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Point to Ponder

On the Use of Den and Resting Site Terminology for Species in the *Martes* Complex

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Abstract

We review den and resting site terminology used in 121 scientific publications related to species of the subfamily Guloninae (hereafter *Martes* Complex, *sensu* Proulx and Aubry 2017). These indicate that the term den has been used both to describe structures used by females to give birth and/or raise their kits, or by both sexes to sleep or rest. The term resting site has been used to describe locations where animals are inactive for varying durations, but no unilateral and systematic link with the den terminology has been established. In the absence of unambiguous, explicit definitions in 53–65% of papers, the lack of consensus on the meaning of these terms hampers efforts towards intra- and interspecific comparisons and sound management plans. Based on the literature and current knowledge on the biology and spatial ecology of species of the *Martes* Complex, we propose a series of unequivocal definitions for resting (rest) site, den, reproductive den, natal den, and maternal den, and show how these terms are interrelated. We recommend that these definitions be used in future studies, or else that researchers define explicitly these terms in papers dealing with the resting ecology of this group of mesocarnivores.

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INTRODUCTION

Murphy and Noon (1991) suggested that if 10 biologists were asked to define a single term commonly used in wildlife science, they likely would invoke 10 different definitions − uncertainty in the wildlife sciences includes the basic terminology we use. The word den originates from the Old English *denn*, defined as "the lair of a wild usually predatory animal" or "a hollow or cavern used especially as a hideout" (Merriam-Webster Dictionary 2020). This suggests that the term *den* is a *structure* that provides shelter and protection.

During a round table organized at the 7th International *Martes* Symposium in 2018 (Ashland, Wisconsin, USA), a discussion on the proper terminology in resting ecology raised the issue that there was occasionally a lack of clarity associated with, and therefore apparent misunderstandings in, the use of the terms *den* and *resting site*. Occasionally, the term *den* has been used either to describe structures used by females to give birth and/or raise their kits (i.e., with a reproductive purpose), or by both sexes to sleep or simply rest, with no reference to reproduction (Arthur *et al.* 1989; Lachat Feller 1993; Green *et al.* 2017; Joyce *et al.* 2017). In some studies, both categories of behaviours and structures have been grouped under the generic term den (Birks *et al.* 2005). The matter is further complicated by the fact that the term resting site may be more appropriate to describe structures where animals sleep/rest but do not reproduce (Birks *et al.* 2005; equivalent to "day hide" in Stier 2000), and dens used for reproduction are equally used for resting/sleeping. Hence, because similar structures may be used by *Martes* species for different purposes such as mating, resting, eating (Green *et al.* 2017; Joyce *et al.* 2017), it is important to properly define dens and resting sites in order to develop habitat management programs that acknowledge the importance of defendable cavities, especially for breeding females (Ruggiero *et al.* 1998). Researchers should adopt standardized terminology to facilitate comparisons among studies (Facka and Moriarty 2017). However, as knowledge of resting ecology develops, terminology must be adapted to different research goals (and resolutions), as well as new *Martes* life histories, phenologies, locations and den uses. Researchers aware of this should provide explicit definitions.

In this Point to Ponder, we review den and resting site terminology used in scientific publications related to species in the *Martes* Complex, which includes the American marten (*Martes americana*), the Pacific marten (*M. caurina*), the European pine marten (*M. martes*), the stone (beech, house) marten (*M. foina*), the Japanese marten (*M. melampus*), the yellow-throated marten (*M. flavigula*), the Nilgiri marten (*M. gwatkinsii*), the sable (*M. zibellina*), the fisher (*Pekania pennanti*), the wolverine (*Gulo gulo*), and the tayra (*Eira barbara*) (Proulx and Aubry 2017). Our objective is to provide definitions that result in an unambiguous distinction of existing den types and resting sites, in the hope to provide a baseline for resting terminology, and hence guide future usage with those definitions or neologisms.

WEB SEARCH and RESULTS

Number of papers

We censused the English language scientific literature (1950 to present) on the Web of Science (Full Collection) platform (Clarivate) using the following terms: den* (the asterisk indicates that any term containing "den" was included), rest*, sleeping, cavity, cavities, reproduction, reproductive, breeding, parturition, natal, maternal, birth, and newborn in either the title or abstract with a clear focus on the species in the *Martes* Complex. Additional articles and technical reports, some in French language, were identified based on our knowledge of scientific literature related to the *Martes* Complex.

