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**BURROW MORPHOLOGY, BURROW PRESERVATION,
AND EVIDENCE OF DIGGING BEHAVIOUR
IN GROUND-DWELLING SQUIRRELS (SCIURIDAE)**

by

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**A thesis submitted to
The Faculty of Graduate Studies and Research
in partial fulfilment
of the requirements for the degree
of Master of Science**

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ABSTRACT

Fossil burrow casts provide valuable evidence of behavioural evolution inasmuch as they reflect the morphology of the original burrow and of the tracemaker, and its digging motions. The fidelity of the cast to original dimensions of the burrow was investigated by comparing open and filled burrows of two extant sciurid species, *Marmota monax* and *Tamias striatus*. A new mapping technique for imaging filled burrows in non-lithified sediment has been introduced. The filled burrows were studied by serial sectioning and three-dimensional reconstruction, and open burrows were cast with plaster. Burrow width was found to differ less between the open and filled burrows than height, suggesting that it is less affected by taphonomic processes and should be preferentially used for identification of the tracemaker.

The digging movements were reconstructed for one of the study species, *Marmota monax* from the variation of claw mark morphology on the surface of the burrow. A preliminary kinematic model was developed linking the geometry of claw marks with digging movements. One of the three morphological types of claw marks recognized on the burrow were interpreted as a previously undescribed wrist-only digging movement that may be common for woodchuck and possibly for a larger group of scratch-diggers.

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METHOD OF THESIS PRESENTATION

The main body of the thesis is presented as two papers, which are preceded by a background chapter and followed by a synthesis chapter.

Chapter 1 describes the current state of the fossil burrow research, the thesis objectives, and gives background information on the two burrowing species studied in this thesis, woodchuck (*Marmota monax*) and chipmunk (*Tamias striatus*). Chapter 2 examines the history of burrows created by the studied species through the morphology and morphometry of the burrows, reconstructs architecture of palaeoburrows created by these two species through the analysis of serial vertical soil sections and interprets taphonomic changes occurring in burrows after their abandonment. Chapter 3 focuses on one element of palaeoburrow morphology, claw marks, and reconstructs digging movements through the analysis of claw marks. Chapter 4 provides conclusions of both chapters.

The burrow reconstruction was created in Rhinoceros 3D vector editing software, it is provided in digital form on CD. Also included on the CD is the Poches software (developed together with Paul Milovanov) that was used to generate synthetic claw marks in Chapter 3.

CHAPTER 1

Current state of fossil burrow research

INTRODUCTION

Most geologists are familiar with trace fossils left by marine invertebrates and most commonly used as indicators of palaeoecology or palaeodepth. This thesis is concerned with tetrapod burrows, terrestrial trace fossils that have been used for palaeoecological reconstructions, but primarily for reconstruction of behaviour.

The aim of the thesis has been to enable a more precise description and interpretation of fossil burrow morphology by the study of modern analogues. Two aspects of burrow morphology that can be easily quantified within a single burrow are the diameter of the burrow and the shape of surficial markings (the shape and size of claw and incisor marks on the surface of the burrow). This led to a two-part subdivision of the thesis. The subject of the first part is the modification of original cross-sectional dimensions of the burrow through its history. Measurements of abandoned open burrows are compared to those of filled burrows for each of the two study species: *Marmota monax* and *Tamias striatus*. The results are used to assess the value of the fossil burrow's width and height for reconstructing the original size of the burrow. The second part of the thesis is devoted to quantification of the morphology of surficial marking in burrows of *Marmota monax*. The variability of claw marks is interpreted with respect to digging behaviour. Forelimb movements are reconstructed using a preliminary kinematic model that links them with the geometry of claw marks.

TRACE FOSSILS AND VERTEBRATE BEHAVIOUR

Behaviour of fossil vertebrates has usually been inferred from the morphology of body fossils. Body fossils have two major limitations that are inherent to them and therefore cannot be overcome by refining the study methods. Firstly, if behavioural adaptation precedes morphological adaptation, the initial period of behavioural evolution is not reflected in body fossils (Boucot 1990). Therefore, the origins of a particular behaviour cannot necessarily be studied from body fossils alone. Secondly, body fossils preserve morphological adaptation but usually only indirectly preserve evidence of behavioural adaptation. Behaviours that modify the environment and allow the animal to escape certain selective pressures without causing morphological change are poorly reflected in the body fossil record. This concerns especially behaviours related to construction and use of shelter. For instance, Odling-Smee et al. (2003) have recently hypothesized that environment-altering behaviours, which they group under the term *niche construction*, may be an important evolutionary feedback mechanism. Such hypotheses can not always be tested with body fossil evidence alone.

For example, it is known that modern vertebrates can be effective burrowers with very few morphological specializations (Goldstein 1968). One unspecialized burrower known from the fossil record is *Diictodon*, a Permian dicynodont. Coiled skeletons of this animal have been found in helical burrow casts preserved in flood plain deposits of the Karoo Sequence of South Africa (Smith 1987). A recent functional re-analysis of *Diictodon*'s morphology has not discovered any evidence of fossorial specializations (Ray and Chinsamy 2003).

The availability of evidence complementing the body fossil record depends on the type of behaviour. Certain behaviours produce artefacts such as cut marks on wood or

traces such as trackways and burrows, some of which can be preserved as fossils. Burrow casts are especially likely to be preserved as trace-fossils because they are sedimentary structures. Because fossil burrows are preserved *in situ*, their interpretation can be correlated with the interpretation of the environment from the sediments or palaeosols that burrows are found in (Hasiotis and Bown 1992).

Burrow casts have the potential to allow the study of the aspects of the evolution of behaviour that are inadequately covered by the body fossil record. However, if fossil burrows are to serve as evidence independent from body fossils, their tracemaker has to be identified not solely from body fossils found inside the burrow, or in the same stratigraphic layer, but from the interpretation of burrow morphology itself. Whereas qualitative morphological features such as large-scale architecture and presence of chambers can serve as evidence for particular behaviours (hibernation, food caching, etc.), quantitative features may allow the identification of the animal that excavated the burrow and reconstruction of its digging movements.

Even qualitative descriptions of fossil burrow morphology are scarce. The quantifiable features of fossil burrows that have been previously used to identify the tracemaker are the cross-sectional diameter (either width or height or both) and surface marking. Surface marking includes claw marks and incisor marks left on the sides of the fossil burrow cast during the excavation of the burrow. Only the width of incisor marks has been used as a quantitative characteristic serving to identify the tracemaker (Martin and Bennett 1977, Gobetz and Martin 2005).

Burrow cross-sectional diameter is the most readily available characteristic of fossil burrows. The diameter of the burrow is expected to reflect the dimensions of the

tracemaker. Before the relationship between cross-sectional diameter and tracemaker's dimensions can be studied, it is necessary to examine the way in which burrows are modified as they are preserved into burrow casts. An understanding of the modification of the burrow dimensions as it is preserved as a burrow cast can be reached through the study of modern analogues.

Identification of the tracemaker depends on the establishment of a link between animal morphology, burrow dimensions, and burrow taphonomy. In this thesis, taphonomy with respect to fossil burrows is understood as the transformation of burrow morphology following its abandonment. As a result of this transformation, an initially hollow burrow is often preserved as a cast within geological deposits. The taphonomic element of the interpretation has previously been little considered. In Chapter Two of this thesis, taphonomic differences between burrows of the same species are described for the first time.

In the case of surficial marking, behavioural reconstruction depends on the establishment of a link between animal morphology, digging movements, and the morphology of the surficial marking. In Chapter Three of this thesis, surficial marking morphology within a single burrow is described qualitatively and quantitatively, and related to the known morphology of the tracemaker species and the digging movements described in the literature.

VERTEBRATE BURROWS AND BURROWING

The previous study of fossil vertebrate burrows has concentrated on interpreting behaviour and ecology (e.g. Dinesman 1968, Heinrich 1977, Burns et al. 1989, Burns 1996), rather than on identifying the tracemaker and separating out the taphonomic

overprint. This focus is partly explained by the influence of marine invertebrate ichnology which is better developed than the study of vertebrate burrows (Shult and Farlow 1992). However, marine invertebrate burrows have two important differences from vertebrate ones. First, marine burrows remain open for a relatively short time. The only exception is borings, but they occur in hard substrates, so that taphonomic processes affecting them are slow, and collapse is not likely to obscure the structure of the trace. Secondly, and most importantly, invertebrate burrows are described independently from the tracemaker. Indeed, the tracemaker is generally unknown, and similar traces can be produced by animals belonging to different orders (Bromley 1996).

