GEORGETOWN SCIENTIFIC RESEARCH JOURNAL
Volume Five
Edition One
Fall 2024

Variation in body size introduces behavioral and adaptive constraints in morphologically similar Felidae species

Dilara Kamrava, Emily Williams, and Alexandra DeCandia

Variation in body size introduces behavioral and adaptive constraints in morphologically similar Felidae species

Dilara Kamrava[1], Emily Williams[1], and Alexandra DeCandia[1,2]

[1] Georgetown University, Washington DC, United States
[2] Center for Conservation Genomics, Smithsonian's National Zoo and Conservation Biology Institute, Washington DC, United States
Email: dck48@georgetown.edu
https://doi.org/10.48091/3ss4sx15

Abstract

Species within the mammalian family Felidae present a unique opportunity to study the relationship between interspecies morphological and ecological variation due to their high phenotypic trait conservation. Despite a long list of shared characteristics, felids display tremendous diversity in body size, with an almost 300 kg difference between the largest and smallest species. However, extensive research into potential interactions of body size with other traits across felids as a whole has yet to be completed. In this review and collection of exploratory analyses, we examined whether variation in body size introduces ecological constraints on how felids use their common traits, particularly regarding ambush hunting behavior. We collated and explored metadata about numerous morphological and ecological characteristics (including average weight, prey selection and killing strategy, pelage characteristics, habitat preference, and conservation status) for all 41 currently recognized species. We found that felid body size influences prey selection and primary dispatch strategy, with larger felids employing suffocating throat bites while smaller felids preferred nape bites. We also found that larger body sizes seemed generally associated with lower prey capture rates, although data collection on more felid species is necessary to confirm whether this trend holds across the family. We further documented high variation in pelage characteristics and preferred habitat types, suggesting that the near universal need for camouflage in ambush predators exerts a stronger influence on pelage color and pattern than body size. Finally, we reported a relationship between body size and conservation status, as 100% of large species and 84% of small species are currently experiencing population declines. While midsize species fare slightly better with only 56% of species showing declines, all felids face significant threats from habitat loss and other anthropogenic pressures. By collating metadata and exploring patterns relating felid body size to ecological and behavioral traits alongside population trends and conservation status, we aimed to improve our understanding of these charismatic and ecologically important animals, while inspiring further study into the eco-evolutionary implications of body size.

Keywords: behavior, conservation, ecology, Felidae, ambush hunting, phenotypic variation

1. Introduction

Species within the mammalian family Felidae serve as ambassadors for wildlife conservation and, in the case of *Felis catus*, beloved household pets. They are found on almost every continent, consistently rank among the most well-known and charismatic species, and even fuel online procrastination in the form of cat videos.[1,2,3] Yet there remain understudied aspects of felid ecology, behavior, and conservation that can provide further insights into these fascinating and enigmatic species.

The Felidae family is a monophyletic clade derived from a relatively recent common ancestor 10-15 mya, and is divided into two subfamilies: Pantherinae and Felinae (Figure 1).[1,4] The Pantherinae subfamily consists of seven species in the two genera Panthera and Neofelis, which are respectively characterized by large and midsize cats. In contrast, the Felinae family contains the remaining 34 species in 12 genera of varying body sizes. There are currently 41 recognized species within Felidae, although this number is frequently adjusted based on shifting taxonomic classifications. For example, the placement of jaguarundi (*Herpailurus yagouaroundi*) in its own genus or within its current sister group *Puma* remains controversial.[4]

The Felidae family is distinguished by phenotypic trait conservation among its members.[5] In general, felids have a highly similar body type, possessing a notably shortened rostrum and a lithe body shape that facilitates jumping, speed, and agility. With the exception of cheetahs (*Acinonyx jubatus*), all felid species also possess protractile claws that passively retract when not in use to allow felids to disguise the noise of their movements and maintain claw health.[6] Excellent night vision allows felids to spot prey from a distance during their preferred crepuscular hunting periods, and during the kill, felids deploy premolars and lower molars as carnassial teeth adept at quickly shearing through flesh.[7,8] The sharp papillae on felid tongues rip meat from prey and allow felids to self-groom, which reduces parasites and dampens scent.[9] Apart from four species within the *Panthera* genus that can only roar (i.e., *P. leo, P. tigris, P. pardus*, and *P. onca*), all felid species communicate by vibrating elastic vocal cords to purr.[10]

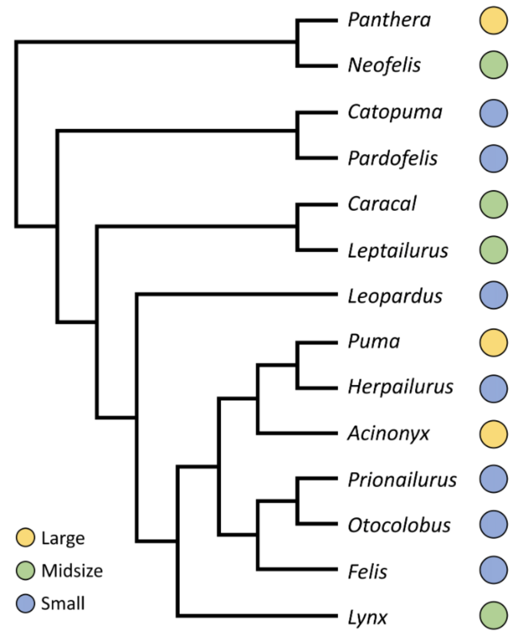

Figure 1. Current taxonomic classification of genera within Felidae.[4] All genera contained felid species only belonging to a single size class overall.

