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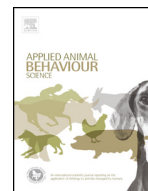
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A standardized ethogram for the felidae: A tool for behavioral researchers

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ABSTRACT

Standardized ethograms offer many practical benefits to behavioral researchers, and several examples exist today for various species and taxa. Despite historic evidence that suggests the family Felidae share similar behavioral repertoires, no standardized ethogram providing comprehensive behavioral definitions exists. In order to create a working ethogram for the Felidae, we conducted a thorough literature review of published articles and books containing behavioral definitions designed for felid species. A total of 95 documents qualified for inclusion, and each was evaluated to identify the terminology used in its behavioral definitions, along with any categorization implemented. The articles included the behaviors of 30 species and 40 subspecies of felids, with the most frequent single study species being the domestic cat (*Felis catus*), followed by several “big cats”. The results were organized into the following mutually exclusive groups for comparison: domestic cat studies, big cat studies, and small cat studies excluding domestic cats (i.e. small exotic cats). Systematic review of definitions confirmed that researchers tend to define felid behavior in similar manners, although some divergence was found between the inclusion of behaviors in domestic and exotic (non-domestic) cat studies. Information from the literature review was used to create a standardized, universal ethogram for use in future felid behavioral studies. The final ethogram suggests the use of “base behaviors” which can be altered using pre-defined modifiers in order to accommodate the requirements of individual studies while retaining consistent terminology. Common behavioral categories are also defined, and suggestions of behaviors that qualify within each category are presented to further assist researchers when developing their study. The ethogram was designed to be user-friendly with clear definitions for each behavior, which should be coherent to a diverse range of observers. We anticipate that use of this ethogram will save researchers time and effort in creating behavioral definitions for their study, while also assisting in unifying felid behavioral research.

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1. Introduction

Ethograms permit the accurate documentation and measurement of observed behaviors, thus, their construction is of fundamental importance in the design of any ethological study (Jennings, 1906; Lorenz, 1973; Tinbergen, 1959, 1963). Typically, ethograms consist of a list of behaviors exhibited by a species, with corresponding

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definitions of each using descriptive terms and phrases (Martin and Bateson, 2007). Although ethogram development is a common research technique, the variation in behavioral definitions across studies can cloud the literature, making comparisons difficult.

Most researchers only develop partial ethograms with regard to the specific needs of their study (Martin and Bateson, 2007). While more comprehensive ethograms may be utilized, their extended length may exclude them from publication, as space is limited in many scholarly journals. Consequently, instead of a study-by-study incremental gain in knowledge, individual studies often remain disconnected, limiting the advancement of beneficial knowledge for a species. Standardization of behavioral terminology within ethograms could help alleviate this issue by increasing inter-observer reliability, giving researchers more confidence that observed behaviors were consistent between studies.

An effort to create a standardized ethogram for all animal species by Schleidt et al. (1984) was met with opposition (see Drummond, 1985; Gordon, 1985; Leonard and Lukowiak, 1985), however, many attempts have been made to develop species- and taxon-specific ethograms (e.g. equids: McDonnell, 2003; common marmoset [*Calithrix jacchus jacchus*]: Stevenson and Poole, 1976; domestic cat [*Felis catus*]: U.K. Working Cat Behaviour Group [UKCBWG] (1995); coyote [*Canis latrans*]: Way et al., 2006). Additionally, there has been a recent push by academic and zoo communities to promote consistent ethogram use. Established in 2006, the “Ethogram Archive Project” has resulted in the web-based tool, EthoSearch (www.ethosearch.org), which serves as a repository for ethograms submitted by different authors (Ross et al., 2010). Similarly, “Etho-Trak” (www.brookfieldzoo.org/pgpages/pagegen.71.aspx), a PDA-based software system, allows individuals at participating zoos to use standardized terminology to collect and share basic behavioral data on their animals (Atsalis et al., 2005). Standardized ethograms may be especially beneficial for captive populations where behavioral issues often affecting reproduction and welfare exist (Clubb and Mason, 2003). With the assistance of Taxon Advisory Groups (TAGs) through the Association of Zoos and Aquariums (AZA) and the European Association of Zoos and Aquaria (EAZA), these ethograms could become easily circulated among members, encouraging the collection of behavioral information within and between institutions.

Although their phylogeny is still debatable, the family Felidae is typically regarded as consisting of one domestic and 36 exotic, or “non-domestic” species (O’Brien and Johnson, 2007). With the exception of size and pelage, all modern felids are remarkably similar in terms of morphology, as the constraints of being an ambush predator has limited the adaptive radiation of this family (Kitchener et al., 2010). Most felid species are solitary, with the exception of lions (*Panthera leo*) and a few other species that form less conspicuous groups, such as domestic cats and cheetahs (*Acinonyx jubatus*) (Macdonald et al., 2010a). Historic information on felids suggests that while some variation exists in vocalizations and hunting strategies (Leyhausen, 1979), felids share very similar behavioral repertoires (Bradshaw and Cameron-Beaumont, 2000; Estes, 1991;

Ewer, 1973; Kitchener, 1991; Leyhausen, 1979; Macdonald, 1992; Sunquist and Sunquist, 2002; Wemmer and Scow, 1977), making this family an excellent candidate for standardized ethogram development. Furthermore, while animals born and reared in captivity may be behaviorally distinct from their wild counterparts (Carlstead, 1996), captive studies have shown that different species of exotic felids exhibit very similar behaviors to each other, as well as to their domesticated relatives (Cameron-Beaumont, 1997).

While a standardized ethogram has been developed for use in domestic cat studies (UKCBWG, 1995), and efforts to promote standardized behavioral research (Mellen, 1988; Szokalski et al., 2012) and personality studies (Gartner and Weiss, 2013) on exotic felids have been made, no general ethogram exists for exotic felids. As the majority of exotic cats warrant conservation concern (International Union for Conservation of Nature [IUCN], 2014), advancing our knowledge of their behavior has important implications not only for their survival in the wild, but also for their management in captivity. Indeed, the AZA’s Felid TAG has identified a universal felid ethogram as a priority to help standardize felid behavior and personality research (Felid TAG, 2011). By implementing a new approach to ethogram development, whereby the universal ethogram draws upon existing behavioral terminology, we estimate that researchers may be more willing to adopt the final product for their own use. Thus, the aim of this study was to conduct a review of the literature on felid behavior and create a universal ethogram for the family Felidae.

2. Methods

Two phases of research were necessary to achieve the goals of this study. First, a literature review facilitated the collection of felid ethograms, which were analyzed for similarities and differences as described below. This motivated the second stage, which involved construction of the final ethogram for practical use. Sufficient rigor during this process should give confidence to researchers when adopting appropriate felid behavioral terminology and definitions, and when selecting which behaviors to be measured in their study.

