a planet, and where we are going.

This is also what the authors think through in their concluding section, which is packed with food for thought. Their final provocation is to move us toward "a better theory of mutuality, participation, or coconquest carried out among a relatively small collective of species that is, for the time being, disproportionately making the Earth what it is"—to see, for instance, cats and pigs and mosquitoes as more than foot soldiers in the story of colonial exploitation and planetary destruction but rather, by harnessing their kin relations with humans and with their agency in mind, complicit actors in it.

I am excited by this line of thinking in part because it offers a rounder version of what human-animal relations look like and do—for better or worse. In multispecies scholarship, relationality has, I think, too often been framed as a panacea for an Anthropocenic world. Entangled relations are often seen as something to be fostered without question, a way to care for others across difference and through connection, which is precisely what we have been told our troubled world needs to flourish: more attachment, more connection, more relations.

While there is much to like about this sentiment of connection, I also know from my work on multispecies care in Jordan that more entanglement or more relationality is not an appealing solution—or a relevant one—for many humans or even potentially for many cats. In Jordan, domestic cats are also everywhere. While some people feed and care for them, they are usually left to their own devices: roaming, reproducing, and encountering and enacting violence and affection along the way. They are treated as agents in this sense, and too much direct human meddling in their lives—sterilization, euthanasia, limiting their movement—is widely viewed as unethical. These are cat-human relations still, but they are often partial, shifting, and uneven, just as other kinds of kin relations typically are. Lynch and Kelty's recognition of the impact of human-animal kinship and agency is refreshing not only because it centers relations but also because it does so without framing their explanatory power as complete or redemptive.

At its core, this article is an invitation to take cats and their relations seriously in the making of this world. I wonder what this recognition might mean as we, in our human-cat mutuality, imagine alternative planetary futures. If cats are indeed complicit in our collective march into increasingly dystopic futures, how might we enact something different together?

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Feline Trouble

Reports recently resurfaced online about Goff Elementary School in Washington State needing to shut down because of the threat of a mountain lion stalking its campus and potentially endangering little human children. It turned out that the calls reporting the big cat on the prowl were wrong. The feline was not a wildcat but a feral domestic cat, one who had gotten fat and was spotted eating a rat (Shauman 2023).

Whether or not the story is true, it illustrates an important argument made by Lynch and Kelty: given that domestic cats are genetically very close and "almost indistinguishable" from wildcats and that domestic cats have a "remarkable ability to go back and forth across the feral-tame spectrum," cats take advantage of kin relations with humans and have uniquely constructed a niche in contemporary ecologies profoundly shaped by political-economic impacts in this contemporary epoch. In homage to John Waters's (1974) campy classic film *Female Trouble*, my commentary engages Lynch and Kelty's argument and further underscores how cats pose their own kind of wily disruptions of neat boundaries. Their disruptions offer alternative ways for anthropologists and other readers of *Current Anthropology* to think about ideas of nature vis-à-vis domestication and perversity as well as ideas of individualized nonhuman experience.

Pawing Nature

For Lynch and Kelty, niche construction functions as a corridor between biological and cultural wings of anthropology, one that works as both a biological analytic and as a social theoretical concept. Following advocates of the new synthesis school of biology who see environments as crucial for evolution instead of a Darwinian and neo-Darwinian emphasis on genetic inheritance, niche construction is the demonstration of how environments are subject to change by a variety of organisms.

How does this work as a social theory? Recognizing cats' actions in constructing a niche, Lynch and Kelty pave a way forward between an "impersonal" genetic, evolutionary determinism on one hand and an anthropocentric, anthropogenic understanding that sees cats as subjects of human-directed artificial selection and control on the other. Niche construction, in more cultural anthropological terms, accounts for nonhuman agency. The Anthropocene is not entirely about anthropogenic impacts but also about other critters who are readily able to pounce and exploit the conditions created by transoceanic shipping networks, the spread of grain cultivation, concentrated human settlement, and suburban sprawl.

This suggests, as the authors argue, that domestication is a form of niche construction. So, if niche construction were to replace the work domestication does in its bridging biological, social, archaeological, and linguistic wings of the discipline, then what might be lost through its adoption?

I worry that niche construction would become a hegemonic way of understanding survival, livability, or relations. Its ecological, metaphoric framework could overlook the possibilities underlying the metaphoric framework of domestication and its critiques of what constitutes households, dwellings, relations, and social reproduction, all of which are all too often unquestionably naturalized and whose questioning and prodding or pawing are methods of queer and feminist social and cultural analysis. The critiques evocative of *Female Trouble* would get supplanted with feline trouble—in a time when gender trouble is too troubling amid transphobic culture wars (Butler 1990, 2024).