Such striking trait conservation among felids is particularly notable given their cosmopolitan distribution. Felids collectively range from the southern tips of South America and Africa to the arctic plains of northern Canada and Russia. Thus, conserved traits likely serve important functions that help cats succeed as predatory mammals across multiple latitudes and disparate habitat types. For example, felids consistently deploy an ambush-like form of hunting, where they maintain camouflage and silence before making the killing strike, whereas canids often rely on strength, speed, or group coordination to bring down prey.[1,5] Furthermore, unlike canids, all felid species barring one (*P. leo*) hunt solitarily.[11] The ubiquity of solitary ambush hunting strategies is likely to be one of the primary drivers behind character similarities, as many of these traits are required for their shared prey acquisition strategy.

Despite widescale similarities, felid species exhibit high variability in body size. At one end of the spectrum rests the smallest felid, the male rusty-spotted cat (*Prionailurus rubiginosus*), which barely tops 1 kg; at the other end of the spectrum lies the largest felid and third largest terrestrial carnivore, the tiger (*P. tigris),* which weighs an average of 280 kg—nearly 300 times the weight of the rusty-spotted cat.[12] The remaining 39 felid species exhibit small, midsize, and large body sizes distributed between the two extremes. Such conspicuous variation in body size likely influences different aspects of felid ecology, behavior, and conservation, such as prey capture rate, prey size, kill method, pelage pattern, and preferred habitat – all of which can affect population viability in increasingly human-modified landscapes.

In the present review, we explored felid body size as it relates to felid ecology, behavior, and conservation. We first searched through several sources in the literature for information on phenotypic, behavioral, and ecological traits of felids.[5,12-15] Focal traits included felid weights, prey characteristics, prey capture rates, kill methods, pelage patterns, preferred habitat, and conservation status. We collated this information (with references) in Supplemental Table S1 to provide an accessible resource for Felidae researchers, and subsequently explored preliminary relationships between traits of interest. Although previous work has examined felid morphology and behavior, much less is known about how phenotypic traits may constrain or modify one another.[16-21] By studying these traits, we can gain a more comprehensive understanding of interspecific variation within Felidae. This, in turn, can inspire further research and targeted conservation efforts to protect these charismatic and ecologically important animals.

2. Trait Documentation and Comparison

To assess body size, we compiled body weights as the expected average weight of a male member of each felid species. We subsequently grouped genera into three weight-based size classes: small (<15kg), midsize (15-50 kg), and large (>50 kg; Table 1). We performed this classification at the genus level because genera within Felidae exhibit a high degree of homogeneity in body weight, and there were no instances of two species within the same genus falling into clearly different size classes. We chose lower size limits for midsize species, as felids that weigh above 15 kg (though not considered "big cats") possess a distinct body type characterized by stocky chests and thicker legs. One exception to this pattern is the slim serval (*Leptailurus serval*), which is a midsize cat closely related to stocky caracals (*Caracal caracal*).[5] We chose 50 kg for the upper size limit of midsize cats because there was a significant gap in body weight between the largest midsize felid (25 kg, *Neofelis diardi*) and the smallest large felid (50 kg, *P. uncia*).

Table 1. Classification of felid species into weight-based size classes at the genus level. Body weights used to classify genera represented the average weight of a male in each species.[12] Genera containing only one species were taxonomically named as the species rather than the genus, and subspecies were not included in the reported species count.

Size class	Weight	Genus or species
Large (7 species)	>50 kg	• *Puma concolor* (Cougar) • *Acinonyx jubatus* (Cheetah) • *Panthera*
Midsize (9 species)	15-50 kg	• *Leptailurus serval* (Serval) • *Lynx* • *Caracal* • *Neofelis*
Small (25 species)	<15 kg	• *Otocolobus manul* (Pallas's cat) • *Herpailurus yagouaroundi* (Jaguarundi) • *Pardofelis marmorata* (Marbled cat) • *Felis* • *Prionailurus* • *Leopardus* • *Catopuma*

Using the IUCN Red List of Threatened Species and existing literature, we compiled the following ecological information for the 41 currently documented felid species: main prey category, prey size (binary: small or large), primary kill method, prey capture rate, pelage color and pattern, preferred habitat, geographic range, conservation status, and population trends (Table S1). We recorded information about pelage pattern since ambush hunting requires felids to maintain effective camouflage, and the diversity of felid coat patterns and colors reflects the wide range of habitats they collectively occupy. Kill method refers to which approach felid species primarily adopt for dispatching prey, including the nape bite, which swiftly severs the spinal cord between the vertebrae, or the throat bite, which requires the felid to clamp the prey's windpipe closed to suffocate them.[5] Finally, we recorded each species' conservation status to assess any patterns between current population trends and felid body size.

After summarizing the collated information into Supplemental Table S1 with references, we imported a modified version of that table into R 4.2.1 for preliminary analysis of patterns and data visualization.[22] Due to small within-group sample sizes, we used non-parametric tests to explore preliminary associations between variables of interest. We used Fisher's Exact tests when comparing two categorical variables, Kruskal-Wallis χ^2 tests when comparing a categorical and continuous variable, and Spearman's ρ tests when comparing two continuous variables, all with a significance threshold of 0.05.

It is important to note that our study is not a formal meta-analysis and does not meet the requirements for a systematic review of metadata.[23] Instead, our main objective was to explore whether felid body size may constrain or modify felid ecology, behavior, and conservation through preliminary analyses of collated information. We therefore used figures and statistical analyses to identify potential patterns that may motivate future comparative analyses inspired by the present study. Our study is limited in scope, and there are a number of additional ecological, physiological, or morphological factors not examined here that may influence the relationships reported. However, in collating numerous traits from the literature into a freely accessible table (which, to our knowledge, is among the first of its kind), our study provides a comprehensive resource for mammalogists interested in pursuing further research on the relationship between felid body size and numerous eco-evolutionary factors. These may include (but are not limited to) hunting behavior and prey choice, habitat preference and pelage characteristics, and conservation status of trends, each of which are explored below.