Some differences in felid behavior, such as in reproduction, hunting, and vocalizations, are often related to differences between species grouped as “big cats” or “small cats” (e.g. Leyhausen, 1979; Peters and Hast, 1994). Therefore, for the purpose of this review, the big cats were defined as those included within the Pantherinae (*Panthera* and *Neofelis*), while small cats are considered to be those in the Felinae (*Acinonyx*, *Caracal*, *Felis*, *Leopardus*, *Lynx*, *Otocolobus*, *Pardofelis*, *Prionailurus*, and *Puma*) as according to Johnson et al. (2006). Additionally, the process of domestication forced cats to co-exist in higher densities with one another and with humans, resulting in intra- and interspecific communication signals that may be absent in exotic felids (Bradshaw and Cameron-Beaumont, 2000). As a consequence of these two factors, the data were organized into the following mutually exclusive groups for comparison:

domestic cat studies, big cat studies, and small cat studies excluding domestic cats (i.e. small exotic cats).

2.1. Literature review

Searches were conducted using several academic databases (Science Direct, Scopus, Springer Link, Web of Knowledge, and Wiley Online Library), as well as Google Scholar. Separate searches were conducted for each felid genus recognized by [Wilson and Reeder \(2005\)](#) and [Johnson et al. \(2006\)](#), along with the truncation of the word ethogram ([Table 1](#)). Terms were entered in the most general search field, which differed between databases (e.g. “topic”, “all fields”, “with all of the words”). In any instance where an author gave reference to another source in the construction of their ethogram, that reference was sought out from the literature and considered for inclusion in the review. Additionally, each document found in the searches that met inclusion criteria ([Table 2](#)) was then searched for in Google Scholar to discover if it had been cited by more recent articles, and if not already included, these articles were considered for inclusion as well. Ethograms stored on the EthoSearch database were also reviewed, and ethograms that pertained to any felid species were selected for consideration. Lastly, authors were periodically contacted for copies of their articles, and if the authors provided additional articles that were not requested nor initially found during the searches, these articles were also considered for inclusion.

Data were collected by systematically recording information from each document, including: reference information (e.g. source, title, authors, year), study type, study species, behavioral categories (if applicable), behavior titles, definitions (if applicable), degree of definition completeness, and the originality of the ethogram (i.e. if the author[s] referenced other sources in the completion of their ethogram or not). Each behavioral definition obtained was deconstructed into its most significant components by separating out mutually exclusive descriptive words and phrases. These descriptive components, usually comprised of physical characteristics, were included as separate entries within each corresponding behavior. Similarly, if the behaviors were categorized in some manner within an article, the behavioral category was also recorded with its corresponding behavior title.

2.2. Construction of universal ethogram

In order to construct a universal ethogram based upon the information gathered in the literature review, all behaviors and behavioral definitions were condensed and organized into a practical catalog. Next, useful behavioral categories were established, and all final behaviors were placed into categories based upon their use within the literature.

2.2.1. Pooling titles and selecting behaviors

Equivalent behaviors and behavioral categories with differing titles but describing similar phenomena were identified and pooled under a single, universal title. The universal title was selected by considering the frequency

of each behavior's title within the review, the exclusivity and clarity of the titles, and the accuracy of the title when compared to historical accounts of the behavior. For example, the behavior “alogroom” appeared within ethograms 15 times, while many similar behaviors existed in smaller frequencies, which described the same phenomenon (i.e. “cat grooms” [$N=1$], “groom” or “grooming” [$N=3$], “groom conspecific” [$N=1$], “groom other cat” [$N=2$], “social groom” [$N=6$], and “social licking” [$N=2$]). After analysis of each term, we determined that “alogroom” would be selected for a single, universal title of this behavior.

After titles of all the behaviors were pooled, the process of selecting which behaviors were to be included on the final ethogram began. Initially, any behavior with a frequency <2 was excluded, as these behaviors were not present on multiple ethograms and thus provided no evidence suggesting that they could be shared between groups of species. However, because the omission of behaviors from an ethogram in a particular study could be due to the objective of the study, rather than imply the absence of the behavior in the study species's repertoire, all behaviors were reviewed on an individual basis before exclusion from the final ethogram.

Next, a threshold was determined within each species group (i.e. domestic, big, or small exotic cat) by identifying behaviors used in at least 10% or more of studies for each group. Pairwise comparisons were then performed to determine the extent that behaviors were shared between species groups. Additionally, the proportion of studies in which a particular behavior occurred was calculated for each species group. For instance, if the behavior “alogroom” occurred in 10% of studies on big cats, that behavior was allocated a score of 0.1. These proportions were cast into a matrix of behavior by species group and hierarchical cluster analysis (Euclidean distance measure, Ward's linkage method) was implemented using RStudio 0.98.1028 ([RStudio, 2012](#)).

2.2.2. Defining and categorizing behaviors

Defining behaviors was accomplished by identifying which physical characteristics were essential to each behavior, and how they were best communicated. The descriptive components of these physical characteristics were evaluated with regard to their meaning, clarity, and ability to accurately communicate what the animal is doing, as well as the frequency of their use. Additional historic sources of information on felids were frequently consulted in order to verify the descriptions of the behaviors and investigate any species-specific tendencies, including: [Bradshaw \(1992\)](#), [Estes \(1991\)](#), [Ewer \(1973\)](#), [Kitchener \(1991\)](#), [Leyhausen \(1979\)](#), [Macdonald and Loveridge \(2010\)](#), [Sunquist and Sunquist \(2002\)](#), [Turner and Bateson \(2000\)](#), and [Wemmer and Scow \(1977\)](#).

Selection of useful behavioral categories began by identifying the 20% most commonly used in the literature reviewed ($N=22$). For clarity, behavioral categories were defined based on descriptions provided, and additional sources ([Barrows, 2011](#); [Immelmann and Beer \(1989\)](#); [oxforddictionaries.com](#)) when necessary.

Table 1

Number of hits resulting from the literature search protocol.

Search Terms	Google scholar	Science direct	Scopus	Springer link	Web of knowledge	Wiley online library	Genus totals
"Ethogram" AND "Acinonyx"	88	19	10	2	0	17	136
"Ethogram" AND "Caracal"	16	2	0	2	0	1	19
"Ethogram" AND "Catopuma"	1	0	0	0	0	0	1
"Ethogram" AND "Felis"	271	83	34	12	1	44	445
"Ethogram" AND "Leopardus"	46	10	3	2	1	5	67
"Ethogram" AND "Leptailurus"	7	1	1	0	1	1	11
"Ethogram" AND "Lynx"	117	11	0	7	0	14	149
"Ethogram" AND "Otocolobus"	6	0	0	0	0	0	6
"Ethogram" AND "Pardofelis"	4	0	0	0	0	0	4
"Ethogram" AND "Prionailurus"	14	0	0	0	0	3	17
"Ethogram" AND "Profelis"	2	1	0	0	0	1	4
"Ethogram" AND "Puma"	69	8	4	4	0	15	100
"Ethogram" AND "Neofelis"	29	3	1	0	0	4	37
"Ethogram" AND "Panthera"	255	45	21	7	1	33	362
"Ethogram" AND "Uncia"	27	3	0	2	0	8	40
Search engine totals	946	186	74	36	4	146	1398

3. Results

3.1. Literature review

The primary search resulted in a total of 1398 initial hits. After the removal of duplicates and thorough review of each result, 95 documents qualified for final analysis (see Appendix A), including 83 articles from peer-reviewed journals, 10 student theses, and two ethograms published in books (Fig. 1). There were 15 authors contacted directly to request copies of their work, eight of whom responded, leading to the addition of five articles. A total of 40 ethograms on felids existed in the [EthoSearch](#)

database (as of July 2012), 37 of which were duplicates already found as a result of the primary searches. The remaining three ethograms were excluded as two were not published in English, while the third lacked appropriate reference material which, after further investigation, led to the conclusion that it had not been previously peer-reviewed.