We identified 340 refereed articles, book chapters, and technical reports of which 121 (36%; see Appendix) were pertinent to the subject treated in here. The Pacific marten from western North America was only recently recognized as a separate species from American marten (Carr and Hicks 1997; Dawson and Cook 2012). Because most publications for this region predate the new classification, we pooled *M. caurina* with *M. americana*. Some papers included more than 1 species of the *Martes* Complex, and the sum of papers related to martens, fishers, and wolverines amounted to 126: *M. americana* and M. *caurina*, 29 (23%); *M. martes*, 17 (13.5%); *M. foina*, 10 (8%); *M. zibellina*, 3 (2%); *P. pennanti*, 39 (31%); and *G. gulo*, 27 (21.5%). Ten (8%) papers were from the 1980s. All others (111 or 92%) were published between 1991 and 2020. Due to the very low number of papers for *M. zibellina* we did not produce species-specific pie charts for this species, but included results in the all-species pie charts.

Number of clear definitions

For all papers included in the analyses, we determined whether the terms related to dens and resting sites were defined, and if so, if the definitions provided were unambiguous with regard to function and/or location / structure. The number of papers with clear

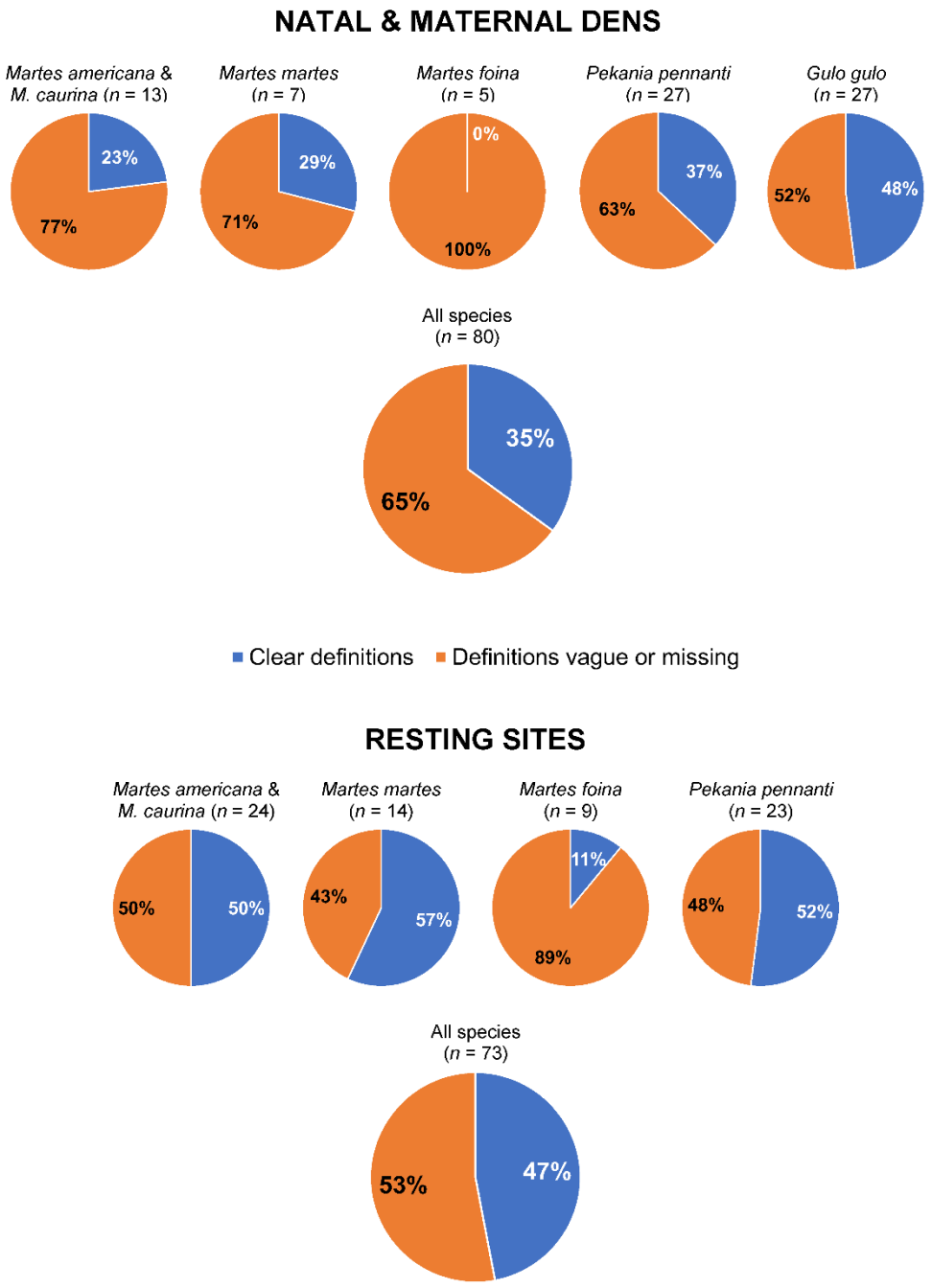

Figure 1. Proportion (%) of papers with clear vs. vague or missing definitions of natal and/or maternal dens, and resting sites in species of the *Martes* Complex. The all-species pie chart for dens include data on *Martes zibellina* (*n* = 1), while that for resting sites include data on both *M. zibellina* (*n* = 2) and *Gulo gulo* (*n* = 1).

definitions related to structures where reproductive females give birth, i.e., natal dens, and raise their kits, i.e. maternal dens, was relatively low for *Martes* species and *Pekania pennanti*, i.e., ≤ 37% of the papers. Nearly half of the wolverine papers had explicit definitions (Figure 1). Overall, only one-third of definitions used for dens in publications related to the *Martes* Complex were explicit (Figure 1).

The majority of papers either did not provide a definition, or the terminology employed was vague and could refer to either natal or maternal dens; maternal dens; resting sites; or all of these. With the exception of *M. foina*, the number of papers with unambiguous definitions for the term resting site was ≥ 50% (Figure 1). In the case of wolverine, the term resting site was rarely used (Wright and Ernst 2004), and researchers used rendezvous sites for post-maternal (post-weaning) dens (Magoun and Copeland 1998), as it was used by Mech (1970) for wolves (*Canis lupus*).