3. Hunting Behavior and Prey Choice

We first examined the relationship between body size and hunting behavior. Here, we found that several aspects of foraging ecology were associated with felid size. As might be expected, larger felids tend to target larger prey such as ungulates, whereas midsize and small felids target a range of smaller species like leporids and rodents, respectively (Fisher's Exact Test, $p < 0.001$; Figure 2a). This relationship makes intuitive sense, as large felids are able to better overcome prey defenses. Large prey in particular present formidable opponents – for instance, giraffes (*Giraffa camelopardalis)* have been known to severely injure and even decapitate hunting lions (*P. leo*) with their powerful kicks.[24,25] Larger prey are also more likely to attract other competing predators. For example, cheetahs hunting for food have had their cubs targeted and killed by nearby hyenas (*Crocuta crocuta*) and lions.[26] As larger felids are better able to overcome these challenges posed by large prey and competitors, they can obtain higher calorie kills as a result. Small to midsize felids likely vary their prey choice accordingly, focusing on the smaller to midsize prey that they are better equipped to dispatch.

Interactions between felid predators and their prey are not just informed by the circumstances preceding an attack, but also by the attack itself. We therefore explored whether felid size significantly influenced how these predators deliver the killing blow to their prey. Dispatch methods include the swift nape bite or the suffocating throat bite.[5] Nape bites are advantageous because the prey is dispatched quickly, whereas throat bites require prey to be subdued for several minutes while slowly suffocating.[27] The inability to perform a killing nape bite arises when the felid's teeth are not large enough, or its bite force not strong enough, to crack open the prey's cervical vertebrae and sever the spinal cord. This situation arises when the prey animal is relatively large compared to the felid. We might expect that small felids, which primarily hunt small mammals and rodents, can more easily deliver a killing nape bite. In contrast, large felids exclusively targeting ungulates as their main prey are faced with significantly thicker and sturdier prey vertebrae. As such, we might expect larger felids to kill their prey by wrapping their jaws around the prey animal's neck and slowly squeezing the windpipe closed.[27] Examination of the collated metadata presented herein supported these expectations, as we observed significant associations between felid size and primary kill method. Large felids use throat bites as their primary kill method, and small felids exclusively use nape bites as their primary kill method (Fisher's Exact Test, $p < 0.001$; Figure 2b). Mid-size felids adopt both approaches, likely due to their intermediate size. Classification of primary prey into binary size classes (small and large) confirmed that larger prey species were more likely to receive throat bites, whereas small prey were dispatched using nape bites (Fisher's Exact Test, $p < 0.001$; Figure 2c), with predators targeting a mix of small and large prey often using either approach.

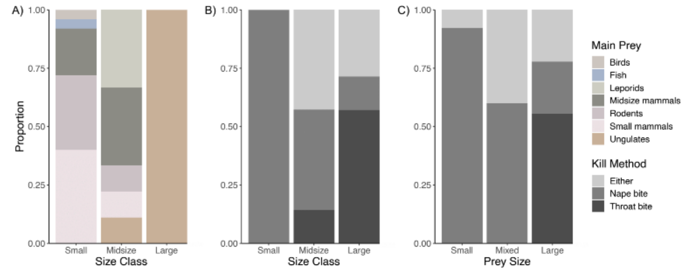

Figure 2. Main prey and primary kill method differ between felid size classes. (A) Large felids primarily target ungulates as their main prey, whereas midsize and small felids primarily target midsize and small prey, respectively. The primary kill method adopted by felids was significantly associated with (B) felid size class (Fisher's Exact Test, $p < 0.001$) and (C) the size of their prey (Fisher's Exact Test, $p < 0.001$)

The final facet of hunting behavior that we examined in the context of felid size was hunting success. We collected prey capture data for the 14 felid species with information available where prey capture rate was measured as the proportion of successful prey captures out of the total observed number of attempts.[5,28-34] Using log-transformed felid weights, we found that prey capture rate appeared to show a generally negative trend as felid size increased (Spearman's $S = 645.630$, $\rho = -0.419$, $p = 0.136$; Figure 3a), with that trend also seeming to appear when felids were grouped into size classes (Kruskal-Wallis test, $\chi^2 = 1.679$, $df = 2$, $p = 0.432$; Figure 3b). However, it is important to note that neither of these results meet the criteria for statistical significance, and should not be interpreted as conclusive. At present, our statistical analyses of felid prey capture rate faced limitations due to low intragroup sample sizes; for instance, out of a possible 25 small felid species, data on prey capture rates was only available for four.