The majority of empirical studies conducted ($N=91$) were performed in captive settings ($N=80$), while the remaining were conducted in the wild ($N=11$). While some studies had multiple research objectives (e.g. enrichment and reproduction: [Mollá et al., 2011](#)), the majority of studies involving exotic cats focused on either enrichment

Table 2

Inclusion and exclusion criteria applied to each article found in literature search results.

Criteria	Description
Inclusion	
<i>Ethogram</i>	The article must have contained either an ethogram, or a list of behaviors recorded, in either a tabular form or included within its text.
<i>Relevant species</i>	The ethogram within an article must have pertained to at least one member of the Felidae family. Articles containing multiple species (felid or otherwise) were included, so long as the behaviors listed apply to at least one Felidae member.
<i>Publication</i>	Articles must have been published in a peer-reviewed journal. Post graduate theses (contributing toward the completion of a Master's or Post-Doctoral degree) were also included, so long as the quality of their behavioral descriptions was apparent.
<i>English language</i>	Articles must have been either published in English, or have been translated reliably.
Exclusion	
<i>Irrelevant species</i>	Articles that discussed felid behavior but solely in comparison to non-felid subjects without a felid-specific ethogram were excluded.
<i>Failure to list behaviors</i>	Articles that reference previous ethograms but failed to list any of the behaviors recorded in their study were excluded. Additionally, any study that described felid behavior yet did not provide a title for said behavior was excluded (e.g. Cat-Stress-Score; Kessler and Turner, 1997).
<i>Veterinary manipulations</i>	Studies that examined the behaviors of subjects after the application of veterinary procedures or medications, whereby the behaviors recorded were specific to the treatment administered, were excluded. However, if some of the behaviors recorded were identified by the article's author(s) as existing within the natural repertoire of the species, these behaviors were included.
<i>Author duplications</i>	In the case where multiple articles written by the same author(s) listed the same behaviors, only one of the articles will be included in the study to avoid pseudoreplication.
<i>Books</i>	Books that described felid behavior at length were not included in the review, however they were consulted when constructing the final ethogram.
<i>Hunting</i>	Due to the species-specific variation in hunting behavior (Leyhausen, 1979), articles that described behaviors associated with the take down of prey at length were not included.
<i>Unavailability</i>	Articles were subject to availability through university, colleague, and general internet access, as well as direct communication with the author(s). If an article could not be obtained through one of these avenues, due to resource availability, it was excluded.

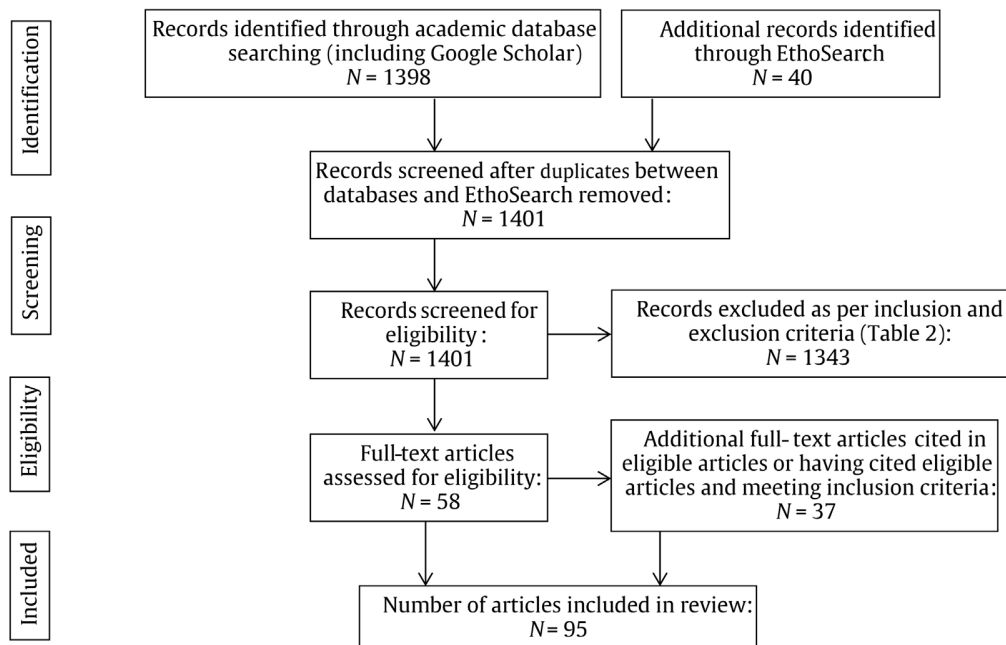


Fig. 1. Flow of article evaluation in order to obtain relevant felid ethograms.

Table 3
Frequencies of study-type with regard to domestic and exotic cat subjects.

Study Type	Domestic	Exotic	Domestic and exotic
Activity Budget	0	16	0
Enrichment	4	23	0
Model	1	2	1
Reproductive	0	6	0
Social	18	7	2
Temperament	3	2	0
Veterinary	2	1	0
Behavior (other)	3	4	0
Total	31	61	3

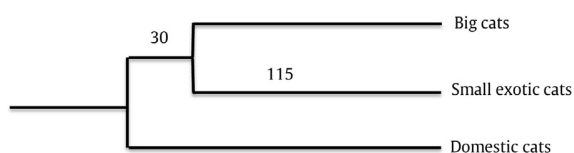


Fig. 2. Hierarchical cluster analysis showing three distinct groups classified as big, small exotic, and domestic cats. Behaviors analyzed were those identified within a 10% threshold for all groups. Hierarchical cluster analysis, measure; complete linkage (branch lengths not to scale).

practices ($N=23$) or building activity budgets ($N=16$). In contrast, research investigating social behaviors ($N=18$) was most common in domestic cat studies (see Table 3). Cluster analysis of the behaviors included on each ethogram collected revealed that big and small exotic cat ethograms were more similar to each other than either was to domestic cat ethograms (Fig. 2).

The articles included a total of 30 species and 40 sub-species of felids (see Fig. 3). The most frequently occurring species was the domestic cat ($N=31$), followed by several

big cat species (tiger [*Panthera tigris*] [$N=17$]; lion [$N=12$]; snow leopard [*Panthera uncia*] [$N=9$]; leopard [*Panthera pardus*] [$N=8$]) and the cheetah ($N=9$) (see Table 4). Together, articles on these five exotic species appeared in over half of the total articles ($N=55$). A total of eight multi-species studies utilized a single ethogram for subjects within the same genus, while the remaining studies ($N=10$) included study subjects from at least two genera.