Vertebrate burrows produced by different taxa have distinct morphologies (architecture, depth, diameter) specific to a genus or species (Hickman 1990), so that the identification of the tracemaker is possible in most cases. Vertebrate trace fossils are used to expand the knowledge of the behaviour for low-level taxa, which makes the identification of the tracemaker crucial.

In contrast to invertebrate burrows, vertebrate burrows can be inhabited for thousands of years (Dinesman 1968, Burns 1996). Over this time, segments of the burrow become abandoned, renewed, enlarged, or filled. Such modifications, occurring over long time intervals and under subaerial conditions, are different from those common in subaqueous burrows (Candisani et al. 2001). Therefore, the study of taphonomy is important for interpreting the morphology of fossil vertebrate burrows.

Among vertebrates, tetrapods, and mammals in particular, are the group in which burrowing is most common (Voorhies 1975). Burrowing and burrow use is especially widespread among mammals living in grasslands, where no other shelter can be found

(Kucheruk 1983, Formozov 1966). Mammals excavate burrows by breaking up soil using a combination of claws, incisors, and the head, and expulsing soil with the hind limbs, the head, or the mouth (Gambaryan 1960). Burrowers are grouped into three main categories according to their digging method (Hildebrand 1974, Nevo 1999). The most common type of digging, which occurs in unspecialized as well as specialized diggers, is scratch-digging, in which soil is broken up with the claws of the manus. Scratch-digging is used by badgers (*Taxus*), armadillos (*Dasypus*), and most burrowing rodents (Lehman 1963, Puttick and Jarvis 1977). Incisor-diggers break-up soil with their incisors, although some also use claws. Incisor-digging is found in rodents, such as the water vole (*Arvicola*) and mole-rats (*Spalax*). Finally, head-lift diggers use the head as a wedge to excavate the burrow, but may use claws in hard substrate. This is the rarest behaviour out of the three types. It is found in some mole-rats (*Nannospalax*, *Myospalax*), the bamboo-rats (*Rhizomys*), and the mole-vole (*Ellobius*) (Howe 1975, Stein 2000).

In mammalogy, burrowing and associated animal morphology has been studied much more systematically than the resulting burrows. Burrowing adaptations in distantly related mammal lineages have been a classic subject of functional morphology (Gambaryan 1960, Hildebrand 1974, Nevo 1979, 1999).

Palaeobiological studies of fossil and subfossil burrows have interpreted their geometry as a reflection of the morphology, digging movements, behaviour, and the life history of its architect. Mammal burrows reflect *tracemaker morphology*, because animals construct a burrow that corresponds closely to their size (Andersen 1982). This correspondence is generally explained by the minimization of energy expenditure during excavation, but is also important for protection. For instance, foxes will dig burrows that

are smaller than those of coyotes, and thus escape predation from coyotes. Burrows of coyotes, in turn, will be smaller than those of wolves, which prevents wolves from entering the burrows and preying on coyotes (Henry 1993). Burrow geometry reflects *digging movements*, because burrows are a result of a digging sequence. The digging movements together with the animal's dimensions determine the smallest possible diameter of a burrow for a particular species (Toots 1963). Burrows also reflect *behaviour* insofar as an important part of the animal's life is spent underground.

Individual or communal hibernation, aestivation (Hembree et al. 2004), food caching (Gee et al. 2003), belowground rearing of the young (Burns et al. 1989, Burns 1996), and belowground feeding (Scheffer 1940, Romañach and Le Comber 2004) are types of behaviour reflected in the burrow structure and infill. For instance, vertical exits (called plunge holes) identify hibernation burrows, whereas the presence of food caches within such burrows suggests that the hibernator would awaken during the winter (Kucheruk 1983, Reichman and Smith 1990). Evidence of ontogeny of digging behaviour may also be preserved in some cases in the form of "practice pits" excavated by the young of the species (Burns 1996).

SURFICIAL MARKING

An individual surficial marking on fossil burrows, in the form of a claw mark or an incisor mark are believed to be reflections of a single movement. Therefore, some aspects of the morphology of the tracemaker can be reconstructed more easily from surficial marking than from the burrow diameter, because the burrow diameter is the product of multiple movements, multiple passages, and may be subject to change from wear and collapse.

Claw marks have been studied in caves (Bachofen-Echt 1931), open burrows (Quintana 1992), and burrow casts (Groenewald et al. 2001). In open burrows and caves, claw marks appear in negative relief (as grooves), whereas on burrow casts, claw, beak, and incisor marks stand in positive relief (as ridges). Not all fossil burrows have surficial marks, suggesting that claw mark preservation depends on the coherence of the sediment, which in turn depends on the grain size and the moisture content (Gobetz and Martin 2005).

Surficial marking of fossil burrow casts can be used to identify the tracemaker and to reconstruct elements of the digging sequence of the animal (Martin and Bennett 1977, Gobetz 2005, Gobetz and Martin 2005). For example, it is from the incisor marks that the Miocene helical burrows of Nebraska were positively identified as belonging to *Paleocastor* (Martin and Bennett 1977). Quintana (1992) identified the excavator of an empty Pleistocene burrow from grooves on the burrow walls that he identified as claw marks of a large armadillo (Dasypodidae).

When a burrow cast is eroded out of the outcrop, its surficial morphology (relief and texture of the surface of the burrow cast) is more easily studied than where a single cross-section of the burrow is exposed. On perpendicular cross-sections, claw marks appear as serrations of the burrow contour, commonly on a subcentimetre-scale (Hasiotis et al. 2004: Figures 3C and D) and may be easily overlooked. Cross-cutting relationships of claw and incisor marks have been used to infer the sequence of digging movements (Martin and Bennett 1977), and the direction of movement (Gobetz and Martin 2005).

Although the width of claw marks has been used to confirm the identification of the tracemaker (Gobetz 2006), no quantitative link between the digging movements and the

morphology of the claw marks has been suggested. The first step towards establishing such a link is the recognition of shape characters related to aspects of digging movements and the quantification of their variation among claw marks from a single burrow.

Previously, the variation of claw mark shape has been quantified in terms of range, mean value and standard deviation of the length and width of the claw mark (Martin and Bennett 1977, Gobetz and Martin 2005, Gobetz 2006). Groenewald et al. (2001) measured claw mark height in relief and its angle relative to the long axis of the burrow. In Chapter Three of this thesis, the variability of claw mark morphology is described from four parameters, a preliminary geometric model for claw mark production is proposed, and is used to reconstruct the variability of movement from the variability of claw marks.

FOSSIL TETRAPOD BURROWS

Published descriptions of fossil tetrapod burrows are generally scarce (Table 1-1). More fossil burrows have been found than have been described (S. Lucas; R. Damiani; L. Tanner, personal communication, 2007). Descriptions have been mostly published when the tracemaker has been found preserved in the burrow, an occurrence much rarer than the fossil burrows as such. Among the finds listed in Table 1-1, only the *Daimonelix* burrow was identified based on incisor marks, rather than body fossils. When burrows are found without a skeleton inside, confusion with root casts or sedimentary structures (e.g. cryogenic wedges) is possible. Ichnologists have formulated characteristics distinguishing invertebrate burrows from other three-dimensional bodies (e.g., root casts)

Table 1-1. Fossil tetrapod burrow descriptions in the palaeontological literature. Identifications made from body fossils are shown in bold.

Period	Formation	Location	Taxonomic group	Reference
Pleistocene	Chapadmalal Formation	Mar del Plata, Buenos Aires Province, Argentina	Mammalia: Edentata: Dasypodidae	Quintana 1992
Late Early Pliocene	Ash Hollow Formation	Nebraska, USA	Mammalia: Rodentia: Heteromyidae: <i>Perognathus</i>	Voorhies 1974
Miocene	Pawnee Creek Formation	Colorado, USA	Rodentia: Sciurognathia: Protrogomorpha: Aplodontoidea: <i>Mylagaulus laevis</i>	Gobetz 2006
Early Miocene	Harrison Formation	Nebraska, USA	Mammalia: Carnivora: Amphicyonidae	Hunt et al. 1983
Early Miocene	Harrison Formation	Nebraska, USA	Mammalia: Rodentia: Geomyidae: <i>Gregorymys</i>	Gobetz and Martin 2005
Early Miocene	Bear Dog Hill Formation	Agate Ntl. Monument, Nebraska, USA	unidentified	Hunt 1993
Oligocene	White River Formation	Wyoming, USA	Rodentia: Myomorpha: Geomyoidea: Eomyidae: <i>Heliscomys</i> , <i>Adjidaumo</i> , <i>Paradjidaumo</i> , <i>Eumys</i> ; Protrogomorpha: Aplodontoidea: <i>Prosciurus</i>	Sundell 1996
Oligocene	White River Formation	Wyoming, USA	Artiodactyla: Tylopa: Merycoidodontidea: Oreodonts	Sundell 1997
Oligocene	White River Formation	near Douglas Wyoming, USA	unidentified	Sundell 1998

Table 1-1 continued. Fossil tetrapod burrow descriptions in the palaeontological literature. Identifications made from body fossils are shown in bold.