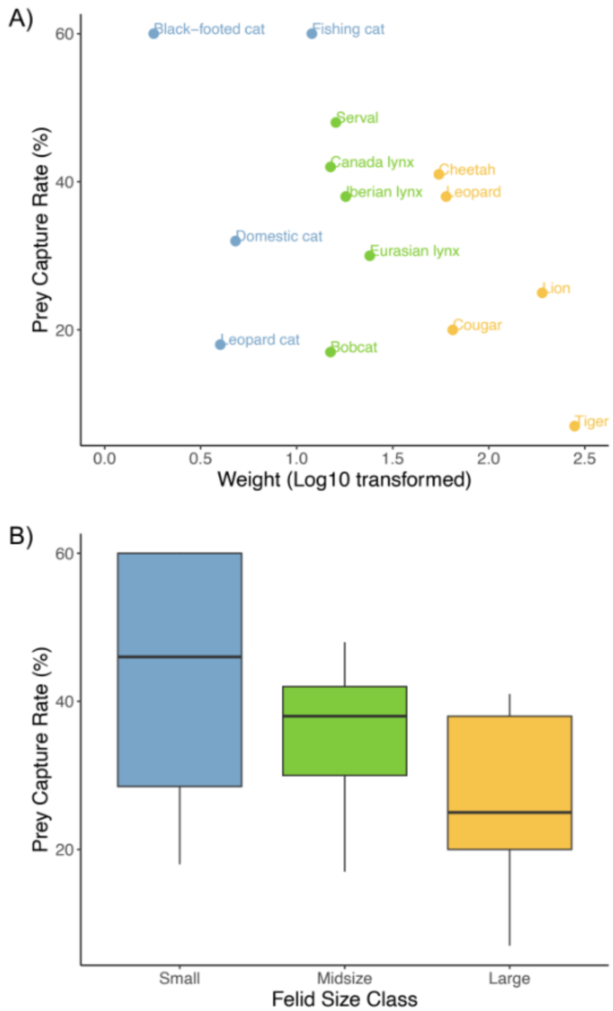

Figure 3. Prey capture rates show a non-significant inverse relationship with felid body size. As felid size increases, prey capture rate seems to decrease non-significantly when measuring size as (A) log- transformed felid weight (Spearman's S = 645.63, ρ = - 0.419, p = 0.1359) and (B) categorical size class (Kruskal-Wallis test, $\chi 2$ = 1.679, df = 2, p = 0.432). Small sample size may have contributed to the non-significance to this trend, as only 14 species had available data on prey capture rate.

We recommend additional data collection in this area, as the emergent trends examined herein with 14 species likely reflect a larger-scale trend observed within Felidae. It makes intuitive sense that larger felids may have lower prey capture rates than smaller felids. This may be caused by prey defenses, but could also relate to ambush hunting behavior, as it is harder to hide larger cats. We see evidence of this universal need for crypsis among felids in the wide array of pelage patterns across size classes that aid in camouflage. For example, tigers rely on their distinctive stripes to blend into the background.[35] While smaller felids also rely on pelage patterns for camouflage, they often occupy concealed spaces that require no visual exposure to the prey, such as tree holes and small burrows abandoned by other fossorial species.[36] The implication of varied ambush success means that the hunting attempts of many large felids may be foiled before they even begin, potentially explaining why species like tigers have lower success rates. We recommend further study of the relationship between felid size and prey capture rates as data is collected for additional species in order to assess whether the observed trend represents a true reality.

4. Pelage Characteristics and Habitat Preference

Given the importance of camouflage for successful ambush hunting, we next explored the relationship between felid size, pelage characteristics, and habitat preference. Across size classes, felids exhibited a broad array of pelage colors from sandy beige (*Lynx pardinus*) to chestnut (*Catopuma badia*) to orange (*P. tigris*), with some small felids exhibiting high intraspecific variation (F. catus; Figure 4a). Pelage patterns similarly varied across size classes, with plain pelage consistently poorly represented (Figure 4b). Although fine-scale habitat preference (i.e., whether felids are primarily arboreal, scansorial, or terrestrial) was not dependent upon felid size class (Fisher's Exact Test, p = 0.805), it was associated with pelage pattern (Fisher's Exact Test, p = 0.047). For example, rosetted patterns typified arboreal or scansorial felids; out of eight felid species with rosetted pelage, only one was terrestrial (*Leopardus guttulus*; Table S1). This suggests that the need for habitat-specific camouflage – rather than overall felid size – exerts a stronger influence on pelage characteristics. This bears out when considering pelage in each felid species' unique contexts. For example, the sand cat's (*Felis margarita*) light sandy striped pelage provides ample camouflage within the North African and West-Central Asian deserts it inhabits.[27] In contrast, arboreal and scansorial cats living in forests often have disruptive dark-spotted or blotched pelage patterns, which match dappled light coming through vegetation.

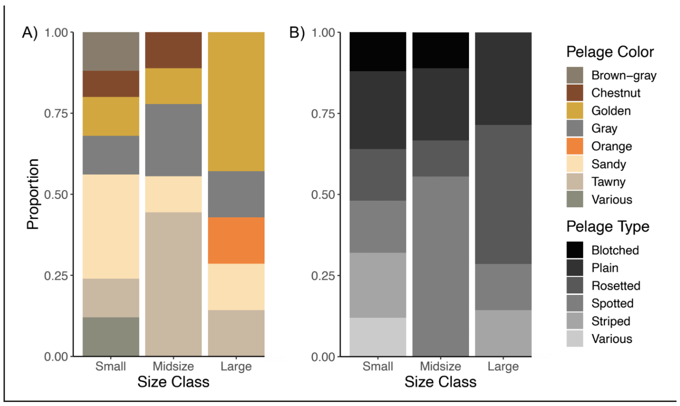

Figure 4. Felids display a wide variety of pelage colors and patterns across size classes. (A) Pelage colors golden, sandy, tawny, and gray can be found in species of all body size classes, with additional colors present in a subset of felids. (B) Pelage patterns plain, spotted, and rosetted can similarly be found in species of all body size classes, with additional patterns present in a subset of felids. Over 50% of midsize felids have spotted pelage.