3.2. Construction of universal ethogram

In regards to the originality of definitions, 56 studies had created their own ethogram, while 39 cited at least one other source in the creation of their ethogram. In terms of definitions provided, 51 studies offered definitions for every behavior listed, 30 studies offered partial definitions (i.e. some behaviors were defined while others were simply listed, or defined as: “as implied”), and 15 studies listed behaviors without providing any definitions. The majority of studies included a single species ($N=77$), while the rest employed a single ethogram for observation of multiple species ($N=18$).

A total of 575 single behaviors were collected from the articles. Over half of the behaviors ($N=347$) were found once, and not repeated within any other study. However, despite the variety of definitions created for each behavior, initial review proved many behaviors to be extremely similar, even across different species. For example, different terms would often be used to describe the same part of the body (e.g. back legs, hind legs, rear legs) or certain environmental factors (e.g. floor, ground, substrate). Further examination also revealed many definitions to be variations of other behaviors, differing by method of behavioral description (e.g. structure or consequence: Hinde, 1970;

Table 4

Total number of articles containing each felid species which qualified for inclusion in this study.

Species	Common name	Total
Domestic cat lineage		52
<i>Felis catus</i>	Domestic cat	34
<i>Felis silvestris</i>	European wild cat	7
<i>Felis libyca</i>	African wild cat	1
<i>Felis bieti</i>	Chinese desert cat	0
<i>Felis margarita</i>	Desert cat	3
<i>Felis nigripes</i>	Black-footed cat	3
<i>Felis chaus</i>	Jungle cat	4
Leopard cat lineage		11
<i>Octocolobus manul</i>	Pallas cat	2
<i>Prionailurus rubiginosus</i>	Rusty spotted cat	2
<i>Prionailurus bengalensis</i>	Asian leopard cat	3
<i>Prionailurus viverrinus</i>	Fishing cat	4
<i>Prionailurus planiceps</i>	Flat-headed cat	0
Puma lineage		13
<i>Puma concolor</i>	Puma	3
<i>Puma yagouaroundi</i>	Jaguarundi	1
<i>Acinonyx jubatus</i>	Cheetah	9
Lynx lineage		9
<i>Lynx pardinus</i>	Iberian lynx	0
<i>Lynx lynx</i>	Eurasian lynx	4
<i>Lynx canadensis</i>	Canada lynx	3
<i>Lynx rufus</i>	Bobcat	2
Ocelot lineage		17
<i>Leopardus pardalis</i>	Ocelot	4
<i>Leopardus wiedii</i>	Margay	4
<i>Leopardus jacobita</i>	Andean mountain cat	0
<i>Leopardus colocolo</i>	Pampas cat	1
<i>Leopardus geoffroyi</i>	Geoffroy's cat	5
<i>Leopardus guigna</i>	Kodkod	0
<i>Leopardus tigrinus</i>	Tigrina	3
Caracal lineage		7
<i>Caracal caracal</i>	Caracal	3
<i>Caracal aurata</i>	African golden cat	1
<i>Caracal serval</i>	Serval	3
Bay cat lineage		1
<i>Pardofelis badia</i>	Bay cat	0
<i>Pardofelis temminckii</i>	Asian golden cat	1
<i>Pardofelis marmorata</i>	Marbled cat	0
Panthera lineage		54
<i>Panthera leo</i>	Lion	12
<i>Panthera onca</i>	Jaguar	4
<i>Panthera pardus</i>	Leopard	8
<i>Panthera tigris</i>	Tiger	16
<i>Panthera uncia</i>	Snow leopard	9
<i>Neofelis nebulosa</i>	Clouded leopard	5

spatial relation: Martin and Bateson, 2007), and/or by the employment of modifiers.

In regards to behaviors with a frequency ≥ 2 ($N = 228$), the majority occurred between at least two or three species groups ($N = 159$). Of the multiple species studies ($N = 18$), all used a single ethogram despite the fact that some of these studies included domestic and exotic ($N = 3$), big and small exotic ($N = 5$), or felid and non-felid ($N = 2$) species.

3.2.1. Pooling titles and selecting behaviors

After similar behavioral titles were combined, the total number of behaviors decreased from 575 to 447 (22% reduction), and 164 of these behaviors had a frequency ≥ 2 . This included two non-behavioral entries (e.g. "other" and "out of sight"), which serve as alternatives that could be scored on a working ethogram.

From this list of 164, behaviors occurring in at least 10% of studies for each species group were identified. Domestic cats had the highest number of mutual behaviors occurring within this threshold ($N = 66$), followed by big cats ($N = 38$), and then small exotic cats ($N = 33$). Pairwise comparisons revealed that of those behaviors with a frequency ≥ 2 ($N = 164$) occurring in ethograms across all studies in this review, 69 behaviors occurred in all three mutually-exclusive species groups, and 45 occurred within at least two species groups (see Appendix B). This left 47 occurring in just one single group, and three behaviors ("snap bite", "sniff nose", and "tail under") that only occurred in multi-group studies.

Behaviors that occurred in at least two or three species groups and were within the 10% threshold ($N = 79$) were included in the final ethogram, as we deemed their communal use a fair representation of the studies within the review. Behaviors that occurred in less than 10% of the studies, but had a frequency ≥ 2 ($N = 85$), as well as those with a frequency of 1 ($N = 283$), were reviewed on an individual basis. Many of these were selected for inclusion based upon their relevance and adaptability for multiple species ($N = 18$). Additionally, the behaviors "head-rolling", "ground slapping", and "self-mutilation", although never included in any articles, were also added to the ethogram as they have been discussed in the literature elsewhere (e.g. Eaton, 1971; Shyne, 2006).

3.2.2. Defining and categorizing behaviors

Many behaviors may be performed using similar body movements, despite the difference in context. The repetitive use of certain modifiers (i.e. words which change or clarify the description of a behavior) within the ethograms in this review suggested that creating standardized definitions of both "base behaviors" and "modifiers" would provide flexibility for researchers wishing to clarify the context of the behaviors without sacrificing consistency between studies. Thus, three different categories of modifiers (Table 5) were created for use in conjunction with definitions of base behaviors (Table 6) for further clarification. *General modifiers* define possible items that a cat may come into contact or interact with ("cat", "human", "object", or "surface"). *Status modifiers* communicate the social status of the individual, even if the cats are not actually interacting with one another ("social" or "solitary"). *Dispositional modifiers* were defined to specify the individual's state of attention, and to distinguish between behaviors performed with playful versus serious intent ("alert", "rest", or "play").