Period	Formation	Location	Taxonomic group	Reference
Late Oligocene to Early Miocene	Harrison Formation, Monroe Creek Formation	NW Nebraska, USA	Mammalia: Rodentia: Castorimorpha: Castoridae: <i>Paleocastor</i>	Martin and Bennett, 1977
Early Tertiary	DeBeque Formation	W. Colorado, USA	unidentified	Turnbull 1970
Eocene	Jebel Quatrani Formation	Egypt	Mammalia: Rodentia	Bown and Kraus 1983
Early Eocene	Willwood Formation	NW Wyoming, USA	Mammalia	Bown 1982
Late Cretaceous (Campanian)	Two Medicine Formation	Choteau, Montana, USA	?Mammalia	Martin 2001
Middle Cretaceous	Blackleaf Formation	Montana, USA	Dinosauria: Ornithischia: Ornithopoda: Euornithopoda: <i>Oryctodromeus cubicularis</i>	Varricchio et al. 2007
Late Jurassic	Salt Wash Member, Morrison Formation	SE Utah, USA	Reptilia: Rhynchocephalia: Sphenodontidae	Hasiotis et al. 2004
Jurassic	Escalante Member, Estrada Formation	Utah, USA	unidentified	Loope 2006
Late Triassic	Owl Rock Member, Chinle Formation	SW USA	unidentified	Hasiotis et al. 2004
Early Triassic	Palingkloof Member, Balfour Formation	Free State Province, South Africa	Reptilia: Cynodontia: Trytilodontoidea: Trirachodontidae: <i>Trirachodon</i>	Damiani et al. 2003

Table 1-1 continued. Fossil tetrapod burrow descriptions in the palaeontological literature. Identifications made from body fossils are shown in bold.

Period	Formation	Location	Taxonomic group	Reference
Early Triassic	Fremouw Formation	Shackleton Glacier, Transantarctic Mountains, Antarctica	Reptilia: Therapsida	Miller et al. 2001 Hasiotis et al. 2004
Early Triassic	Katberg Formation	SW Karoo, South Africa	Reptilia: Anapsida: ?Procolophonidae	Groenewald 1991
Late Permian	Teekloof Formation, Adelaide Subgroup, Lower Beaufort Group	Reiersvlei, Teekloof Pass; SW Karoo, South Africa	Reptilia: Cynodontia: Diictodontia: Diictodontidae: <i>Diictodon</i>	Smith 1987
Early Permian	Speiser Shale	Kansas, USA	Lepospondyli: Lysorophia: Lysorophidae: <i>Brachydectes elongatus</i>	Hembree et al. 2004, Hembree et al. 2005

(e.g. Plaziat 1971), but have not discussed the same problem for vertebrate burrows (cf. Voorhies 1975, Miller et al. 2001). Without a body fossil inside, the burrows have been attributed only to high-level taxa (Table 1-1). Quantitative characteristics measured in fossil burrows include the entrance ramp angle, the cross-sectional diameter, the width-height ratio, and the whorl radius for helical burrows (Smith 1987, Groenewald et al. 2001).

Most tetrapod fossil burrows found to date come from flood-plain deposits (e.g., Smith 1987, Hasiotis et al. 2004). Loope (2006) describes Jurassic burrows of unknown affinity from aeolian deposits. The process of burrow filling is poorly understood, although most burrow casts are interpreted as resulting from flash floods. Burrow fill sometimes includes sedimentary structures such as lamination, cross-stratification, and rip-up clasts. In a study of therapsid burrows, Groenewald et al. (2001) describes a general fining trend away from the opening of the burrow, but notes that the terminal chamber is filled with coarse sand. This may suggest that different filling processes account for the structure of the fill depending on the location within the burrow.

Fossil burrows in hard sediments have been described where there is a grain size contrast between fill and matrix (Miller et al. 2001). Burrows in soft sediment have been commonly recorded in palaeosols, but have not been described in three dimensions because of the difficulties of mapping, quantitative description, and interpretation. Chapter Two of this study introduces a mapping technique for imaging filled burrows in soft sediment.

MODERN ANALOGUES

Modern analogues of fossil burrows are both open burrows and filled burrows of extant species in non-lithified sediments. Open burrows provide an analogue to those burrows that have been commonly described in the fossil record, ones filled in one fast event. Filled burrows are an analogue to a type of burrow cast originating from a burrow filled slowly through sifting from the surface or backfilled by the animal. Although fossil burrows have been commonly encountered in the fossil record, few have been described in detail and many may have been overlooked, because the contrast between the fill and the encasing deposits is often less than in the case of catastrophically filled burrows.

Open burrows of many mammals, including those of woodchuck and chipmunk, have been studied by biologists (Fisher 1893, Hamilton 1934, Allen and Shapton 1942, Grizzell 1955, Bruleigh and Vandruff 1998; Panuska and Wade 1956, Thomas 1974). Trackers and field naturalists have established rules of thumb for identifying animals from the diameter of burrow entrances (Elbroch 2003). The architecture of burrows has been described for individual species in terms of branching, presence of chambers, vertical shafts, and so forth (Hickman 1990). In the boreal forest region, where the number of burrowing species is small, these descriptions would be expected to suffice for identification of the tracemaker. But even within this small set of species, the diameter of the opening alone does not always permit species identification. Since burrow openings become enlarged with wear, field naturalists use other characteristics, such as the frequency of cleaning and the shape and size of the throw mound to complement identification from the diameter of the opening (Elbroch 2003).

Studies of open burrows have focused on the architecture of the burrow rather than its diameter. Although some elements of the burrow geometry are species-specific,

Kucheruk (1983) cites evidence from different taxa showing that the same species can produce a variety of burrow types depending on the burrow function, on the location within the geographic range and the availability of other shelter. Therefore, the geometry of the burrow may reflect the function of the burrow more than the morphology of the tracemaker.

Other features of burrows reported in the biological literature include the presence of earth plugs, latrines, caches, spirals and anastomosing tunnels (Hickman 1990). Although these features can be species-specific, they are not related to animal morphology and therefore cannot be used for identification of the tracemaker except for extant species, for which the occurrence of particular features is known.

Filled burrows are known as *krotovinas* to soil scientists who study them as a factor in the turnover and mineralization rate of organic matter, as well as in inorganic mass movement (Retallack 2001). Quaternary palaeontologists and paleoecologists have studied filled burrows as a site of possible concentrations of bones and other organic remains (Dinesman 1968, Dinesman and Shterenberg 1967, Heinrich 1977, Jäger 1977). The morphology of filled burrows, however, has so far received little attention. Burrows become filled either passively by colluvial deposition from the surface, or actively by the animal itself. The way a burrow is filled determines the degree of its preservation, because colluvial deposition must fill voids incompletely and preferentially closer to the entrance. Besides being determined by the environment, the mode of fill is dependant on the animal. Some animals are known to make extensive earth plugs and dig new burrows every year, shifting soil into unused parts of the burrow (woodchucks), others tend to reuse the same burrows over long periods of time (wolves).

The plugged parts of the burrow are most conspicuous in soil, and it is upon these, and not the passively infilled burrows that the Quaternary palaeontologists have most often chanced upon (Dinesman 1968, Burns et al. 1989, Burns 1996). Subterranean animals often plug large portions of their burrows, producing a great number of filled tunnels over time. Filled mole-rat burrows of different ages cover every ten centimetres of a section wall in areas where this species is found (Formozov 2006).

The third type of filled burrows represents a rare event that is, however, well known from the palaeontological record. Flash-floods and ash falls fill burrows with a homogeneous infill that is distinct from the surrounding soil in grain size and colour.