As such, we see that the adaptive value of different pelage colors and patterns can vary by environmental context. This has high relevance to felid ecology and evolution, as felids are known to occupy a wide variety of contexts. On a broad geographic scale, species within Felidae exist on almost every continent and in numerous habitat types including forests, shrublands, grasslands, savannas, deserts, inland wetlands, and rocky areas (Figure 5). While we observed some patterns relevant to size class (e.g., all large cat species can be found in shrublands and grasslands), we also observed a remarkable range of habitat types within species, and particularly within large-bodied species. For example, Sumatran tigers (*P. tigris sondaica*) inhabit tropical rainforests where monthly average temperatures never dip below 22°C, while the Amur tiger (*P. tigris tigris*) inhabits areas of northeastern China where temperatures can plunge as low as -53°C in the winter.[37] The range of pumas (*P. concolor*) spans most of the Americas, with the South American cougar (*P. concolor concolor*) occupying the Amazon rainforest and Andes mountains while the North American cougar (*P. concolor cougar*) inhabits spaces from Central America to the Rocky Mountains in British Columbia.[38] In fact, large leopards (*P. pardus*), lions (*P. leo*), cheetahs (*A. jubatus*), and jaguars (*P. onca*) all possess multi-continental distributions across their subspecies; except for the jaguar, which is monotypic.[39]

In contrast to these broad-reaching distributions of large felids, almost one-quarter (24%) of small felids are exclusively found in the forests of Southeast Asia, with some species, such as the bay cat (*C. badia*), restricted to only one island.[4,5] Additionally, the Andean mountain cat (*L. jacobita*) is only found in the rocky hills of the Andes mountains, and the kodkod (*L. guigna*) is limited to shrubland and forest in southern Chile.[39,40] On average, small felids tend to be more specialist in their habitat requirements than wider-ranging large felids, which can have important implications for the conservation monitoring and management of species within each size class.

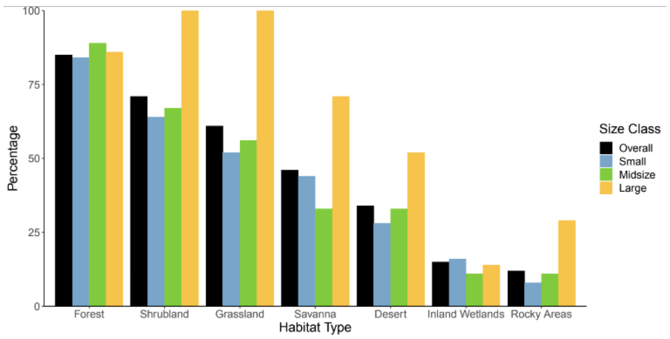

Figure 5. The majority of felid species can be found in forest, shrubland, and grassland habitats. Each bar represents the percentage of total felid species (black) or the percentage of small (blue), midsize (green), and large (yellow) felid species found in each habitat type.

5. Conservation Status and Trends

Across all habitat types and size classes, felid species face the risk of local extirpation and range-wide extinction. According to the International Union for Conservation of Nature, the majority (71%) of large felid species are currently listed under a threatened category (i.e., Vulnerable or Endangered; Figure 6a). In contrast, 44% of midsize felid species and 36% of small felids were classified under threatened categories; yet all size groups had at least one Endangered species (Table S1). Overall trends place midsize felids as faring the "best" of the size classes, as 66% of midsize species are classified as Least Concern. However, population trends provide reason for concern, as roughly 80% of felid species are currently experiencing population declines. Large felids are particularly at risk, as 100% of species in this size class have decreasing population trends (Figure 6b). Small felids exhibit a similar trend, with 84% of species experiencing population declines and only one species (*P. bengalensis*) exhibiting stable population trends. Midsize felids again seem to be faring the "best" of the three size classes, as three out of the four felids with stable population trends are classified as midsize. However, over 50% of midsize species are nonetheless experiencing population declines, underscoring the troubling population trends exhibited across all three felid size classes.

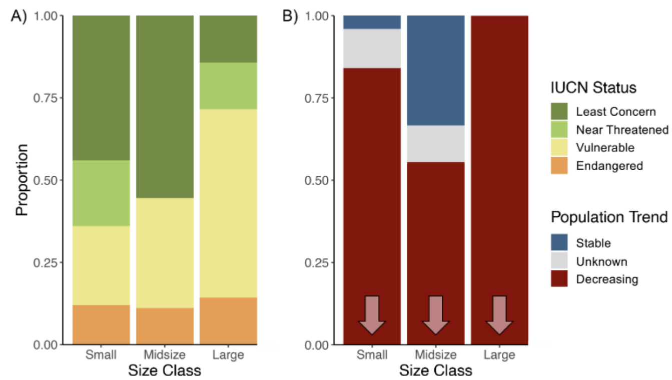

Figure 6. Felid species of all size classes are experiencing significant conservation challenges. (A) The majority of large felid species are listed in a threatened category (i.e., Vulnerable or Endangered) by the IUCN Red List, with a significant proportion of small and midsize species also listed as threatened. (B) All large felids exhibit decreasing population trends, with 84% of small felids and a little over 50% of midsize felids similarly decreasing.

These troubling conservation trends may relate to the factors previously considered in this review. For example, if large felids have lower hunting success rates than smaller species, big cats will necessarily require a larger territory in order to access a wider berth of prey and avoid resource competition. This reveals a potential driver for decreasing population trends observed in every large felid species, as undisturbed, contiguous habitat is diminishing quickly. For example, it is estimated that there will be no remaining suitable habitat for Bengal tigers (*P. tigris tigris*) in southern coastal Bangladesh by 2070.[41] For jaguars (*P. onca*), habitat fragmentation was found to be a greater threat than habitat loss; out of 28 surveyed subpopulations separated by fragmentation, only two were found to be viable in the long term.[42] While small and midsize felids may be able to survive in smaller home ranges (possible due to higher hunting success rates), habitat loss and fragmentation threaten their long-term viability, as well. For example, species inhabiting one or a few isolated areas have few to no options for dispersal should their habitat be destroyed or modified for anthropogenic use.