Pouncing on Perversity

I was surprised to learn that spaying and neutering encourages the growth of cat communities (or "colonies" as Lynch and Kelty call them). They cite a study about cat populations where all members had gone through trap-neuter-return and yet grew at faster rates (Gunther, Finkler, and Terkel 2011). Apparently, intact males prefer these groups and dominate others through such behaviors as marking, which neutered cats *are said* to seldom indulge. The emphasis is on "said" because anecdotal evidence from cat-loving friends suggests otherwise. Giving Gunther, Finkler, and Terkel (2011) benefit of doubt, Lynch and Kelty write, "All of this looks like a perverse version of domestication. Instead of controlled breeding for the production and enhancement of particular traits, it increases the quality of individual cats' somatic life while constraining their ability to

produce offspring or genes in future generations." What domestication is not perverse? Is it not perverse that many humans steal milk that would have gone to baby bovines? What makes the support of a living animal's welfare in exchange for their reproductive capacity more perverse than a system that forces the bearing of offspring without any care about the welfare of the ones giving birth, as I have asked in my work (Parreñas 2018)? As any fan of *Female Trouble* would ask, is not everything about contemporary life perverse?

Prodding Individuality

In an effort to truly go beyond the "impersonal luck of genetics" as an explanatory model, Lynch and Kelty admirably consider the way cats have increasingly moved around the world, fraught as it is with histories of exploitation. Their units of cat analysis are both individuals or populations and species. Yet readers do not really get the sense of individual life, save for the remains of a juvenile bobcat found in a precolonial mortuary pit in present-day Illinois and dating from 25 to 79 CE. Individual cats may be unique only insofar that they as a species, arbitrarily delineated as a species, are not that different from each other, and yet they live in quite varied climes, conditions, and interspecific relations. In our conversations across subfields and between biological and cultural theories in the places they meet, I do hope that we can foster an openness to recognize odd, idiosyncratic, perhaps even perverse characters who make for memorable stories and lessons—like the domestic cat who could pass as a mountain lion.

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Human-Nonhuman Collaborations

Lynch and Kelty present their thesis that domestic cats (*Felis catus*) have flourished alongside humans because they have expanded their niche into new human-facilitated spaces by collaborating with humans. They argue that cats possess their own agency and are neither simply biologically adapted to human spaces nor merely domesticated. They present compelling evidence by examining the cat's niche along its various dimensions.

Central to their thesis is the idea of collaboration between humans and cats. At different points, it has been understood as kinship, partnership, compatibility, and more broadly as forms of relating in multispecies associations. They suggest that a range of other animals could be understood in similar terms and mention the domestic dog as the most obvious case.

I assess a range of species and examine their niche changes in recent history (~10,000 years) to understand their forms of relating to humans and how this may have contributed to their persistence, even success, in the Anthropocene. The domestic dog (*Canis lupus familiaris*) and humans have been associated with each other for 15,000–40,000 years (Perri et al. 2021). During this time, the dog's niche has expanded along multiple dimensions, including diet, hunting behavior, habitat, geography, lifespan, social behavior, and morphology (Young et al. 2011). Efforts similar to trap-neuter-return (TNR) mentioned by Lynch and Kelty are widespread in efforts to control free-ranging dog populations. In India, with an estimated population of 59 million free-ranging dogs, these programs are called "animal birth control" or ABC (Gompper 2014). In an ABC program, nongovernmental organizations, municipal administrations, and volunteers capture and surgically spay or neuter dogs and release them at the site of capture. Like TNR, ABC is controversial, and there is little evidence that it works; in all likelihood, it exerts a selection pressure in favor of dogs avoiding capture and keeping a distance from human settlements (Aredath and Vanak 2023). Like TNR, the ABC program allows humans to avoid killing dogs, attempts to reduce aggressive behavior in dogs, and increases the affective interactions between citizens and dogs by creating a need to care for and feed a large number of dogs (>300,000 in Bangalore; Bhalla et al. 2021). I can discuss the case of the dog in detail, but it is no surprise that all of Lynch and Kelty's arguments about the cat hold true for the dog as well.