The variety of infill processes must create a spectrum of taphonomic burrow facies within a single burrow, from collapsed burrows to partially filled burrows to fully filled ones. How the filling proceeds has not been studied. It is often implicitly assumed that infill occurs always in a catastrophic event and the rest of the burrow is lost to collapse, which is believed to occur after the abandonment of the burrow.

The discovery of open burrows of a Pleistocene ground sloth in Argentina (Saffer et al. 2004) suggests that burrows, even of a very large diameter, can remain intact for thousands of years, at least where high concentration of soil carbonate favours rapid hardening. On the other hand, collapse is known to occur during the occupation of a burrow. Even in calcareous soils of southern Saskatchewan, collapse can be a major cause of mortality in ground squirrels, which get buried when soils become saturated by water in the spring (P. Fargey, personal communication 1999).

It can be assumed that the prolonged use of the burrow decreases the fidelity of the burrow to the dimensions of its constructor. Gambaryan (1960) writes that the mole-

rat feeding burrows (constructed during foraging and relatively short-lived) fit this animal so closely that any forward movement of the pelvis causes the knee to hit the side of the burrow or the femur to come against the body of the animal. This can be contrasted with burrow systems of wolves, badgers, and Eurasian marmots. Such burrow systems are often continually used for hundreds and even thousands of years and their diameter may in some parts of the burrow become enlarged relative to the size of their inhabitant (Dinesman 1968, Heinrich 1977). Burns (1996) studied a fossil prairie dog town, where the age of individual tunnels ranged from 33,650 to 22,000 years. Refitting, collapse and subsequent clearing of debris must imprint multiple signatures on the burrow that was initially excavated by a single animal. A study of the infilling processes in modern burrows with a smaller life-span would allow for better distinction between different taphonomic signatures.

This thesis examines the burrows of two living rodents, woodchuck (*Marmota monax*) and chipmunk (*Tamias striatus*), to offer a quantitative assessment of the taphonomy of cross-sectional characteristics of mammal burrows (Chapter Two) and a quantification of claw mark features (Chapter Three).

MARMOTA AND TAMIAS

The two most common burrowers in temperate and boreal eastern North America are the woodchuck (*Marmota monax*) and the chipmunk (*Tamias striatus*), both members of the subfamily Marmotini within the family Sciuridae (Woods 1980). They represent two distinct size classes, so their burrow sizes never overlap (Elbroch 2003). Both are solitary, relatively unspecialized burrowers and because they are relatives, they may be expected to exhibit similar digging behaviour.

The tree-dwelling forms are primitive within the family Sciuridae (Mercer and Roth 2003, Herron et al. 2004, Steppan et al. 2004). Among the ground-dwelling forms, the degree of adaptation to digging and commitment to life underground increases from chipmunks (tribe Tamiini) and North American ground squirrels to Eurasian ground squirrels (both belonging to the genus *Spermophilus*), prairie dogs (*Cynomys*), and marmots (*Marmota*). Adaptation to terrestrial locomotion can be estimated by the ratio between the hind and the front limbs. Hind limbs are 23.5% longer than front limbs in chipmunks, but only 9.2–11% longer in marmots (Bibikov 1967). Although these more advanced forms do not reach the level of adaptation observed in those rodents that obtain their food below the surface, such as the gopher (*Geomys*) or the mole-rat (*Spalax*), burrows do play an important role in their life history. Burrows provide shelter throughout the year, a site for hibernation in the winter and for rearing the young in the spring. Most of the ground-dwelling sciurids spend more than half the year below the ground.

Chipmunks are known since the early Miocene of North America and Eurasia. The tribe Tamiini occupies morphologically an intermediate position between the burrowers and the climbers. Though chipmunks are believed to be weak diggers, the underground excavations of *Tamias striatus* can be up to 10 m long (Panuska and Wade 1956). During hibernation, chipmunks enter a shallow torpor, from which they periodically awaken to feed. While other hibernators, including marmots, survive the winter on accumulations of fat, chipmunks rely on nuts cached in special chambers inside the burrow.

Table 1-2. Characteristics of chipmunk burrows.

	Simple system (caches, no nest)		Extensive system (caches and nest)	
	Range	Mean	Range	Mean
Entrance diameter (cm)	5.1–6.4 ¹ , 3–15 ²	5.8	4–7.5	5.9
Plugged entrances	0–1	0.1	0–4	0.9
Depth (cm)	30.5–76.2 ¹ , 7.5–62.5 ²	20.6	61–86 ¹ , 12.5–42 ²	25.3
Anastomosing	Yes ²			
Entrances	1–3	1.4	1–4	2.7
Nesting	Present			
Defecation chambers	Commonly none			
Ramp	45°			
Number of living chambers			1–4	1.9
Number of caches	0–1	0.1	0–3	0.5
Total length (m)	0.125–1.25	0.545	max 8.84 ¹ , 1.65–10.09 ²	4.157

(¹Panuska and Wade 1956, ²Thomas 1974).

Table 1-3. Characteristics of woodchuck burrows.

	Range	Average	Notes
Entrance diameter, (cm)	13–40 ¹ , 23x11.5 ⁵	25 ¹	
Plugged entrances	Present in hibernation burrows		
Depth (cm)	100–150 ¹ , –195 ²		
Anastomosing	No		
Entrances	1–5	1.8	Less on slopes and in the woodland, more on flat open areas. More in wet areas
Nesting	Dried and shredded leaves, sometimes bare		
Defecation chambers	Latrine or buried in the mound		
Downshaft diameter (cm)	10 ² , 15 ¹		
Number of living chambers	1-2		
Total length (m)	0.8-6.4 ⁵	4.95 ¹ , Median 4.8 ⁵	n=21 ¹ , n=9 ⁵
Total volume (cm ³)		315000 ¹	

(¹ Grizzell 1955, ² Hamilton 1934, ³Bruleigh and Vandruff 1998, ⁴Allen and Shapton 1942, ⁵Fisher 1893)

Marmots are known since the late Miocene of North America, but all the extant species are young, dating back only to the Pleistocene (Armitage 2000). *Marmota monax* is the most divergent form of this otherwise homogeneous group. It is the only inhabitant of the forest zone, and the only solitary species. It is also smaller than most other marmots, weighing 3–4 kg, and only in rare cases attaining 7 kg (Hamilton 1934, Bibikov 1967).

Tables 1-2 and 1-3 show characteristics of chipmunk and woodchuck burrows pooled from several studies of the burrow architecture of these species. Both chipmunks and woodchucks, and likely ground-dwelling sciurids generally, often excavate nests next to stones or walls, below roots of a tree or other dense natural objects (Bihr and Smith 1998). In addition to providing structural stability, such arrangement protects the animal against predators that dig for their prey (coyotes and badgers).

Chipmunk burrows contain multiple nut caches which are stored in special chambers and in the galleries themselves. Latrines have only been reported once by one author (Calahane 1947) and have been found missing in several extensive studies of chipmunk burrows (Elliott 1978, Panuska and Wade 1956, Thomas 1974). The presence or absence of latrines is often a species-specific characteristic of burrows (Hickman 1990). Entrance ramps are quite steep (around 45°), but there are no shafts. Chipmunk nests are found in the deepest part of the burrow, but still often lie above the depth of frost penetration. In winter, this necessitates the use of nesting litter, which can allow the temperature in the chamber to be raised by 10°C (Panuska and Wade 1956). Earth plugs are made not only in the burrows used for hibernation, but also in simple systems

containing storage chambers. Blocking the entrance to such burrows prevents them from getting plundered (Thomas 1974).

Woodchuck burrows always contain latrines, usually in blind pockets 30–100 cm long. The angle of descent is 35–40°. Those burrows used for hibernation sometimes contain a plunge hole, or shaft, which extends almost vertically from the surface to the depth of 0.5–1.0 m, where it ends in a turnaround chamber. These three features are shared with the other members of the genus (Letov 1950).

The distance to the first turn and the number of turns is commonly reported as a stable characteristic for Eurasian marmots, but neither has been measured for the woodchuck. Where a plan view is available, it is possible to calculate this value for woodchuck burrows. On Fisher's (1893) figures VI-VIII, the first turn occurs at 90-110 cm in most cases, in some cases 70 cm, in one case in only 30 cm (a 45° turn). Another feature that has not been measured but may be characteristic for the species is the distance from the entrance to the earth plug. Some species put the plug flush with the surface, some even push it above the surface in a crest, others leave 20–100 cm, still others several metres (Davydov et al. 1978, Kizilov and Berendiaev 1978). The structure of the plug is not described for the woodchuck, but it is known that some other species specially prepare or save earth balls 0.5 and 5 cm in diameter which, when put together in a plug, let some air through (Letov 1950, Davydov et al. 1978).