Yet even if the extent of a species' range is not impacted, other factors can seriously decrease the quality of available habitat and reduce the available area where a species can thrive. Pollution, in particular, affects small and midsize felids by increasing disease and spreading risks across wide swaths of habitat. For example, fishing cats (*P. viverrinus*) that partially rely on estuary mangrove habitats were found to be threatened by heavy metal contamination.[43] Similar dynamics were found in urban-dwelling bobcats (*L. rufus*), where exposure to anticoagulant rodenticides led to increased disease severity.[44-46] As apex predators, felids are especially susceptible to bioaccumulation, which can be heightened for small felid species (e.g. *P. bengalensis*) that primarily prey on secondary consumers such as birds or fish. These effects are particularly striking in urbanized areas, where felids can experience increased exposure to toxins amid additional threats, such as car strikes, poaching, illegal snares, and culling for the pelt trade.[47,48] This latter threat poses a large risk to felids of all size classes, as many fall victim to the trapping and fur industries due to their elaborate pelts.[49] Irrespective of the specific underlying cause, the decreasing population trends observed across all size classes are concerning for Felidae species and their interacting partners, as felids often important roles as apex predators in their ecosystems by promoting interspecies coexistence and revitalizing habitats in unexpected ways.[50-53]

6. Conclusion

In the present review, we examined the potential role that felid body size plays in hunting behavior, habitat preference, and conservation status. We collated information from the scientific literature regarding numerous ecological variables – such as prey characteristics, capture rates, kill methods, pelage patterns, habitat preferences, and population trends – and populated a summary table containing all 41 currently recognized Felidae species (Table S1). We reported preliminary relationships between felid size class and preferred prey, prey size, and kill method, with all size classes exhibiting a diverse array of habitat preferences and pelage characteristics. Finally, we reported concerning population trends across all three felid size classes, with 100% of large felid species, over 50% of midsize felid species, and over 80% of small felid species exhibiting population declines.

Our findings regarding the relationship between felid body size and numerous aspects of their ecology, behavior, and conservation suggest that body size does influence eco-evolutionary dynamics between felids and their prey. While we identify several important patterns, our results should be considered preliminary and are meant to inspire future research that considers additional variables and species-level data. At the time of this study, small and midsize cats had considerably lower amounts of available data compared to large cats. This was exemplified by prey capture rates, where we collated information for 4 small felid species and 5 large felid species, despite small species outnumbering large species 25 to 7. This discrepancy in data availability may be due to small cats' elusive nature, distribution in remote locations, or small numbers. However, their further study is critically important, as the more we know about each felid species, the better informed our conservation actions can be. This is particularly relevant given the sobering population trends reported herein across all three size classes.

Despite the stated limitations of this study, the relationship between felid body size and numerous ecological traits has not previously been reviewed to this extent. Our study therefore represents an important step towards a more comprehensive understanding of species within Felidae and the many associations between their body size and ecology, behavior, and conservation. As the majority of felid species experience population- and species-level threats, their continued study – particularly for chronically understudied small to midsize cats – is paramount to designing effective conservation strategies and enabling long-term persistence of felids. We hope these qualitative analyses and summative table of collated metadata present a valuable resource to the Felidae research community and inspire further study and conservation action of these charismatic and ecologically important species.

References

1. Feldhamer, G.A., Merritt, J.F., Krajewski, C., Rachlow, J.L., Stewart, K.M. (2020). Mammalogy: Adaptation, Diversity, Ecology. Fifth Edition, Johns Hopkins University Press, Baltimore.
2. Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., Macdonald, D.W. (2015). Conservation inequality and the charismatic cat: *Felis felicis*. *Glob Ecol Conserv 3*: 851–866. https://doi.org/10.1016/j.gecco.2015.04.006
3. Myrick, J.G. (2015). Emotion regulation, procrastination, and watching cat videos online: Who watches Internet cats, why, and to what effect? *Comput Human Behav 52*: 168–176. https://doi.org/10.1016/j.chb.2015.06.001
4. Kitchener, A.C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N., Abramov, A. V, Christiansen, P., Driscoll, C.A., Duckworth, J.W., Johnson, W.E., Luo, S.J., Meijaard, E., O'Donoghue, P., Sanderson, J., Seymour, K., Bruford, M.W., Groves, C., Hoffmann, M., Nowell, K., Timmons, Z., Tobe, S.S. (2017). A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News* (11).
5. Sunquist, M., Sunquist, F. (2002). Wild Cats of the World. University of Chicago Press, Chicago.
6. Bryant, H.N., Russell, A.P., Laroiya, R., Powell, G.L. (1996). Claw retraction and protraction in the carnivora: Skeletal microvariation in the phalanges of the Felidae. *J Morphol 229*(3): 289–308. https://doi.org/10.1002/(SICI)1097-4687(199609)229:3<289::AID-JMOR4>3.0.CO;2-U
7. Ewer, R.F. (1998). The Carnivores. Cornell University Press, Ithaca.
8. Wittenberg, P.A. (1995). Phylogenetic, behavioral, and dietary constraints on felid masticatory morphology. Thesis: Duke University.
9. Goździewska-Harłajczuk, K., Barszcz, K., Klećkowska-Nawrot, J., Hamouzová, P., Čížek, P., Kuropka, P., Kvapil, P. (2023). Comparative study of lingual papillae, lingual glands and lyssa of the tongue of selected wild felids (Carnivora, Felidae) in biological aspects. *Biology 12*(4): 516. https://doi.org/10.3390/biology12040516
10. Hast, M.H. (1989). The larynx of roaring and non-roaring cats. J Anat 163: 117.
11. Krofel, M., Kos, I., Jerina, K. (2012). The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behav Ecol Sociobiol 66*: 1297–1304. https://doi.org/10.1007/s00265-012-1384-6
12. Lamberski, N. (2015). Felidae. Fowler's Zoo and Wild Animal Medicine, Volume 8: 467.
13. Mattern, M.Y., McLennan, D.A. (2000). Phylogeny and speciation of felids. *Cladistics 16*(2): 232–253. https://doi.org/10.1006/clad.2000.0132
14. Rinaldi, A.R., Rodriguez, F.H., Carvalho, A.L., Passos, F.C. (2015). Feeding of small Neotropical felids (Felidae: Carnivora) and trophic niche overlap in anthropized mosaic landscape of South Brazil. *Biotemas 28*(4): 155–168. https://doi.org/10.5007/2175-7925.2015v28n4p155
15. Skinner, J.D., Chimimba, C.T. (2005). The mammals of the southern African sub-region. Cambridge University Press, Cambridge.
16. Day, L.M., Jayne, B.C. (2007). Interspecific scaling of the morphology and posture of the