For behavioral categories, once titles were combined, the total number decreased from 113 to 101 (11% reduction). Each of the 20% most commonly used behavioral categories ($N = 22$) were reviewed and, after the pooling of titles, the categories "play", "rest", "social", and "solitary", were removed and reassigned as the modifiers mentioned above. Additionally, while "Calm" fell outside the top 20%, we determined it was an appropriate category for relaxed behaviors, thus was added to the list. The final behavioral categories selected for inclusion on the final ethogram include: Active, Affiliative, Aggressive, Agonistic, Calm, Exploratory, Fear, Feeding, Inactive,

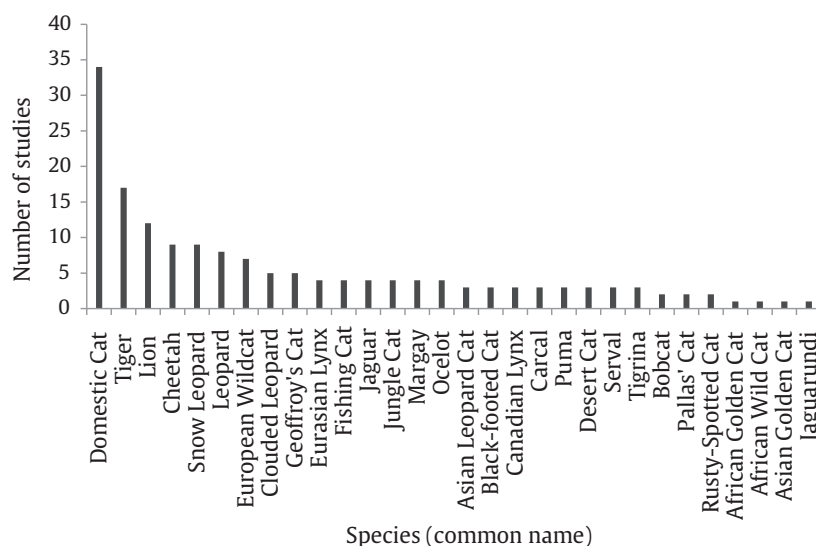


Fig. 3. Number of articles containing felid species subjects which qualified for inclusion in this study. Species are arranged by highest frequency, then follow alphabetical order when occurring in equal amounts.

Table 5

Descriptions of modifiers to be used in conjunction with base behaviors.

Modifier	Description
General	
<i>Cat</i>	Another individual of the same species (i.e. conspecific). Additional information can be provided to explain the relationship between individuals by labeling the cat using broad titles (e.g. "mother," "new individual," "breeding partner," "offspring"). The common name for the study species can be used in lieu of "cat."
<i>Human</i>	Any human involved with the study. For additional clarity, broad titles for caregivers can be used (e.g. "observer," "keeper," or "owner").
<i>Object</i>	Any object the cat appears focused on and/or is in contact with. For additional clarity, broad titles for objects can be used (e.g. "branch," "mesh," "ball").
<i>Surface</i>	Any external surface that the cat appears focused on and/or is in contact with, whether it is horizontal or vertical.
Status	
<i>Social</i>	Cat is in close proximity of another individual. ^a
<i>Solitary</i>	Cat is alone.
Dispositional	
<i>Alert</i>	Cat is vigilant and attentive to surroundings, with eyes open, ears forward, mouth closed or slightly open, and head up. Cat's eyes may be focused in a specific direction, or scanning the area accompanied by head and possibly ear movement.
<i>Rest</i>	Cat is stationary and generally inactive, typically in a lying or sitting posture. Eyes may be closed or open, and head may be up or down and performing minimal movement.
<i>Play</i>	Cat is performing a behavior in a "non-serious" or playful manner (Recommended for use when distinguishing between affiliative and aggressive or agonistic social interactions). Observer must have certainty that the cat has no intention to harm. May look for facial expressions indicating play, such as mouth slightly open without showing teeth, ears and eyes appear relaxed or fairly alert (Estes, 1991).

^a Close proximity may be subject to experimental conditions, however it would typically imply that the cats are within one or two body lengths of each other.

Locomotion, Maintenance, Marking, Reproductive, Stereotypic and Vocalization (Table 7). Base behaviors that were previously categorized in the literature reviewed were maintained within those categories. Additional behaviors not categorized by ethograms in this review were placed within categories based on historic felid literature referenced previously (for more detailed information and suggestions for use see Guidelines for Ethogram Use in the online [supplementary material](#)).

3.2.3. Vocalizations

A range of vocalizations were captured on ethograms during this review, although their frequencies were very low in most cases. While felids employ a range of close, medium and long-distance acoustic signals, they are all

said to share a basic repertoire of vocalizations (e.g. Peters, 2002; Sunquist and Sunquist, 2002). Therefore, it was determined that vocalizations which appeared commonly on ethograms within the review, as well as most of the vocalizations included in the literature on felids (Bradshaw and Cameron-Beaumont, 2000; Peters, 2002; Peters et al., 2009; Sunquist and Sunquist, 2002) would be defined and are included on the final ethogram (Table 8).

4. Discussion

4.1. Trends in felid behavioral studies

The literature review suggested that a trend toward selecting certain species as study subjects exists. Out of the

Table 6

A standardized ethogram for the Felidae including definitions for all base behaviors. Definitions are provided for all words listed in bold font.

Title	Definition
Allogroom	Cat licks the fur of another cat's head or body.
Arch back	Cat curves back upwards and stands rigidly.
Approach	Cat moves toward (modifier) while looking at it.
Attack	Cat launches itself at (modifier) with extended forelegs and attempts to engage in physical combat.
Avoid	Cat moves, or changes direction while moving, in order to keep away from (modifier).
Bare teeth	Cat opens its mouth slightly while pulling lips back to expose teeth.
Bite	Cat snaps teeth at and is successful in biting (modifier).
Body rub ^a	Cat rubs any part or entire length of body against (modifier).
Body shake	Cat rotates its abdomen from side to side.
Carry	Cat picks (modifier) up off the ground and moves it to another location.
Charge	Cat rushes toward (modifier).
Chase	Cat runs rapidly in pursuit of (modifier).
Chew	Cat grinds an object in its mouth using the teeth.
Clawing	Cat drags front claws along an object or surface, likely leaving visual marks behind.
Climb	Cat ascends and/or descends an object or structure.
Copulation	Male mounds female and intromission is achieved.
Crouch	Cat is alert and positions the body close to the ground, whereby all four legs are bent, and the belly is touching (or raised slightly off of) the ground.
Cuff	Cat strikes at (modifier) with forepaw and contact is made. Claws are usually extended.
Defecate	Cat releases feces on the ground while in a squatting position.
Dig	Cat breaks up or moves substrate around with its paws.
Displace	Cat provokes an avoidance behavior from another cat.
Drag	Cat moves (modifier) from one location to another without picking it up off the ground.
Drink	Cat ingests water (or other liquids) by lapping up with the tongue.
Ears back	Ears are held at the rear of head (UKCBWG, 1995).
Ears erect	Cat points its ears upward (UKCBWG, 1995).
Ears flat	Cat flattens its ears to its head, so that they tend to lie flush with the top of the head (UKCBWG, 1995).
Ears forward	Ears are held at the front of head (UKCBWG, 1995).
Eat	Cat ingests food (or other edible substances) by means of chewing with the teeth and swallowing.
Excess salivation	Cat salivates heavily.
Explore	Cat moves around attentively while sniffing the ground and/or objects.
Fight	Cat engages in physical combat with another cat.
Flehmen	Cat makes a grimaced facial expression, where the mouth is open, upper lip is elevated, and tongue may protrude out of the mouth.
Flee	Cat runs away from (modifier).
Flinch	Cat approaches and/or sniffs (modifier), but abruptly stops and retreats or flees from (modifier).
Flirting run	Female cat feigns running away from a breeding partner.
Forage	Cat searches for food or other edible substances.
Follow	One cat travels closely behind (modifier).
Freeze	Cat suddenly becomes immobile with body tensed (UKCBWG, 1995).
Fur-plucking	Cat excessively grooms a specific area of its body. This can include any tail- and paw-sucking actions. May result in the removal and visible loss of fur, as well as skin irritation.
Groom	Cat cleans itself by licking, scratching, biting or chewing the fur on its body. May also include the licking of a front paw and wiping it over one's head.
Groom (anogenital)	Cat grooms its own genitals.
Ground slapping	Cat slaps its front paws or stomps its feet against the ground.
Head butt	Cat briefly pushes its head against (modifier).
Head-rolling	Cat tosses its head in a circular motion.
Head rub ^a	Cat rubs its head against (modifier).
Head shake	Cat rotates head from side to side.
Hiding	Cat occupies a location away from a specific stimulus (or modifier).
Hind feet scraping	Cat scrapes hind feet on the ground in a backwards direction, shuffling one foot after the other.
Huddling	Cat is at rest , lying or sitting with body in contact with (modifier).
Hunt	Cat actively pursues live prey. Includes movements such as crouching , stalking , or any other species-specific behavior.
Investigate	Cat shows attention toward a specific stimulus by sniffing and/or pawing at it.
Intromission	The male's penis enters the female's vagina.
Jumping	Cat leaps from one point to another, either vertically or horizontally.
Kneading	Cat pushes forepaws into the ground or (modifier) in a rhythmic, kneading motion.
Kill bite	Cat delivers a strong bite to (modifier), that which may be equal to a bite used to take down and kill prey.
Lick	Cat's tongue protrudes from mouth and strokes (modifier).
Lordosis	Female cat raises hindquarters while lowering forequarters to the ground, presenting genitals to male. Tail is often averted to one side. The position is sometimes accompanied by treading of the hind legs.
Lying	Cat's body is on the ground in a horizontal position, including on its side, back, belly, or curled in a circular formation.
Manipulate object	Cat uses any part of body to touch, hold, move, or pick up, an object.
Mount	A male cat attempts intromission by straddling over the female with front and hind feet. In "small" cats, this may be accompanied by a nape bite and/or treading movements of the hind feet.
Nape bite (small and domestic cats)	The male grips the back of the neck of a female with his mouth while mounting , and may continue holding on during copulation .