Although Merriam (1884) and Grizzell (1955) found some nests only 45 cm below the surface, woodchuck nests, unlike those of chipmunks, are generally found close to or below the frost line. However, nests are not found in the deepest part of the

burrow, either. Higher positions may be colder in the winter but are less likely to be flooded in the spring (Thomas 1974).

In addition to species-specific characteristics, descriptions of burrows reveal the variability in architecture that reflects the life-history characteristics of the animals, the history of burrow use and remodelling, and the particular physical environment. Both marmots and chipmunks generally survive to the age of three years in the wild (Grizzell 1955, Linduska 1950). The chest girth changes throughout the animal's life span, especially in the woodchuck, which goes through seasonal cycles of weight gain and loss. However, this change is probably reflected in the size of only some burrows and then only to a limited degree. Hibernation burrows are generally excavated when the animals are fattest. The young of the year do not dig a summer burrow, but occupy an abandoned one until the fall (Grizzell 1955). The young fatten up later into the fall than the adults, so that when they lie down in hibernation, the difference in mass between the two groups is not large. At the end of the year, the young are about 1 kg lighter than the yearlings and the adults. Hamilton (1934) believes that young animals dig smaller, shallower burrows.

Chipmunks tend to stay in the same area throughout the year, but woodchucks, except for rare cases (e.g. Grizzell 1955), choose different sites for summer and winter burrows, so that remodelling of a simple system into a hibernation burrow is less probable. However, since summer burrows are not occupied by the woodchuck in winter, they are often used by other animals (skunks, rabbits: Allen and Shapton 1942).

Soil hardness affects both the ease of excavation and the wear of the burrow opening. In sand, woodchucks dig to the depth of 200 cm, but in gravelly soil, the depth of their constructions rarely exceeds 120 cm (Hamilton 1934). Wear explains why the

entrance diameter is usually larger (sometimes three times larger) and more variable than tunnel or vertical shaft diameter (Grizell 1955, Panuska and Wade 1956). Bihr and Smith (1998), however, found the diameter of the tunnels to be more variable between burrows (for *Tamias minimus*, $\bar{X} = 3.7 \pm 1.08$, $n=21$) than the diameter of the entrances ($\bar{X} = 4.4 \pm 0.70$). Unfortunately, it is the entrance diameter that is most commonly reported in life-history and ecology studies (Laundré 1989). In one marmot species (*Marmota caudata*), soil moisture is reported to be associated with burrows having more entrances, which helps air circulation, drying and thawing (Kizilov and Berendiaev 1978), but such association has not been found in woodchuck burrows. In addition to difference between burrow systems, burrow diameter is reported to vary within the same burrow, and some authors mention that it decreases with depth (Hamilton 1934, Kizilov and Berendiaev 1978), but no data substantiating this has been published.

The process of burrow construction has received less attention than the architecture of burrows. Digging movements of marmots are not well known with the exception of short descriptions by Hamilton (1934), Gilbert (1940) and Gambaryan (1960). In addition to these descriptions, the digging sequence of the closely related prairie dogs (Stalheim-Smith 1984) can be used as a close analogue for both woodchucks and chipmunks. Woodchucks are reported to use incisors in addition to claws during digging (Agrawal 1967). It is possible that unlike true incisor-diggers, woodchucks only use incisors to cut roots when starting to excavate a burrow (Hamilton 1934,).

Evidence for digging movements in *Tamias* is provided only by traces on burrows observed by Panuska and Wade (1956). Traces include longitudinal furrows, which they interpret as claw marks and small pockets, possibly representing bite marks. Soil has

been observed being evacuated by forward pushing and backward kicking. Some observers have suggested that soil is also removed in cheek-pouches, but this seems unlikely (Panuska and Wade 1956, Allen 1938).

The anatomy of *Marmota monax* is well described (Bezuidenhout and Evans 2005), and limb anatomy has been described for all sciurids, including *Tamias striatus* and *Marmota monax* (Thorington et al. 1997). From the literature review, the published descriptions of burrows and morphology of the two species appear sufficient for the identification of their burrows in open and filled state. Woodchuck and chipmunk are therefore suitable animals for the study of taphonomic differences between open and filled burrows.

THESIS OBJECTIVES

In this thesis, modern analogues of fossil burrows are used to study the morphology of burrows in relation with its tracemaker. The objectives are to:

- 1) Describe the architecture of filled woodchuck and chipmunk burrows and their geological context.
- 2) Test differences in cross-sectional diameter between abandoned open and backfilled burrows of woodchuck and chipmunk.
- 3) Explore the variability of claw marks on a woodchuck burrow and to interpret it in terms of digging movements.

The first two objectives correspond to the first part of the study and are described in Chapter Two. The last objective corresponds to the second part of the study and is described in Chapter Three of this thesis.

CHAPTER 2

Spatial variability of filled and open burrows of woodchuck (*Marmota monax*) and chipmunk (*Tamias striatus*)

INTRODUCTION

Vertebrate fossil burrows are biogenic sedimentary structures that can be used to reconstruct behaviour (Hasiotis 2002). In order to relate the reconstructed behaviour to an animal taxon, it is necessary to identify the tracemaker. Skeletons of tracemakers are only rarely found in fossil burrows, so that the identity of the tracemaker has to be inferred from the cross-sectional size of the burrow. Mammals are believed to construct tunnels to match their dimensions (Nevo 1999); however, the formation of the burrow cast is poorly understood, and it is not clear how closely the dimensions of the fossil burrow reflect those of the original excavation.

This study compares differences in cross-sectional width and height between open and filled burrows. Woodchuck (*Marmota monax*) and chipmunk (*Tamias striatus*), two species of sciurids, were selected to contrast taphonomic differences within burrows of different diameter classes. In this study, burrows and their sedimentary contexts are described. Filled burrows have not previously been mapped in soft sediment, and open burrows have been studied from excavations focused on descriptions of plan geometry rather than cross-sectional variation. The results of the study are used to discuss the published interpretation of a fossil burrow.

BACKGROUND

Burrows are constructed by representatives of most orders of modern mammals for temporary shelter, raising their young, hibernation or aestivation, and foraging or hunting prey (Reichman and Smith 1990). The use of burrows is common in the temperate regions generally and prevalent in grasslands (Formozov 1966). By constructing or adopting a burrow, animals escape some of the selective pressures of their environment (Nevo 1999).

In the last two decades, a growing number of descriptions of fossil vertebrate burrows have been published. With the exception of two studies (Martin and Bennett 1977, Gobetz 2006), the tracemaker was identified from the skeleton found inside the burrow (e.g. Groenewald 1991, Groenewald et al. 2001, Damiani et al. 2003, Varicchio et al. 2007). Vertebrate burrow trace-fossils complement the body-fossil record by providing information on behaviour, such as hibernation, aestivation, food caching and belowground feeding (Quintana 1992, Burns 1996, Gee et al. 2003, Hembree et al. 2004). Most importantly, fossil burrows provide direct evidence of behaviour that can be compared with inferences made from body fossil morphology. For instance, the skeletal morphology of the identified tracemaker can be analyzed for evidence of digging adaptations (Ray and Chinsamy 2003, Smith 1987).

In order to be used as independent evidence for behaviour, burrows have to be identified not from body fossils but from their own morphology. The tracemaker becomes fossilized in its burrow only in the rarest cases, and a much greater number of burrows can be taken into account if the tracemaker is identified from their architecture, surface marking, and cross-sectional diameter (Doonan and Stout 1994, Damiani et al. 2003, Martin and Bennett 1977). *Architecture* can be species-specific, but also varies

depending on its function (hibernation, shelter, raising young), location within the geographic range (related to the availability of other shelter), and substrate conditions (Hickman 1990). Architecture is strongly dependent on the history of a particular burrow, as an existing burrow can be refitted to serve a new function as new tunnels and chambers are added and others backfilled (Kucheruk 1983). *Surficial markings* are left by the burrower's claws or teeth, and therefore closely reflect the morphology of the tracemaker (Martin and Bennett 1977, Gobetz 2006). However, claw and tooth marks are not always found on fossil burrows, because their preservation depends on the substrate (Loope 2006) and wear (see Chapter Three). *Cross-sectional size* of the burrow is the most easily obtained and the most commonly reported characteristic of a fossil burrow. For reasons of energy minimization, it is closely related to body size of the burrower (Reichman and Smith 1990, Nevo 1999).