limbs during the locomotion of cats (Felidae). *Journal of Experimental Biology 210*(4): 642–654. https://doi.org/10.1242/jeb.02703
17. Lanier, D.L., Dewsbury, D.A. (1976). A quantitative study of copulatory behaviour of large Felidae. *Behavioural Processes 1*(4): 327–333. https://doi.org/10.1016/0376-6357(76)90014-0
18. Mellen, J.D. (1993). A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats (Felis). *Am Zool 33*(2): 151–166. https://doi.org/10.1093/icb/33.2.151
19. Peters, G., Tonkin-Leyhausen, B.A. (1999). Evolution of acoustic communication signals of mammals: friendly close-range vocalizations in Felidae (Carnivora). J *Mamm Evol 6(*2): 129–159. https://doi.org/10.1023/A:1020620121416
20. Randau, M., Goswami, A. (2017). Morphological modularity in the vertebral column of Felidae (Mammalia, Carnivora). *BMC Evol Biol 17*: 1–12. https://doi.org/10.1186/s12862-017-0975-2
21. Sicuro, F.L., Oliveira, L.F.B. (2011). Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zool J Linn Soc 161*(2): 414–462. https://doi.org/10.1111/j.1096-3642.2010.00636.x
22. R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org/.
23. Haddaway, N.R., Bethel, A., Dicks, L. V, Koricheva, J., Macura, B., Petrokofsky, G., Pullin, A.S., Savilaakso, S., Stewart, G.B. (2020). Eight problems with literature reviews and how to fix them. *Nat Ecol Evol 4*(12): 1582–1589. https://doi.org/10.1038/s41559-020-01295-x
24. Hayward, M.W., Kerley, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *J Zool 267*(3): 309–322. https://doi.org/10.1017/S0952836905007508
25. Pickard, A.R., Holt, W. V, Green, D.I., Cano, M., Zoo, T., Rose, P., Roffe, S. (2014). Clawing their way to the top: Lion vs. giraffe! Newsletter of the IUCN SSC Giraffe & Okapi Specialist Group 44: 19.
26. Hunter, J.S., Durant, S.M., Caro, T.M. (2007). To flee or not to flee: predator avoidance by cheetahs at kills. *Behav Ecol Sociobiol 61*: 1033–1042. https://doi.org/10.1007/s00265-006-0336-4
27. Kitchener, A.C., Van Valkenburgh, B., Yamaguchi, N., Macdonald, D., Loveridge, A. (2010). Felid form and function. *Biology and Conservation of Wild Felids*: 83–106. https://www.researchgate.net/publication/266753114_Felid_form_and_function
28. Funston, P.J., Mills, M.G.L., Biggs, H.C., Richardson, P.R.K. (1998). Hunting by male lions: ecological influences and socioecological implications. *Anim Behav 56*(6): 1333–1345. https://doi.org/10.1006/anbe.1998.0884
29. Ganguly, D., Adhya, T. (2022). How fishing cats *Prionailurus viverrinus* (Bennett, 1833) fish: describing a felid's strategy to hunt aquatic prey. *Mammalia 86*(2): 182–189. https://doi.org/10.1515/mammalia-2020-0133
30. Herbst, M., Mills, M.G.L. (2010). The feeding habits of the Southern African wildcat, a facultative trophic specialist, in the southern Kalahari (Kgalagadi Transfrontier Park, South Africa/Botswana). *J Zool 280*(4): 403–413. https://doi.org/10.1111/j.1469-7998.2009.00679.x
31. Hilborn, A., Pettorelli, N., Caro, T., Kelly, M.J., Laurenson, M.K., Durant, S.M. (2018). Cheetahs modify their prey handling behavior depending on risks from top predators. *Behav Ecol Sociobiol 72*: 1–10. https://doi.org/10.1007/s00265-018-2481-y
32. Ivan, J.S., Shenk, T.M. (2016). Winter diet and hunting success of Canada lynx in Colorado. *J Wildl Manage 80*(6): 1049–1058. https://doi.org/10.1002/jwmg.21101
33. Lamichhane, B.R., Kadariya, R., Subedi, N., Dhakal, B.K., Dhakal, M., Thapa, K., Acharya, K.P. (2016). Rusty-spotted Cat: 12th cat species discovered in Western Terai of Nepal. *Cat News 64*: 30–36.
34. McGregor, H., Legge, S., Jones, M.E., Johnson, C.N. (2015). Feral cats are better killers in open habitats, revealed by animal-