Recommended definitions and relationships between resting sites and type of dens (Figure 2)

Resting (rest) site – In more than 50% of publications of most species, the term resting site is not defined (Figure 1), likely because resting is the dominant behaviour observed routinely in radio-tracking studies. However, this term is somewhat misleading. While animals may be resting or sleeping at these sites, they may also use them for eating or temporarily retreating from a predator (Green *et al.* 2017; Aubry *et al.* 2018). Also, while researchers consider that animals are inactive and stationary (Table 1), there is no single criterion indicating for how long the animals must be inactive before a structure is identified as a resting site. While some researchers do not specify a minimum time period of inactivity (e.g., Green *et al.* 2017; Aubry *et al.* 2018), others associate resting sites with a minimum inactivity period of 60 s (Buskirk *et al.* 1988; Chapin *et al.* 1997; Wilbert *et al.* 2000), 10 min (Raphael and Jones 1997), 15 min (Martin and Barrett 1991), 30 min (Pereboom *et al.* 2008; Larroque *et al.* 2017), and 1 h (Steventon and Major 1982) or more (Zielinski *et al.* 2006), depending on species, study objectives, instruments and methodology. The time period may be variable depending on the specific use of those locations, e.g., protection against inclement weather or a predator, caching or eating prey, vigilance or rest/sleep *per se*. If the specific behaviour cannot be identified, which is common with radio-tracking studies, the stationary location of animals during short periods of inactivity (e.g., 60 s) may wrongly be presumed to correspond to a resting site, which may bias a (micro-)habitat selection study. In addition, it is likely that at least some resting sites used for short time periods (i.e. "lie-ups" *sensu* Bright and Smithson 1997) during the nocturnal active period differ in their characteristics from that used for the extended diurnal rest. Regarding the latter, some researchers did not include locations where martens simply laid on the ground, on tree branches, or at other exposed sites, even though they do rest in this way (Buskirk 1984); others used residency times, based on the age of tracks entering and leaving a structure, to identify resting sites (Powell 1994). Several researchers recognized the challenge of approaching such resting structures without disturbing the animal. In this case, this can result in an incomplete sampling of resting sites used by the animals, and thus a partial knowledge of resting ecology, and less information for the development of comprehensive management programs.