The variation in burrow dimensions for a single species may be related to the age of the animal, the length of occupation of the burrow, and the substrate properties, although these relationships are poorly tested. The narrower the size range of digging individuals within a species, the less variability can be expected in the burrow dimensions. It is common for young-of-the-year to occupy existing burrows, so that burrows are excavated only by mature animals with a size range narrower than that of the entire population (Reichman and Smith 1987). Substrate is also believed to play some role in the variability of burrow size. Laundré (1989) studied the dimensions of burrows of five small rodent species (Townsend's ground squirrel, *Spermophilus townsendii*; Wyoming ground squirrel, *Spermophilus elegans*; deer mouse, *Peromyscus maniculatus*; Ord's kangaroo rat, *Dipodomys ordii*; and montane vole, *Microtus montanus*). The study found

that although the effect of bulk density and soil texture on burrow dimensions was statistically significant for some small mammal species, no consistent pattern was observed. In montane voles, horizontal diameter and vertical diameter decreased with greater bulk density. In deer mice, a combined effect of soil texture and bulk density was recognized on vertical diameter, and in three other species, soil characteristics had no effect on burrow dimensions. Variability due to length of occupation has not been quantified, but it can be related to the repair of collapsed or filled portions of the burrow, which may enlarge the burrow. The length of occupation is largely species-specific, with the most short-lived burrows created by the most specialized, often subterranean diggers. Weaker and less specialized burrowers will more often adopt and adapt an existing burrow, sometimes of a different species (Reichman and Smith 1987).

PRESERVATION AND MODIFICATION OF BURROWS

The existing criteria for identifying tracemakers do not account for variation introduced after abandonment and during the preservation of burrow casts. Three interpreted modes of filling are mentioned in descriptions of fossil burrows: rapid passive fill, colluvial fill (a slow passive fill), and active fill. Most burrow casts are found in floodplain deposits and are interpreted to be rapidly filled in a flash-flood (Smith 1987, Hasiotis et al. 2004). Another filling mechanism, called colluvial fill, has been mentioned by Heinrich and Jäger (1975) in a paper devoted to the infill of fossil badger setts (colonial burrows). Colluvial fill involves slow passive fill by sediment movement from the entrance of the burrow. Some animal species are capable of actively backfilling unused portions of their burrows. This type of fill is well known for invertebrate ichnofossils (Hasiotis 2002), but is not mentioned in descriptions of fossil vertebrate

burrows. However, many species of mammals are known to backfill portions of the burrow either seasonally (during hibernation), or while refitting the burrow (for instance, rebuilding a hibernation burrow into a shelter burrow) (Kucheruk 1983, Reichman and Smith 1990).

The mode of infilling defines the relationship between the freshly excavated burrow and the burrow cast. The cast resulting from backfilling is an exact negative of the open burrow. The cast resulting from rapid passive fill reproduces the top part of the burrow but not the bottom, where colluvium has accumulated on the floor of the burrow. The cast resulting from a slow passive (colluvial) fill reproduces the bottom part of the burrow, but not the top, because in many places the burrow remains incompletely filled. All three filling mechanisms can be combined in a single burrow, producing different relationships with the original burrow dimensions. In general, the longer the burrow remains open and uninhabited before being filled, the more modification can be expected to occur. What modifications occur in burrows is not known, but two processes that can be hypothesized based on soil mechanics are failure, most likely in the form of roof collapse, and plastic deformation. Both processes reduce mainly the vertical diameter of the burrow. It can therefore be expected that vertical diameter (cross-sectional height) would be more variable along a single burrow and would differ between open and filled burrows. Horizontal diameter (cross-sectional width) can be expected to be less affected by roof failure and colluvial fill, and therefore vary little both within a single burrow and between burrows in various states of abandonment and infilling.

In this paper, this prediction is tested by comparing width and height between open and filled burrows of two species of rodents. If burrow width is preserved during

filling of the burrow, then the width of open and filled burrows will be statistically indistinguishable. If burrow width is affected by collapse and fill, then a comparison between open and filled burrows will show statistically significant differences.

Because tunnels with a larger diameter can be expected to be more prone to collapse, the species were selected belonging to different size classes with non-overlapping diameters of burrows. The species used in this study belong to sister taxa within the family Sciuridae: the woodchuck (Marmotini: *Marmota monax*) and the chipmunk (Tamiini: *Tamias striatus*) (Mercer and Roth 2003). The woodchuck is a larger (adult weight 2-4 kg), more specialized digger than the chipmunk (adult weight 70-120 g). Although both animals spend most of their life in the burrow, they are morphologically little specialized for digging (Hamilton 1934, Allen 1938).

METHODS

A comparison between burrows at different stages of abandonment and filling required collection of field data to capture burrow geometry. Burrow geometry was described differently for open and filled burrows. Whereas techniques for studying open burrows involve making casts, and are described in the literature, the collection of data from filled burrows required the development of an approach involving cross-sectional reconstruction, described in some detail below.

Study sites

Field data were collected at three study sites:

- 1) a site in Gatineau Park, Quebec (filled burrows of woodchuck and chipmunk);
- 2) a site in Ottawa, Ontario (plaster casts of open woodchuck and chipmunk burrows, partially filled woodchuck burrows);

- 3) a site in Prince Edward Island National Park (chipmunk partially-filled occupied burrows).

Gatineau Park site

The Gatineau Park site is located at 45°37'N, 75°50'W in the Gatineau Hills, Quebec, at the southern border of the Laurentian Uplands in the Boreal forest zone (Figure 2-1). The predominant surface deposits in the Gatineau Park are glaciofluvial ice-contact sands and gravels in unequally distributed eskers and kames, outwash plains and fans (Buckley 1970). To the south and west of the park, the postglacial Champlain Sea has deposited clays that now form a flat plain. The Champlain Sea clays are found 1 km east of the study site, so that it is possible that sands found on the study site were associated with deltas forming into the Champlain Sea (Hogarth 1970, St. Onge 1997). The geological map of the area (St. Onge 1997) shows the sand pit area covered with glaciofluvial deposits.

The Gatineau Park site is situated in the side of an old sand pit excavated into a sand hill surrounded by bedrock. Although the distribution of mammal burrows in the southern part of the Canadian Shield has not been studied, an analogy with eskers in the Slave Geological Province (in the northwest of the Shield) suggested that burrows may be concentrated in sand ridges surrounded by areas of bedrock (Desjarlais 1998, Dinesman 1968). A preliminary survey confirmed the presence of filled burrows at this location.

All genera of digging mammals found in the Gatineau Park (Table 2-1) have a wide Boreal distribution, and it is possible that they have been present in the area at least

Figure 2-1. Location of the three study sites. A. Gatineau Park site and Ottawa site. B. Prince Edward Island site.

since the retreat of the Champlain Sea 9,500 years ago (Banfield 1974). The only exception is the coyote (*Canis latrans*), which has extended its range from the West into the study area in the last century.

Forests in the study area were cut in the middle of the nineteenth century, and agricultural fields were established. The site is found on one of such fields which, although abandoned since the 1940s, has not been overgrown with forest.

Ottawa site

The study site is located on unoccupied lands of the Lebreton Flats in Ottawa, Ontario (45° 25' N; 75° 42' W). It is an old road embankment oriented northwest-southeast and now overgrown with pines and shrubs. Chipmunk and woodchuck burrows are found on a 10° slope of north-eastern aspect. Woodchucks have been last observed occupying burrows on the site two years prior to the study period. The burrows became abandoned as the shrubs have grown high.

Prince Edward Island site

The site is located at 46° 41' N, 63° 8' W in the Prince Edward Island National Park. The partially filled occupied chipmunk burrows were studied in a section 1 × 2 × 2 metres excavated in a forested area of a parabolic dune at an elevation of 5 m above sea-level. The substrate at this site is an anthropogenic mix of sandy loam and aeolian sand associated with an old dry-stone field-dyke.

Table 2-1. The digging fauna of the Gatineau Park region. List compiled from Banfield (1974) and National Capital Commission (2007). Burrow diameters from Elbroch (2003), body weights from Banfield (1974) unless noted otherwise.