A more surprising example is that of two similar-sized big cats: the common leopard (*Panthera pardus*) in the Old World and the cougar (*Puma concolor*) in the New World. Both occupy a similar position in their ecosystems and have recently expanded their distribution to urban and semiurban regions. Pumas now occur in several large cities across North and South America, from Los Angeles to Rio de Janeiro (Pontes et al. 2021; Riley, Sikich, and Benson 2021). Similarly, leopards are found in large Indian cities such as Mumbai and Bangalore (Athreya et al. 2013). Expansion of the niche of these big cats—including changes in social behavior, diets, home range, and hunting behavior—has helped them thrive in suburban and rural areas. These big cats prey on dogs, pigs, cats, and other pets more than deer; they are often less territorial and possess detailed understanding of the rhythms of human activities in cities. However, given that they also sometimes attack and kill (and sometimes eat) humans, it is important to understand how humans and big cats relate to each other. In India, there are cases of people worshipping big cats as gods (Nair et al. 2021), similar to some indigenous peoples in the Americas (Saunders 1994). Lynch and Kelty encourage us to understand and articulate the collaboration between these species and humans to better understand their "success" over the past few decades.

Similarly, Asian elephants (*Elephas maximus*) are (re)colonizing urban spaces with changes to their diets, behavior, and social structures (Srinivasaiah et al. 2019). Humans and elephants have a long (thousands of years) history of interactions, ranging from the taming of elephants for use in wars to reverence and

worship in many Indian cultures. However, the use of urban and suburban areas by elephants is marked by a detailed understanding of these spaces that the elephants have. Removing individual elephants with this knowledge seems to create confusion in the remaining (naive) elephants, which lack the knowledge of how to survive alongside people.

Primates such as rhesus macaques (*Macaca mulatta*) and many other species around the Old World show niche expansion in their diets, ranging, and social behavior to benefit from human projects. However, how they have associated with humans is less understood. In a recently documented example, lion-tailed macaques (*Macaca silenus*), an endangered and endemic species from southern India understood to be a habitat specialist occurring only in pristine rainforests away from human presence, started frequenting a neighboring town and quickly took to spending most of their time inside the town (Dhawale, Kumar, and Sinha 2020). This change in their (and human) behavior may become the difference between its survival and extinction in the region.

Interactions between human and nonhuman animal species in the Anthropocene have often been assessed through a lens of competition, conflict, and the survival of the fittest. However, understanding these relationships through the lens of collaboration, partnership, kinship, or other forms of relating needs further exploration to understand how at least some of these species can flourish alongside humans. What can we say about leopards, elephants, and primates living close to or within human settlements, often with intricate knowledge of navigating these spaces? They clearly possess their own agency, but can this be called collaboration? Lynch and Kelty provide the framework to begin asking the questions: What forms of collaboration exist in multispecies assemblages, especially between humans and nonhuman animals? And how can these collaborations affect mutual flourishing? Andrews, Kelty, and Suryawanshi (2025) argue for the possibility of multispecies societies, and the question of collaboration between species is at the center of it.

Reply

We are very grateful for these generous commentaries that sharpen and confirm the core of our research article. We appreciate the thoughtful responses here and want to amplify the questions they raise.

Above all, it is gratifying to hear from a diverse set of commentators the support for a collaboration across cultural and biological anthropology, suggesting that the discipline is in a different place than it once was. Clearly, there is more space now for thinking in collaborative and recombinant ways than in the past, when the two subfields too often practiced either animosity or mutual indifference. Given that our contribution to one of anthropology's core journals centers on cats, perhaps for the first time, something seems to have changed. The explosion of work in cultural anthropology that focuses on multispecies contexts and the expansion of biological anthropology beyond primates suggests that the discipline's core questions have shifted. The question once thought to define anthropology generally—namely, "What makes us human?"—might no longer be the core question. This is a significant reorientation, one answered only in part by concepts like the Anthropocene or the variety of "post-" humanisms on offer. What, really, might those core questions be now?

The impetus for our own work also comes from, as Ferreira puts it, "major extensions of its [biology's] main models" that have opened up a range of different ways of knowing animals—and not only knowing but also of relating to or interfering with biology and ecological natures. While multispecies ethnography has counseled practitioners to develop "arts of noticing" (Tsing 2015), it is clear that new biological and ecological research affords more than just noticing. As Hansen and Fuentes point out, understanding local and individual cross-species dynamics can be essential for enhancing sustainability across "at least some ecosystems and relations"; at the same time, we appreciate the caution offered by Addison, who pointed out that scapegoating of other animals is a common distraction tactic that tries to hide the fact that human corporate and profit interests affecting climate change and land-use change are truly the main drivers of these ecological shifts and losses.

Conservation and management strategies can all too readily operationalize such new models in biology (see, e.g., van Dooren et al. 2023) without taking seriously "our understanding of how cocreated ecologies, behavioral patterns, and potential cultures function," as Hansen and Fuentes emphasize. Anthropology might be able to position itself differently vis-à-vis conservation, management, and environmental science if we can emphasize that our developing expertise is about these shared forms and emergent practices across species—and not just on any particular species or genus of primates or a restricted notion of culture or social learning. Although it represents a significant development in cultural anthropology, multispecies ethnography goes only part of the way toward such a recognition. As McClellan rightly points out in her commentary, it too often celebrates creating more relationships or becoming entangled with as redemptive, when in fact there are a wide variety of relations (good and bad, for different entities) already in place.