Many detailed definitions were identified for resting sites (Table 1), but there is some technical difficulty associated with the identification of these sites in the field. We propose the following definition on the basis of Gess *et al.* (2003), Green *et al.* (2017) and Aubry *et al.* (2018) (Table 1): *Any place or structure used by stationary males and females between moving bouts, for resting and/or sleeping (prerequisite), as well hiding from predators, sheltering from inclement weather, and sometimes eating prey killed elsewhere (facultative or case-dependent)*. It is important to note that a resting site is not necessarily a shelter or cavity; it could be a nest, a shallow depression in the ground, a branch, or a thicket of dense bushes as well.

Den – A den is a subcategory of resting site characterized by a hollow or enclosed structure (Figure 2). Based on the structures identified in the field and functions reported in the literature, a den can be defined as follow: *Secure cavity that provides shelter and insulation, and is primarily used for rest, sleep and/or reproduction*. Examples are burrows (subterranean), snow tunnels (subnivean), hollow tree trunks/branches (arboreal), rock crevices, caverns and some enclosed human structures.

Reproductive den – This is a subcategory of den (Figure 2). In the analysed literature, this term was used sporadically either when details of reproductive behaviour were not known, or both birthing and raising young occurred in the same den. It can therefore be defined as follows: *Secure cavity that is used either for giving birth and/or raising young*.

Natal den – Many similar, acceptable definitions have previously been published (Table 1). The key word for all these definitions is "parturition". The term reproductive den cannot be used to refer to natal dens specifically, as it also includes maternal dens, which could be selected at a different location and have another function (Green *et al.* 2017). Using the presence of kits or pups at the den to define a natal den is not correct either because the female may have already moved them to a maternal den (see below). With wolverines for instance, confirming the presence of natal dens is not

Table 1. Explicit definitions of natal dens, maternal dens, and resting sites for species in the *Martes* Complex.

Definitions	Species					References
	Martes americana & M. caurina	*Martes martes*	*Martes foina*	*Pekania pennanti*	*Gulo gulo*	
Natal Dens						
Supposed parturition sites where females were first detected and were repeatedly used by an adult female in April or May.	√					Bull and Heather 2000
The first reproductive den (a refuge used by a reproductive female with young that are still dependent and nursing) used by a female in a given year and where parturition occurs.	√			√	√	Green *et al.* 2017; Jokinen *et al.* 2019
Parturition site when female movement and resting patterns become highly localized.	√					Ruggiero *et al.* 1998
Site of parturition and subsequently nursing the litter.		√		√	√	Magoun and Copeland 1998; Kleef 2000; Birks *et al.* 2005; Raley *et al.* 2012; Zhao *et al.* 2012; Matthews *et al.* 2013, 2018; Sweitzer *et al.* 2015; Thompson and Purcell 2016; Niblett *et al.* 2017; Green *et al.* 2018;
Den used during a specific time period corresponding to the winter–spring parturition season.					√	Landa *et al.* 1997; Magoun and Copeland 1998; Aubry *et al.* 2007; Dawson *et al.* 2010; McKelvey *et al.* 2011; May *et al.* 2012; Gervasi *et al.* 2014; Rauset *et al.* 2015; Webb *et al.* 2016; Aronnson and Persson 2018
Den used for parturition				√		Berg *et al.* 2020
Maternal dens						
Sites to which females move the kits after leaving the natal den. Also known as post-natal.	√					Bull and Heather 2000

Table 1. Explicit definitions of natal dens, maternal dens, and resting sites for species in the *Martes* Complex (cont'd).