Latin name	English name	Entrance diameter, mm	Body weight, g	Habitat
<i>Blarina brevicauda</i>	Short-tailed shrew	25-32	18	Broadly terrestrial, esp. damp brushy woodlands, bogs
<i>Canis latrans</i>	Coyote	330–610	15900–20500	Wide range
<i>Canis lupus</i>	Timber wolf	508–889	25000–30000	Wide range
<i>Condylura cristata</i>	Star-nosed mole	25–32	40–50	Semiaquatic
<i>Marmota monax</i>	Woodchuck	133–279	1550–5000 ¹	Forest edges and openings
<i>Microtus pennsylvanicus</i>	Meadow vole	19–35	14–38 ²	Meadows, lowland fields, grassy marshes.
<i>Napaeozapus insignis</i>	Woodland jumping mouse	40	17–26	Boreal habitats
<i>Parascalops breweri</i>	Hairy-tailed mole	25–35	40–65	Hardwood forests, forest edge, meadows
<i>Sorex cinereus</i>	Masked shrew	19–22	3.6 ³	Open and closed forests, meadows, river banks
<i>Sorex fumeus</i>	Smoky shrew	20-25	5 ⁴	Deciduous and coniferous forests
<i>Synaptomys cooperi</i> †	Lemming mouse	20	14–42	Sphagnum bogs, coniferous and deciduous forests
<i>Tamias striatus</i>	Chipmunk	38–51	70–140 ⁵	Open forests
<i>Tamiasciurus hudsonicus</i>	Red squirrel	57–76	200–250 ⁶	Deciduous and coniferous forests; Parks and Hedgerows
<i>Vulpes vulpes</i>	Red fox	152–305	3000–7000	Wide range
<i>Zapus hudsonius</i>	Meadow jumping mouse	43	13.5–26.1 ⁷	Humid habitats with herbaceous cover, open forests

¹Hamilton 1934, Grizzell 1955; ²Iverson and Turner 1974; ³Tuttle 1964, Whitaker 2004; ⁴Morrison et al. 1957, Owen 1984; ⁵Mearns 1891, Panuska 1959, Levenson 1990; ⁶Yahner 1980 ⁷Whitaker 1963. †Has not been observed inside the park.

Burrow characterization

Open burrow casting

Woodchuck and chipmunk burrows were cast with plaster. Previous workers have cast burrows using clay (Panuska and Wade 1956), concrete (White 1962), polyurethane foam (Felthausen and McInroy 1983, Hembree and Hasiotis 2004), and plaster of Paris (Gobet 2006). Plaster was used in this study because it is known to preserve detailed surface structure (Gobet 2006).

All excavations required a crew of 2 persons. Thinly mixed quick-set plaster of Paris was poured into the burrow. One burrow system was excavated for *Marmota monax* and three for *Tamias striatus*. The casts were sawed into sections while still in the ground and extracted piece by piece. Filling the woodchuck burrow with plaster took approximately 10 hours over the period of three days. The excavation of the woodchuck burrow cast, using both large and small hand tools, took approximately 50 hours. The layers through which the burrow passed were recorded as they were exposed during excavation. The filling of three chipmunk burrows took half an hour to an hour each, and their excavation took an hour to two hours.

Filled burrow reconstruction

Quantitative data on the cross-sectional dimensions of filled burrows were collected through excavation and three-dimensional mapping of the subsurface. A $10 \times 1.5 \times 2$ m volume was excavated (about 30 m^3) (Figure 2-2).

Prior to excavation, a 5×10 m area was surveyed in one metre squares using a compass, a measuring tape and an engineer's level equipped with a horizontal Vernier circle. In the course of excavation, some areas outside the surveyed rectangle were

Figure 2-2. The Gatineau excavation site. A. View of the surface grid looking northwest (stakes on the right). B. View of the excavation face looking north.

Figure 2-3. Elevation map of the Gatineau study site. Quadrat names are marked at their northeastern corner. Squares mark the location of three burrow systems (A - woodchuck burrow; B - chipmunk burrow A; C - chipmunk burrow B).

additionally mapped as burrow traces were discovered (See Figure 3-3 for a map of the study site). Each of the one metre squares was referred by a code of the type 1N1, often used in archaeological excavations (Hogg 1980). N stands for north; the first number is the distance in metres east of the zero stake, and the second number, the distance north of the zero stake. A code of the type 1N refers to east-west position only, and a code of the type N1 refers to the north-south position only.

The excavation exposed a section down to a maximum depth of 200 cm below the surface, but the mapped depth depended on the presence of traces, including root casts, because in many cases, burrow traces could be distinguished from root traces only through serial excavation. After a section was documented, the next section was made 2–15 cm inward depending on the density and the size of the traces encountered.

Burrow traces were documented by photographing consecutive vertical section faces with a digital camera (Nikon Coolpix 5700, 5 mega pixels) mounted on a tripod. In total, more than 500 photographs were taken. Care was taken to photograph the sections from approximately the same distance (one metre) and perpendicular to the wall. In order to facilitate subsequent scaling and perspective correction of the images, a wire grid was placed against the wall on each photographed section. Sedimentary layers were described at each vertical section, and a sample was taken for each layer. The grain size composition of sedimentary layers was later determined through dry sieving of the samples.

The site-wide three-dimensional coordinates of each section were recorded from two sources. A surface grid of stakes planted at one metre intervals in lines running north-south and east-west served to establish coordinates in the horizontal plane.

In the field, coordinates in the vertical plane were established relative to the soil surface above the section by measuring distances from the edge of bank to the corners of the wire grid. The grid had a mesh of 10 cm and was mounted on a wooden frame 1×1 m. Another grid was used later in the excavation, with a frame made of aluminium angle. At each section, the grid was levelled using a carpenter's level, the sides were aligned horizontally with an east-west stake line and the corners fixed against the section wall using skewers.

Although an effort was made to make the section wall as vertical as possible, a deviation from the vertical was always present. To calculate the inclination of the section wall relative to the vertical, the horizontal distance from the edge of bank to the point above a corner of the grid was measured ("extension"). We measured extensions above each corner of the grid. In the illustrations, corners are numbered 1,2,3 and 4 and corresponding extension measurements are "extension1", "extension2", etc. In the formulas, a general notation of the type "extensionN" was used, where $N=1,2,3,4$.

The other measurements served to establish the three-dimensional position of each section. Table 3-2 lists and Figure 3-4 illustrates the coordinate measurements. Measurements were taken to the closest stake line for horizontal coordinates (x, z). The vertical coordinate was calculated from several measurements using the formulas shown on Figure 3-4. Vertical measurements include the depth measured down the wall section from the bank edge to a corner of the grid ("DinclN") and the vertical depth of a corner of the grid below the edge of bank measured down a plumb line. The plumb bob was attached to the end of a dowel that was laid on the soil surface perpendicular to the bank edge and moved until the bob touched a corner of the grid. "ExtensionN" was

Table 2-2. Measured and calculated variables for positioning traces in three-dimensional space. Distances measured for each inside corner of the wire grid.

Variables	Explanation	Measurement type
N	Corners of the grid ($N=\{1,2,3,4\}$)	
DinclN	Depth below edge of bank measured along the wall at the N-th corner of the grid	Vertical measurement
yN	Vertical distance from the bank edge to the N-th corner of the grid (measured down the plumb line attached to a dowel)	Vertical measurement
extensionN	East-west distance from the edge of bank to the N-th corner of the grid (measured along the dowel)	Horizontal measurement
x	North-south distance from stake line N0 to the edge of bank above corner 2.	Horizontal measurement
zN	East-west distance from stake line 0N to the bank edge above one of the top corners (negative when east of stake 0N)	Horizontal measurement
elevN	Surface elevation above datum at the N-th corner of the grid	From the elevation map
elev_downN	Surface elevation above datum at the northern end of dowel at the N-th corner of the grid	From the elevation map
elev_bankN	Surface elevation above datum at the edge of bank at the N-th corner of the grid	From the elevation map
dowel_length	Length of the dowel to which plumb bob was attached	Constant
calculated average depth	Depth of the top of the grid below site-wide datum. Average of vertical position estimates for two top corners of the grid	Calculated
extension_downN	“extensionN” corrected for surface slope	Calculated
Δ_{extN}	“Extension_downN” correction related to frame thickness	Calculated
Δy_{downN}	“yN” correction related to surface slope	Calculated
Δy_{fN}	“yN” correction related to the thickness of the grid frame	Calculated
Dincl_trueN	“DinclN” corrected for the thickness of the grid frame	Calculated
y_trueN	“yN” corrected for the thickness of the frame and surface slope	Calculated
extension_trueN	“extension” corrected for the thickness of the frame and surface slope	Calculated

Figure 2-4. Field measurements and calculations (refer to Table 3-1 for explanation of terms). Diagrams not to scale. A, C, D, E, F – side view (looking south). B – front view (looking east).