Table 6 (Continued)

Title	Definition
Nape bite (big cats; including but not limited to <i>Panthera</i> spp.)	The male performs an inhibited nape bite , where he will place his mouth on or around the back of the female's neck at the moment of, or just after, ejaculation, but is unlikely to actually bite down.
Nursing	A mother cat feeds her offspring, whereby the offspring drink milk from her nipples by placing their mouths around her nipples and suckling.
Nuzzle	Cat moves its entire head and nose side to side against one area of the head or body of another cat (or human).
Other	Any behavior that does not fit into one of the descriptions provided.
Out of sight	Cat is not visible to the observer.
Pacing	Repetitive locomotion in a fixed pattern, such as back and forth along the same route. Can include walking , trotting and running . Movement seems to have no apparent goal or function. Must be performed at least two times in succession before qualifying as stereotypic .
Patrol	Cat is alert and walks around in a calm, deliberate manner, periodically stopping to perform investigative or marking behaviors.
Paw ^a	Cat pats (modifier) with its forepaw(s). Claws are usually retracted.
Pelvic thrust	While in a mounted position, the male makes searching and/or thrusting movements with his pelvic region against the anogenital region of the female.
Piloerection	Cat raises the hairs on the nape of its neck, shoulder, back or tail, so that the fur is standing erect.
Play ^a	Cat interacts with something in a “non-serious” manner (i.e. where there is no intention to harm).
Play roll on back	Cat rolls onto its back, with its belly exposed and all paws in the air, within a playful context. All agonistic behaviors are absent (i.e. hissing , ears back).
Pounce	Cat leaps onto (modifier).
raise paw	Cat lifts its forepaw as if to cuff , paw or strike at (modifier) but does not follow through with the action.
Rake	Cat makes kicking movements with one or both hind legs against (modifier).
Rear	Cat stands up on its hind legs with forelegs toward or against (modifier).
Retreat	Cat backs away from (modifier) while watching it.
Roll ^a	While lying on the ground, cat rotates body from one side to another. During the roll , the back is rubbed against ground, the belly is exposed and all paws are in the air. Cat may continue rolling repeatedly from side to side.
Roll on back	Cat rolls onto its back and becomes stationary, with its belly exposed and all paws in the air. The body is usually tense, and may be accompanied by hissing and ears back .
Running	Forward locomotion in a rapid gait, which is faster than walking or trotting.
Scratching	Cat scratches its body using the claws of its hind feet.
Self-biting	Cat bites or chews on an area of its own body, which may result in damage to the fur or skin.
Self-mutilation	Cat performs any self-injurious behavior (including self-biting and fur-plucking), which may result in a visible loss of hair and skin irritation or abrasion.
Sitting	Cat is in an upright position, with the hind legs flexed and resting on the ground, while front legs are extended and straight.
Sleeping	Cat is lying on the ground with its head down and eyes closed, performing minimal head or leg movement, and is not easily disturbed.
Snap Bite	Cat opens its mouth and snaps it shut, as if biting the air (Cameron-Beaumont, 1997).
Sniff ^a	Cat smells (modifier) by inhaling air through the nose.
Sniff air	Cat inhales air through the nose with its head raised and nose not in close proximity of any particular object or surface.
Sniff anogenital	Cat smells the anogenital region of another cat.
Sniff nose	Two cats smell the nasal regions of each other.
Stalk	Slow, forward locomotion in a crouched position directed toward (modifier), with head kept low and eyes focused on (modifier).
Standing	Cat is in an upright position and immobile, with all four paws on the ground and legs extended, supporting the body.
Stare	Cat gazes fixedly at (modifier) and is not easily distracted. In the case of social stare , gaze may be directed at another cat's eyes.
Stretching	Cat extends its forelegs while curving its back inwards.
Strike At	Cat swipes forepaw at (modifier) but no contact is made.
Swimming	Cat propels itself through water using its legs.
Tail bent-up	Tail is bent in an upward curve (Cameron-Beaumont, 1997).
Tail down	Tail is held down with the end kinked out (Cameron-Beaumont, 1997).
Tail half-up	Tail is held at a 45° angle to the tail up posture, or thereabouts (Cameron-Beaumont, 1997).
Tail over	Tail is bent directly over the body (Cameron-Beaumont, 1997).
Tail parallel	Tail is parallel to the ground, sometimes slightly curved (Cameron-Beaumont, 1997).
Tail quiver	Part of, or the entire tail, is vibrated while raised in the up or half-up position (UKCBWG, 1995; Cameron-Beaumont, 1997).
Tail slap	Cat quickly strikes its tail on the ground (UKCBWG, 1995).
Tail swish	A violent swish of the tail; more rapid than a tail wave but smoother than a tail twitch (Cameron-Beaumont, 1997).
Tail twitch	A rapid flick of the tail in either a side to side or up to down motion (UKCBWG, 1995; Cameron-Beaumont, 1997).
Tail under	Tail is tucked right under the body. This position is normally held whilst the cat is crouching in a defensive manner (Cameron-Beaumont, 1997; Bradshaw and Cameron-Beaumont, 2000).
Tail up	Tail is held in an upright position (Cameron-Beaumont, 1997).
Tail wave	A slow and gentle wave of the tail from side to side (Cameron-Beaumont, 1997).
Threaten	Cat directs aggressive behaviors toward (modifier) without making any physical contact with it.
Touch noses	Two cats sniff at and touch each other with their noses.
Treading	Rhythmic, raising and lowering of paws so that cat is stepping in place.
Trembling	Fine muscle tremor or spasm of the body or legs (Griffith et al., 2000).
Trotting	Forward locomotion at a swift gait performed with alternating steps. Movement is faster than walking but slower than running .