Any reproductive den use subsequent to a natal den. Maternal dens are used when kits/cubs are not yet weaned and have limited mobility.	√			√	√	Magoun and Copeland 1998; Ruggiero *et al.* 1998; Inman *et al.* 2012; Zhao *et al.* 2012; Matthews *et al.* 2013, 2018; Thompson and Purcell 2016; Green *et al.* 2017, 2018
Pre-weaning dens.					√	Raley *et al.* 2012; Sweitzer *et al.* 2015
Where kits are raised.					√	Niblett *et al.* 2017; Berg *et al.* 2020
Secondary den.					√	Jokinen *et al.* 2019
Resting (Rest) site						
Structures for resting that provide protection from predation and thermoregulation.	√					Tweedy *et al.* 2019
If animals are inactive.	√	√	√			Steventon and Major 1982; Spencer *et al.* 1983; Spencer 1987; Zalewski 1997, 2001, 2012; Wilbert *et al.* 2000; Gess *et al.* 2013; Larroque *et al.* 2017
When animals are stationary.				√		Weir *et al.* 2012
Where animals rest.	√	√	√	√		Pulliainen 1982; Buskirk *et al.* 1988; Chapin *et al.* 1997; Raphael and Jones 1997; Stier 2000; Pereboom *et al.* 2008; Aubry *et al.* 2013; Truex and Zielinski 2013; Joyce *et al.* 2017; Larroque *et al.* 2017
Daily refuges used by a male or a female at any time during the year. Rest sites may provide thermal and/or physical protection for individuals and are typically used for sleeping, eating, and hiding from predators or inclement weather.	√					Green *et al.* 2017
When it is obvious during tracking that the animal is inactive.	√					Martin and Barrett 1989
Daily refugia.				√		Zielinski and Schlexer 2015
Roosting site.				√		Zielinski and Gray 2018; Zielinski and Schlexer 2019
Used daily between known bouts of activity to provide thermoregulatory benefits and protection from predators.	√					Zielinski *et al.* 2006; Slauson and Zielinski 2009
Where animals are not actively hunting or travelling, they use protected sites for resting that helps them conserve energy, avoid predation, gain thermoregulatory advantages, and consume prey.				√		Aubry *et al.* 2018

always feasible due to the difficulty of observing pups located at the end of long, complex snow tunnels (Aubry *et al.* 2007). However, when researchers know exactly the period of parturition during the winter–spring period, dens found during a specific time period may be identified as natal dens (Table 1). For all species, natal dens may also be identified indirectly through a change in the locomotory behaviour (from highly mobile to predominantly stationary) of radio-tracked females.

On the basis of definitions reported in scientific publications, we believe that a natal den in *Martes* Complex species is perceived and can be defined as follows: *Secure cavity used by a reproductive female for parturition and often initial raising of the kits/pups*. Obviously, this requires the confirmation that parturition did occur at that location.

Maternal den – The majority of definitions of maternal dens relate to structures used by the female to raise her kits/pups after it commonly leaves the natal den. These are post-natal dens where pre-weaned animals with limited mobility are raised. On the basis of definitions reported in scientific publications (Table 1), we believe that a maternal den should be defined as follows: *Secure cavity used by a reproductive female subsequently to a natal den, and where the weaning of the kits/pups generally takes place*.

It is important to note that while a reproductive female will obviously use only 1 natal den during a specific breeding season, she may relocate her kits to different maternal dens several times until they are weaned (e.g., Berg *et al.* 2020). In addition, common to all reproductive den types, any of them can be used as "regular" resting sites outside the breeding period (Birks *et al.* 2005). However, they still qualify to be called "dens" due to their enclosed structure and the enhanced safety and insulation they provide.

DISCUSSION

There has been a lack of clarity in the use of the terms *resting (rest) site*, *den*, *reproductive den*, *natal den*, and *maternal den* for species of the *Martes* Complex. This has been exacerbated recently by the tendency for some authors to incorrectly associate the term "den" only with reproduction. In some other cases, researchers voluntarily overlooked specific den types or resting sites (Wynne and Sherburne 1984; Lachat Feller 1993; Paragi *et al.* 1994). In several cases, authors did not provide definitions perhaps because the terms appeared self-explanatory. The lack or the incompleteness of definitions may not have been detrimental to some coarse-grain habitat studies where researchers tried to identify, for example, the seral stages of forest stands used by the animals or the general distribution of females. However, as pointed out by Ruggiero *et al.* (1998), den or resting structures may have small-scale features (characteristics of the actual structure) and a small-scale context (immediate surroundings) that need to be identified in order to produce effective habitat management programs. This is particularly relevant for the forest-dwelling species of the *Martes* Complex that rely on trees with suitable cavities, which can be in limiting amounts in some managed landscapes (e.g., Berg *et al.* 2020). The nature, attributes, abundance and distribution of natal dens, maternal dens, and resting sites can be pivotal to understanding population dynamics, carrying capacities, and guiding timber and wildlife management programs.