borne video. *PLoS One 10*(8): e0133915. https://doi.org/10.1371/journal.pone.0133915
35. Godfrey, D., Lythgoe, J.N., Rumball, D.A. (1987). Zebra stripes and tiger stripes: the spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biological Journal of the Linnean Society 32*(4): 427–433. https://doi.org/10.1111/j.1095-8312.1987.tb00442.x
36. Happold, M., Happold, D.C.D. (2013). Mammals of Africa. Bloomsbury, London.
37. Luo, S.-J., Liu, Y.-C., Xu, X. (2019). Tigers of the world: Genomics and conservation. *Annu Rev Anim Biosci* 7: 521–548.
38. Gay, S.W., Best, T.L. (1996). Relationships between abiotic variables and geographic variation in skulls of pumas (Puma concolor: Mammalia, Felidae) in North and South America. *Zool J Linn Soc 117*(3): 259–282. https://doi.org/10.1111/j.1096-3642.1996.tb02190.x
39. Day, L.M., Jayne, B.C. (2007). Interspecific scaling of the morphology and posture of the limbs during the locomotion of cats (Felidae). *Journal of Experimental Biology 210*(4): 642–654. https://doi.org/10.1242/jeb.02703
40. Johnson, W.E., Culver, M., Iriarte, J.A., Eizirik, E., Seymour, K.L., O'Brien, S.J. (1998). Tracking the evolution of the elusive Andean mountain cat (*Oreailurus jacobita*) from mitochondrial DNA. *Journal of Heredity 89*(3): 227–232. https://doi.org/10.1093/jhered/89.3.227
41. Mukul, S.A., Alamgir, M., Sohel, M.S.I., Pert, P.L., Herbohn, J., Turton, S.M., Khan, M.S.I., Munim, S.A., Reza, A.H.M.A., Laurance, W.F. (2019). Combined effects of climate change and sea-level rise project dramatic habitat loss of the globally endangered Bengal tiger in the Bangladesh Sundarbans. *Science of the Total Environment 663*: 830–840. https://doi.org/10.1016/j.scitotenv.2019.01.383
42. Zanin, M., Palomares, F., Brito, D. 2015. The jaguar's patches: Viability of jaguar populations in fragmented landscapes. *J Nat Conserv 23*: 90–97. https://doi.org/10.1016/j.jnc.2014.06.003
43. Harika, T.L., Al-Ghanim, K.A., Riaz, M.N., Krishnappa, K., Pandiyan, J., Govindarajan, M. (2023). Fishing cat scats as a biomonitoring tool for toxic heavy metal contamination in aquatic ecosystems. *Toxics 11*(2): 173. https://doi.org/10.3390/toxics11020173
44. Riley, S.P.D., Bromley, C., Poppenga, R.H., Uzal, F. a., Whited, L., Sauvajot, R.M., Service, N.P., Monica, S.. (2007). Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. *Journal of Wildlife Management 71*(6): 1874–1884. https://doi.org/10.2193/2005-615
45. Serieys, L.E.K., Armenta, T.C., Moriarty, J.G., Boydston, E.E., Lyren, L.M., Poppenga, R.H., Crooks, K.R., Wayne, R.K., Riley, S.P.D. (2015). Anticoagulant rodenticides in urban bobcats: exposure, risk factors and potential effects based on a 16-year study. *Ecotoxicology 24*(4): 844–862. https://doi.org/10.1007/s10646-015-1429-5
46. Serieys, L.E.K., Lea, A.J., Epeldegui, M., Armenta, T.C., Moriarty, J., Vandewoude, S., Carver, S., Foley, J., Wayne, R.K., Riley, S.P.D., Uittenbogaart, C.H. (2018). Urbanization and anticoagulant poisons promote immune dysfunction in bobcats. Proceedings of the *Royal Society B: Biological Sciences 285*(1871). https://doi.org/10.1098/rspb.2017.2533
47. Abdukadir, A., Khan, B., Masuda, R., Ohdachi, S. (2010). Asiatic wild cat (*Felis silvestris ornata*) is no more a 'Least Concern' species in Xinjiang, China. *Pakistan Journal of Wildlife 1*(2): 57–63. http://hdl.handle.net/2115/49688
48. Ghoddousi, A., Hamidi, A.K., Ghadirian, T., Assadi, S.B. (2016). The status of wildcat in Iran – a crossroad of subspecies. *Cat News S 10*: 60–63.
49. Smith, N.J.H. (1976). Spotted cats and the Amazon skin trade. *Oryx 13*(4): 362–371. doi:10.1017/S0030605300014095
50. Kamler, J.F., Stenkewitz, U., Sliwa, A., Wilson, B., Lamberski, N., Herrick, J.R., Macdonald, D.W. (2015). Ecological relationships of black-footed cats (*Felis nigripes*) and sympatric canids in South

Africa. *Mammalian Biology 80*: 122–127. https://doi.org/10.1016/j.mambio.2014.11.004

51. LaBarge, L.R., Evans, M.J., Miller, J.R.B., Cannataro, G., Hunt, C., Elbroch, L.M. 2022. Pumas (*Puma concolor*) as ecological brokers: a review of their biotic relationships. Mamm Rev 52(3): 360–376. https://doi.org/10.1111/mam.12281
52. Sarasola, J.H., Zanón-Martínez, J.I., Costán, A.S., Ripple, W.J. (2016). Hypercarnivorous apex predator could provide ecosystem services by dispersing seeds. *Sci Rep 6*(1): 19647. https://doi.org/10.1038/srep19647
53. Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U. (2015). What is an apex predator? *Oikos 124*(11): 1453–1461. https://doi.org/10.1111/oik.01977