Table 6 (Continued)

Title	Definition
Urinate	Cat releases urine on the ground while in a squatting position.
Urine spray	While standing with tail raised vertically, cat releases a jet of urine backwards against a vertical surface or object. The tail may quiver as urine is discharged.
Urine walk	Cat urinates in standing position, usually combined with walking (Fazio, 2010).
Vocalize	Cat produces sounds or calls, originating from the throat and mouth.
Vomiting	Cat ejects stomach contents out of its mouth.
Walking	Forward locomotion at a slow gait.
Watch	Cat observes a specific stimulus (or modifier).
Wrestle	Cat engages in physical contact with (modifier), whereby the cat struggles with (modifier). Can include pulling (modifier) toward itself with its forelegs and perform raking movements with the hind legs.
Yawn	Cat opens its mouth widely while inhaling, then closes mouth while exhaling deeply.

^a Multiple variations of behavior are possible. The use of modifier(s) to clarify context is especially recommended.

Table 7

Base behaviors that fall within each behavioral category. Definitions for each category are listed in the online supplementary material.

Active	Affiliative	Aggressive	Agonistic	Calm	Exploratory	Fear	
Carry	Anogenital sniff	Attack	Approach	Ears erect	Chew	Avoid	
Clawing	Follow	Bare teeth	Arch back	Groom	Dig	Crouch	
Crouch	Gurgle ^a	Bite	Avoid ^a	Kneading	Drag	Ears back	
Defecate	Head butt ^a	Charge	Bare teeth ^a	Lying ^a	Ears erect	Excess salivation	
Drag	Huddling ^a	Chase	Bite	Purr	Ears forward	Flee	
Drink	Lick	Crouch	Chase	Scratching	Explore	Flinch ^a	
Ears erect (alert)	Nuzzle	Cuff	Cuff	Sitting	Flehmen	Freeze ^a	
Ears forward (alert)	Play	Ears back ^a	Displace	Stretching	Investigate	Groom	
Eat	Prusten ^a	Ears flat	Ears back	Yawn ^a	Lick	Head shake	
Explore	Puff ^a	Fight	Fight		Manipulate object	Hiding	
Fight	Play roll on back ^a	Ground slap ^a	Flee		Paw	Hiss	
Forage	Sniff nose	Growl	Ground slap ^a		Rear ^a	Retreat	
Groom	Social groom/allogroom	Kill bite ^a	Growl		Sniff (any)	Tail under	
Hunt	Social roll	Piloerection	Hiss		Watch ^a	Trembling	
Investigate (all types)	Social rub/allorub	Pounce	Piloerection ^a				
Locomotion (all types)	Social sniff	Rake ^a	Raise paw ^a				
Play	Stutter ^a	Rear ^a	Retreat				
Rear	Tail up ^a	Snarl	Roll on back				
Roll (solitary)	Touch noses	Spit	Snap bite				
Rub (object)		Strike at	Snarl				
Scratching		Tail slap ^a	Social stare				
Sniff (all types)		Tail swish	Strike at ^a				
Allogroom		Tail twitch	Tail over				
Standing		Threaten	Tail under				
Stretching		Yawn ^a	Yowl				
Urinate							
Vocalize							
Wrestle							
Feeding	Inactive	Locomotion	Maintenance	Marking	Reproductive	Stereotypic	Vocalizations
Bite	Groom	Approach	Defecate	Clawing	Allogroom ^a	Fur-plucking	Caterwaul
Carry	Lying	Chase	Drink	Defecate	Anogenital groom ^a	Head-rolling ^a	Chatter
Chase	Sitting	Climb	Eat	Hind feet scraping	Caterwaul ^a	Pacing	Chirp
Chew	Sleeping	Flee	Groom	Solitary Roll	Cheek rub ^a	Self-biting	Copulatory Cry
Drag	Standing	Flirting run ^a	Clawing	Rub (object)	Clawing ^a	Self-mutilation ^a	Growl
Drink	Stretching	Follow	Urinate	Urine Spray	Copulation		Grunt
Eat		Jumping		Urine walk ^a	Copulatory cry ^a		Gurgle
Forage ^a		Pacing			Flirting run ^a		Hiss
Hunt ^a		Patrol ^a			Flehmen ^a		Mew
Kill Bite		Retreat ^a			Intromission		Prusten/chuff
Lick		Running			Lordosis ^a		Puff
Nursing		Stalk ^a			Mount		Purr
Pounce		Swimming ^a			Nape bite		Roar
Sniff		Trotting			Pelvic thrust		Snarl
Stalk		Walking			Social roll ^a		Spit
Vomiting ^a					Stutter ^a		Stutter
					Treading		Wah-wah
					Urine spray ^a		Yowl
					Yowl ^a		

^a Behaviors that the authors have placed in categories based on the general felid literature.

Table 8

List of vocalizations based on felid literature. Although many cats share a number of vocalizations, many species-specific vocalizations exist. While this list is not exhaustive, it contains some of the most commonly referenced and recognizable felid vocalizations, and is encouraged for use and future expansion. Definitions are provided for all words listed in bold font.