We believe that the importance of den and resting site definitions has evolved over time. Proulx and Santos-Reis (2012) reported that conservation efforts to properly manage *Martes* populations and habitats started after 1990. In this review, the majority of papers with acceptable definitions for natal and maternal dens, and resting sites, were published after 1990, thus suggesting that researchers and managers recognized the need for detailed, explicit and unambiguous definitions to better manage populations and communities. We hope that our proposal reaffirms definitions of existing terms and encourage their proper use, or the creation of neologisms, as appropriate.

CONCLUSION

Our review of the scientific literature leads us to conclude that until now, a lack of clarity in the use of the terms *resting (rest) site*, *den*, *reproductive den*, *natal den* and *maternal den* for species in the *Martes* Complex has created some uncertainty with regard to their meaning. On the other hand, we detected, and encourage, a more recent tendency among researchers to properly identify these structures in the field. On the basis of many similar and acceptable definitions, we recommend the use of the following definitions (see Figure 2 for relationships between these terms):

Resting site: Any place or structure used by stationary males and females between moving bouts, for resting and/or sleeping (prerequisite), as well hiding from predators, sheltering from inclement weather, and sometimes eating prey killed elsewhere (facultative or case-dependent).

Den: Secure cavity that provides shelter and insulation, and is primarily used for rest, sleep and/or reproduction.

Reproductive den: Secure cavity that is used either for giving birth and/or raising young.

Natal den: Secure cavity used by a reproductive female for parturition and often initial raising of the kits/pups.

Maternal den: Secure cavity used by a reproductive female subsequently to a natal den, and where the weaning of the kits/pups generally takes place.

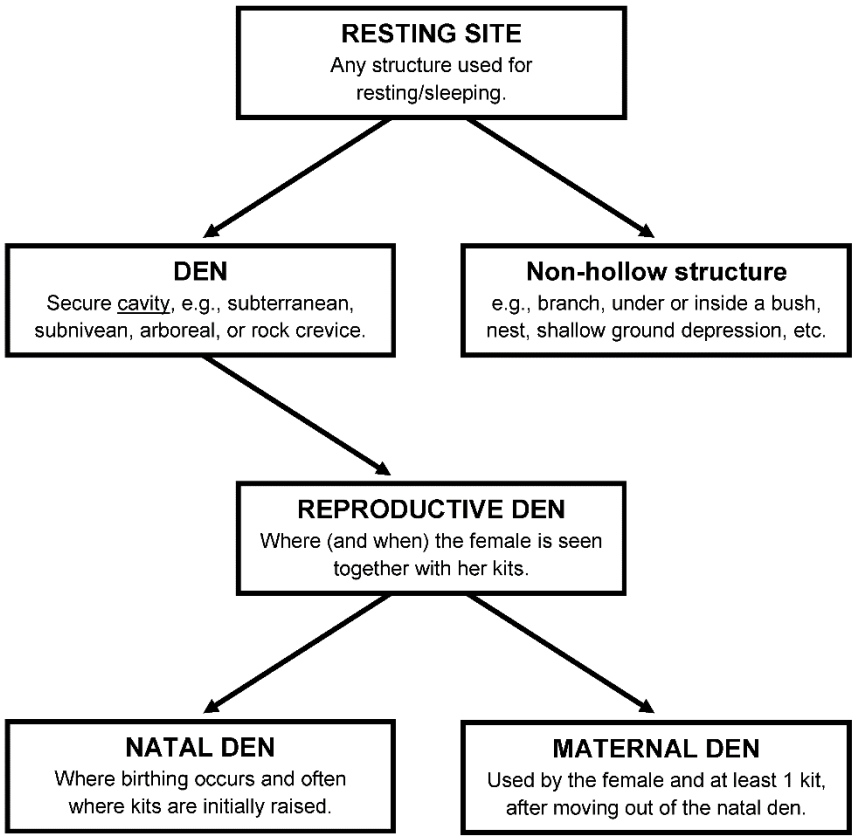

Figure 2. Schematic diagram showing the relationships between the terms defined in this paper. Refer to the text for full definitions.

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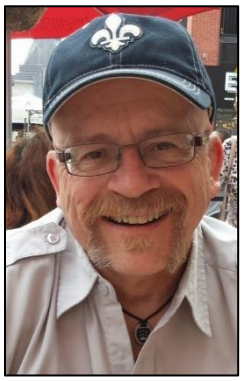

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