There is broad agreement here with our starting point that cats practice more agency than they have been given credit for and humans perhaps practice less. A further question, perhaps, is "what kind of agency?" Here we push back gently against the reduction of our approach to "niche construction." We want to reemphasize our perspective that human-cat collaboration is different from coevolution or symbiosis, different from existing theories of commensalism (Hulme-Beaman et al. 2016), synanthropy (O'Connor 2013), niche construction, or cultural evolution (Laland, Odling-Smee, and Feldman 2000). The concept of "niche construction" is a powerful tool for thinking about how a species transforms an environment just enough to give itself a reproductive or survival advantage (beavers building dams or

earthworms modifying soil chemistry), which in turn can become a heritable capacity ("ecological inheritance"; Boivin et al. 2016; Laland, Odling-Smee, and Feldman 2000).

We agree with Hansen and Fuentes in underlining the need to understand the complexity of human-mediated niche construction, in which animals depend on humans as ecosystem and niche engineers, such as the macaques in New Delhi that profit from human cultural production and practices in temples and markets (Barua et al. 2021). Biological anthropologists have also explored human evolution using a niche construction framework (Fuentes 2016, 2017; Kissel and Fuentes 2018). Such work primarily considers humans as a niche-constructing species affecting itself but has begun to explore how humans construct niches for other animals and act simultaneously as collaborators and competitors to shape new ecologies for a range of species (Boivin et al. 2016). Ellwanger and Lambert (2018) offer guidance for how to study the impact of human niche construction on nonhuman primates at both ecological and evolutionary timescales. As Parreñas sums up here, "Niche construction, in more cultural anthropological terms, accounts for nonhuman agency."

But it is not clear in our case that cats do much in the way of niche construction: cats have repeatedly taken advantage of human alteration of the environment, leading to new ecological opportunities, social dynamics, and selective pressures with the potential to affect evolutionary trajectories as well as forms of social learning and development—but they do not do it themselves. Humans, by contrast, especially modern humans, do so much more than simply altering the environment that the concept of niche construction seems inadequate to describe what modern humans accomplish when they "construct": creating ecological rearrangements that are consequential for a wide range of species, not just cats or other "domesticated" animals.

Do we coconstruct a niche then? This might seem to imply that humans and cats are learning from each other or responding directly to each other in some way. Some species can thrive through social learning and cultural inheritance, including learning from humans, but we do not think that cross-species social learning is cats' forte. The process of domestication and treatment of cats as human companions has certainly provided cats with ample social learning opportunities from humans, but evidence so far is that their use of social learning is quite limited compared with other companion species (Fugazza et al. 2020).

Rather, what we argue here is that cats are very good at "niche expansion" into new human-facilitated niche space and at "niche space saturation" across both new and old niche spaces through individual or population specialization. This saturation across expanded multidimensional niche space serves as a buffer for cats in changing cultural and ecological environments, including even against human attempts to control, limit, or eradicate them (i.e., against local or national turns in humans' biophilia values or stances and resultant shifts in cultural practices, as mentioned by Ferreira).

In terms of social theory (as Parreñas asks), a sharper focus on niche expansion might preserve the focus on the complexity and multiplicity of human relations with cats (from the cats in Jordan that McClellan sees to those in the United States or in Brazil) without needing to identify a particular practice of "co-constructing" niches. Modern cats, rather, are very good, on their own terms, at fitting together with whatever humans do (even when we try to eradicate them), and this is neither simply a genetic inheritance nor a result of humans' intentional intervention.

The concept of niche expansion has been used in biology in a context independent of humans to suggest that if individuals are more variable within populations, the species may occupy a wider niche (Bolnick et al. 2003; Pagani-Núñez et al. 2019; Sjödin, Ripa, and Lundberg 2018; Valen 1965). Here we argue that humans make cat niche width expansion possible on multiple axes because they affect cat individual variation through artificial selection, hormonal manipulation, contact with kittens that results in developmental differences, and degrees of captive control. Cat populations also show the ability to expand into a wider niche space through entering human-transformed and built environments, exploiting changing human cultural practices as well as traveling with humans during geographic expansions. Humans may construct niches for cats both actively through direct feeding and caring and passively through attracting rodents to grain or garbage, but cats' biological flexibility allows this expansion into this new niche space simultaneous with their maintenance of occupancy of their ancestral niche space.