Vocalization	Definition	Context	Species
Caterwaul	Loud, drawn out whine. May be similar to the yowl .	Reproductive (female advertisement call)	Bobcat, domestic cat, puma snow leopard
Chatter	Cat rhythmically clashes the jaws, creating a low-amplitude, smacking sound.	When desiring prey which is out of reach; displacement .	Domestic cat, Eurasian lynx
Chirp	A short, high-pitched call described as similar to a bird chirping.	Contact call; used to locate conspecifics; when something is desired.	Cheetah, domestic cat
Copulatory cry	Cry emitted by female cat during successful intromission. In “small cats” it is described as a low, barely audible growl (Mellen, 1993).	Reproductive (female)	Recorded in some small cats (Mellen, 1993), although variations are likely to exist in most (if not all) species.
Growl	A low-pitched, throaty, rumbling noise produced while the mouth is closed.	Aggressive; agonistic	Most (if not all) cats
Grunt	Short, throaty, atonal call.	Calling to cubs; searching for group members; part of roaring sequence	Jaguar, leopard, lion
Gurgle	Short, pulsed sound, described as similar to a person gargling their throat.	Affiliative; friendly; females with kittens	Most (if not all) “small cats”
Hiss	A drawn-out, low-intensity hissing sound produced by rapid expulsion of air from the cat’s mouth, usually during exhalation.	Agonistic	Most (if not all) cats
Mew	The distinctive “meow” call that is typical of cats. Mews can differ considerably between species, and vary in tone, duration, pitch, and structure.	Many (social; reproduction; contact call)	Most (if not all) cats, however sound varies in intensity and differs between species
Prusten (chuff)	Cat expels jets of air through the nose creating a low-intensity, soft, pulsed sound, described as being similar to the snorting of a horse.	Affiliative; friendly	Clouded leopard, jaguar, snow leopard, tiger
Puff	Cat expels short, explosive jets of air through the nose and lips in rapid, rhythmic sequence of 2–4 sounds. Described as a bout of stifled sneezing.	Affiliative; friendly	Leopard, lion
Purr	Low, continuous rhythmical tone produced during respiration while the cat’s mouth is closed. Creates a murmuring sound.	Friendly; contentment	Most (if not all) “small cats”
Roar	High intensity call that differs between species but consists of a “main call” and grunting sounds. In the lion, the call may be described as moaning, full-throated and thundering.	Long distance; contact or spacing call; possibly more	Jaguar, leopard, lion, tiger
Snarl	Cat bares teeth while emitting a sound similar to a growl , however the mouth is open and the sound is usually louder, shorter and higher in pitch than a growl .	Aggressive; agonistic	Most (if not all) cats
Spit	Cat makes a sudden, short, explosive exhalation resulting in a burst of noise and is often accompanied by a violent movement.	Aggressive	Most (if not all) cats
Stutter (stutter-barking)	Soft, throaty repetitive call typically emitted by a male when interested in female in estrus.	Reproductive; affiliative	Cheetah
Wah-wah	Cat makes a “wah–wah” sound, where each “wah” is muffled, short, atonal, and of low amplitude.	Approach of two individuals; displacement ; may be a mild threat	Some “small cats” (e.g. African golden cat, Asian golden cat, bobcat, caracal, Eurasian lynx, jaguarundi, puma)
Yowl	A long, drawn-out vocalization of variable pitch, intensity, duration and tonality.	Reproductive; mild threat	Bobcat, cheetah, domestic cat, Eurasian lynx, Geoffrey’s cat jungle cat, lion

95 studies examined, domestic cats ($N = 31$) may be the single highest study species for several reasons; specifically, access as study subjects and a stronger ability to manipulate experimental conditions in which they are involved. In regards to exotic species, the observed bias toward the big cats ($N = 46$) as study subjects was not surprising. This trend has been recorded elsewhere (Macdonald et al., 2010b), and is potentially due to their popularity with the general public, and their vulnerable or endangered conservation status (IUCN, 2014).

In terms of the use of ethograms, researchers more often created their own behavioral definitions rather than employ the use of another's ethogram, as more than half of the articles contained ethograms without reference to any other study. In exotic cat ethograms, 18 articles referred to other studies in the creation of their ethogram, while 43 simply created their own. Despite the establishment of standardized definitions for the behavioral repertoire of the domestic cat (UKCBWG, 1995), only seven of the 25 domestic cat articles in this review that occurred after its publication in 1995 utilized it. However, the high frequency of mutual behaviors existing on ethograms pertaining to two or three different felid groups suggests that there is similarity between ethograms of different felid species, regardless of the origin of the ethogram.

Investigation of each behavior identified during the literature review revealed three main trends which suggested similarity in behavioral descriptions: (a) titles varied, although their definitions described similar behaviors; (b) definitions varied in terminology, but described similar behaviors; (c) many definitions utilized modifiers to specify the context of the behavior. Conversely, behavioral categories varied extensively, which initially suggested there was little value in creating standardized behavioral categories, as categorization was dependent on the aim of each study. Nevertheless, some categories appeared routinely on ethograms (e.g. "active", "stereotypic", "reproductive"), despite the variance of behaviors within them. Therefore, we determined that a minimum number of standardized behavioral categories with suggestions of qualifying behaviors may be beneficial and important in standardizing felid research.

4.2. Similarities and differences in ethograms

The differences noted between domestic and exotic cat ethograms, including the definition of the behaviors within them, most likely reflects the diversity of hypotheses being tested and environmental conditions of each particular study rather than fundamental differences in behavior. Although some domestic cat studies in this review investigated the welfare of cats in captive environments ($N = 5$), the inherent value of domestic cats as study subjects allows them to be used to investigate broader topics. For example, dominance and the social structure of cat colonies has been of much research interest (e.g. Macdonald et al., 1987; van den Bos and de Vries, 1996), and is reflected by a greater proportion of social behavior studies seen within the domestic cat group in this review. This principal does not apply to most exotic cats, as the majority live solitary lives in the wild. Studies of exotic felids in

captivity are more applied in focus, often with an aim to develop practical solutions to problems with keeping wild animals in captivity (Mellen, 2011), which could explain the high number of ex situ studies investigating enrichment practices. Therefore, behaviors used for domestic cat studies may be beneficial for studies of exotic felids in a zoo setting. Additionally, while the behaviors included within the ethogram certainly apply to domestic cats, a detailed ethogram exists for this species (UKCBWG, 1995), and should also be consulted given the nature of domestic cat studies.

Most of the behaviors identified in this study were described similarly, and are very likely to apply to most, if not all, felid species. However, it is impossible to state with certainty whether all of these behaviors pertain to all existing felid species, and whether they are commonly displayed by both wild and captive individuals. Researchers should bear in mind that some behaviors listed on the final ethogram may only be seen during ex situ studies due to the effects of captivity (Carlstead, 1996) and thus may not be observed in the wild. Some comparative studies have suggested that certain behaviors are species-specific, as Mellen (1993) demonstrated with "hind feet scraping", however studies examining inter-species behavioral differences such as this are rare in the literature. Therefore, as felid research continues to grow, it is likely that species-specific additions and modifications to the standardized ethogram being proposed will be necessary. Additionally, while certain behaviors may naturally only apply to the social felid species, we suggest that they still be considered for those exotic species in captivity, which are often housed in pairs or trios (Mellen and Shepherdson, 1997). These captive groupings allow individuals to interact more often with conspecifics than they typically would in the wild, and studies have suggested that they may adapt by employing additional social signals in contexts not observed in the wild (for discussion see Bradshaw and Cameron-Beaumont, 2000). This is an interesting point that could be further explored in captive studies of exotic cats.

Ex situ behavioral research is essential to the captive management of felids, and the consistency in behavioral definitions can assist with inter-observer reliability and ease comparisons of data collected across studies over time. This can result in cumulative knowledge that is translated into practical management decisions to improve the welfare of felids in captivity. It may also facilitate behavioral studies on poorly studied species for which little behavioral information is available.

5. Conclusion

The standardized ethogram is designed to be user-friendly with clear, objective definitions. Combining base behaviors with modifiers should provide sufficient flexibility for studies in any environment. It is our hope that publication of this ethogram will make it widely available to those pursuing felid research, and that future developments and modifications would be based on this ethogram to maintain comparability between studies. Such standardization is likely to improve our understanding of felid

behavior and aid in the successful conservation and welfare of the Felidae.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.applanim.2015.04.001>.

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