More than one form of agency is at work here: cats need not be understood, in classic biological terms, as simply competitive or altruistic (i.e., a self/other-directed agency modeled on care or survival), and neither human biophilia nor greed alone account for their outcomes. Agency might also mean simply the ways in which the biological capacities and affordances of a creature enable and expand its ways of living in a world that has been transformed by other creatures. We are fellow travelers (Diamond 1978), but we might not actually be companion species (Haraway 2003) all that often.

It is also clear that such relations differ across different assemblages of human and animal. Evidence from some work in multispecies ethnography clearly demonstrates the ability of some animals to make such expansive choices (Govindrajan 2018; Locke 2017; Parreñas 2018), and here Suryawanshi provides several more mammalian examples of human-mediated niche expansion across different axes. We are excited to continue to develop the exploration of axes of niche expansion for both domesticated and wild species that interact with humans in a way that increases the given species' range, population size, and ecological impact. The study of human-mediated "niche contraction" in other species may seem obvious but must also be of interest to study in parallel.

Our expanded project aims to take the niche dimensions analyzed here for cats and explore them across other wild, domesticated, feral, invasive, and endangered species to understand how human interaction has changed or is changing niche space for them along these same axes: docility and domestication, living quarters, distribution, habitat, circadian rhythm, ecological role and diet, social organization, morphology, lifespan, and

reproductive capacity. We also want to explore whether other axes not important for cats may be essential in understanding changes found in other species' ecologies.

Finally, there is the question of perversion. Parreñas invokes one of the greatest antiheros of modern cinema, Dawn Davenport of *Female Trouble* (Waters 1974), as a way to query what might become of ideas like niche construction or domestication. In particular, she worries that niche construction might "become a hegemonic way of understanding survival, livability, or relations." To take Dawn Davenport seriously as a hero might be the ultimate challenge for our story of livability and more-than-human relations. Davenport rejects and destroys everything: school, family, her child, friends, lovers, law, society, audience, even her own body. Yet (thanks in great part to the incomparable performance of Divine) Dawn emerges successful at each turn. It is a stretch perhaps, but Davenport might be the ultimate niche expander: every norm, every law, and every restriction thrown up around her by society, family, celebrity culture, and elitism becomes a space for her to explore and thrive in, along multiple dimensions of human beauty and horror, up to and including the electric chair that kills her at the end.

McClellan echoes a similar concern: "When we talk about success, what do we mean? Are animals who are decidedly not populous or widely dispersed—who may be endangered or already extinct—failing in some way?" Success for Dawn Davenport looks nothing like what we might mean by the term in biology. There, it can mean increased genetic representation over generations relative to other individuals at the intraspecific level (reproductive success), or when comparing across species over time, it can mean widespread or abundant populations of species that outcompete other similar species and persist over long(er) periods of time (a species' evolutionary success). Such success can create the paradox that successful and expanding species in this last sense may have long-term increasing negative impacts on ecology, habitat, and other species, as is most obvious in the case of humans.

Can we—do we want to—square the success of Dawn Davenport with that of the cat? *Female Trouble* can be a powerful tool of cultural critique, revealing that all of culture is constructed (read: perverse). But it is, alas, limited as a tool of discovery. Insofar as we value the ability that humans have to expand their knowledge and understanding of themselves and other entities, and also want to recognize the ways this expansion is itself consequential (i.e., as Addison points out, it might itself be a way of expanding certain dimensions of a niche), Davenport might be less a critique than simply a patron saint warning us of the Pyrrhic, and all-too-human, nature of flourishing or success. One can imagine Dawn's/Divine's voice perhaps: it ain't easy for a queen to be obscene on a trampoline. But Dawn is just plain mean, self-absorbed to the point of insanity, capitalizing on her own calamity. Is she the epitome of humanity?

Consider, in closing, a different hero: a real mountain lion in Los Angeles named P-22 who was numbered and named by the National Park Service, framed with a radio choke collar in Griffith Park, tamed with trickle-up rat poison, shamed into eating chihuahuas off of pet walker's leashes, maimed by a car when too addled to sprint, famed like no other feline by a sold-out starlit memorial crowd in the Greek Theater, and reclaimed by Tongva and Chumash members for burial in the unceded indigenous lands of the Santa Monica Mountains. P-22 is both victim of human overreach and object of unconditional love. It may well be true that agape enlarges eros—but P-22, Dawn Davenport, and the modern cat remind us that the consequences of unconditional love can be wildly different, depending on its objects and its aims.

—Jessica W. Lynch and Christopher M. Kelty

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