A. Measurements of the section wall orientation. The inclination of the section wall is exaggerated for demonstration purposes.

B. Transformation of individual section measurements with reference to a single datum. In front view, vertical distance “Y” and wall distance “Dincl” completely overlap. Note that the soil surface is inclined in both west-east (soil surface line) and north-south (edge of bank line) directions.

$$\Delta y_{\text{down}} = \frac{(\text{elev_downN} - \text{elev_bankN})}{(\text{dowel_length} - \text{extensionN})} \times \text{extensionN}$$

C.

$$\text{extension_downN} = \left[1 - \left(\frac{(\text{elev_downN} - \text{elev_bankN})}{(\text{dowel_length} - \text{extensionN})} \right)^2 \right] \times \text{extensionN}$$

D.

$$\text{Dincl_trueN} = \sqrt{(\text{DinclN})^2 - 2.54^2}$$

$$\text{extension_trueN} = \text{extension_downN} - \Delta \text{extN}$$

E.

$$y_{\text{trueN}} = yN + \Delta y_{\text{fN}} + \Delta y_{\text{downN}}$$

F.

Figure 2-4 continued. C. Corrections to “yN” due to surface slope. Calculation of “ Δy_{downN} ”. D. Corrections to “extensionN” due to surface slope. Calculation of “extension_downN”. E. Corrections to “DinclN” and “yN” due to thickness of the aluminium grid frame. Calculation of “Dincl_trueN”. F. Calculation of “y_trueN”.

measured as the length of the dowel between edge of the bank and the attachment of the plumb bob string. Additional corrections to measured values had to be calculated to compensate for surface slope and thickness of the frame, which affected some measurements (See Table 3-2 and Figure 3-4 C, D, E, F).

The range of width and height of infilled burrows measured directly off the section wall is much greater than the true variation of cross-sectional characteristics. This is because the wall usually cuts the burrow at an oblique angle (Figure 2-5). In order to obtain a perpendicular section, it is necessary to first reconstruct the three-dimensional shape of the burrow from serial sections. The greater the number of sections used to reconstruct the burrow, the better the inference of the position of the burrow axis and its curvature. Before cross-sectional measurements of infilled burrows could be taken, the geometry of filled burrows had to be reconstructed from photographs of individual sections and from their coordinates recorded in the field.

The photographs were first scaled and rectified in ArcMAP (ESRI 2006) using the wire grid for reference. Layers, sublayers, root casts, fault lines, and burrow contours were then traced from photographs in ArcMAP (ESRI 2006) and imported into AutoCAD (Autodesk 2004), where they were positioned and rotated in three-dimensional model space using coordinates calculated from field measurements and corrections. Each one metre by one metre quadrat was traced separately but later integrated into a single model using the calculated angles and distances. Surfaces were then fitted through the oblique burrow contours in Rhinoceros 3D (McNeel 2006) using the NURBS tool to produce a three-dimensional model of each burrow. Because each tracing affects the inference of

Figure 2-5. Ellipses obtained by intersecting cylinder with planes at various angles. A. The plane passes through the axis of the burrow. Green outline: plane at a horizontal angle with the axis of the burrow. Red outline: plane at a vertical angle with the axis of the burrow. B. The plane intersects the cylinder at two different distances from the axis.

the burrow path at the neighbouring points, the construction of the model required multiple retracing of burrow contours.

Partially filled burrows

Partially filled burrows are burrows modified by collapse or infill. The filling of burrows occurs either actively when the animal backfills portions of its own or an existing burrow, or passively, by colluvial fill (Heinrich and Jäger 1975). An occupied chipmunk burrow was excavated at the Prince Edward Island site to estimate the role of colluvial fill and collapse during the active use of the burrow and aid in the interpretation of processes leading to the formation of burrow traces. Sections exposed partially filled chipmunk burrows and food caches. Segments of the burrow system were photographed on horizontal and on vertical sections. Additionally, partially filled woodchuck burrows were exposed and photographed as part of the excavations at the Gatineau Park site.

Measurement

Burrow cross-sections are not circular; therefore, two measurements are necessary to characterize them: width, or transverse diameter, and height, or ceiling-to-floor diameter. Plaster casts of open burrows were measured directly with a sliding Gneupel calliper. The filled burrows were measured from their reconstructions (computer models). The reconstructed tunnels were contoured perpendicular to the burrow axis in Rhinoceros (McNeel 2006), and the width and height of the perpendicular contours was measured using a routine in AutoCAD (Autodesk 2004). Because the connection of cross-sections into a three-dimensional body involves an interpolation, measurements were taken at the cross-sections, where the interpolation error is smallest.

Statistical analysis

Analysis of quantitative characteristics was limited to cross-sectional width and height. For other quantitative characteristics, such as angles of junction and turn, measurements are not sufficiently numerous in a single burrow to be studied statistically. The measurements yielded eight statistical samples for each of width and height of both filled and open woodchuck and chipmunk burrows. Some of the samples included chambers and branching points in addition to tunnels. In these cases, chamber measurements were excluded from the sample. The normality of the distribution of each sample was tested using the Shapiro-Wilk statistic and the skewness index. Width and height were then compared between open and filled burrows in order to test the prediction that cross-sectional width is better preserved through burrow history than the cross-sectional height. Because all the distributions were found to be non-normal, a non-parametric Mann-Whitney U test was used, at the 0.95 significance level ($p=0.05$). Where both width and height differed between the open and filled burrow, open burrow width was compared to filled burrow height, and open burrow height was compared to filled burrow width, in order to check if in these cases open and filled burrows had the same cross-sectional area.

RESULTS

Stratigraphic context of filled burrows

The geologic features encountered in the Gatineau Park site are soil horizons, sedimentary layers, and trace-fossils. The stratigraphic sequence varies considerably across the ten metre width of the studied section. Figure 2-6 shows the layers and horizons exposed at three points in the study site. Letters mark soil horizons, numbers

Figure 2-6. Gatineau Park site. Stratigraphic section. Letters mark the soil horizons, numbers mark sedimentary layers. Refer to Table 2-3 for descriptions of layers.

mark geologic layers. Soil horizons are named according to the Canadian system of soil classification (Canada Soil Survey Committee 1978).

1. Sedimentary layers. The main kinds of deposits in the section are sands and sandy gravels. Grain size analyses showed that sands range from silty-fine to medium-coarse sands (See Appendix A for grain-size data). Silty-fine to medium sands are either horizontally laminated or contain ripple cross-lamination. Sandy gravels are interpreted as lag deposits (Table 2-3). Clay rip-up clasts are found in patches throughout the study site at the top of the undisturbed section (layer 12: Figure 2-7, Figure 2-8) and locally within layer 3 (Figure 2-9c). The fluvioglacial origin of the deposits at the study site (St. Onge 1997) is confirmed by their high topographic position, occurrence of cross-lamination, and good sorting (Benn and Evans 1998).

The exact sequence of layers varies about every 3 metres north to south. The grain size within an individual layer changes on a slightly smaller scale. The more continuous features of the section are the lag gravels and the sand layer intercalated between the gravels. The sand layer associated with the gravel lag (layer 5) has planar bedding that can be traced for several metres (see Table 2-3). Layer 2 dominates the bottom of the section in the northern half of the site, and is replaced by layer 3 in the southern half. According to compaction, the section can be divided into three zones (marked by horizontal lines in Table 2-3), the top being the least, and the bottom the most compacted. The fluvioglacial deposits are arranged into cross-cutting three-dimensional bodies which are interpreted as outwash channel deposits from their geometry, erosional boundary, and fill. This origin explains the spatial variability observed in the stratigraphic sequence.

Table 2-3. Occurrence of burrows by layer.

Burrows	#	Grain size and colour	Sedimentary structures	Compaction**
+	Ap	Plough layer (grey sand)*	bedding obliterated	Low
+	Bhf	Bioturbated layer (sand)*	bedding obliterated	
-	12	Fine light-brownish grey sand with clay rip-up clasts	massive	Medium
-	11	Fine to medium light-brownish grey sand	massive	
+	10	Medium to very coarse light-brownish grey sand with gravel	planar bedding	
+	9	Fine to medium-fine light-brownish grey sand	planar bedding	
+	8	Medium to coarse grey sand	planar bedding	
-	7	Light-grey medium to coarse sand	planar bedding	High
-	6	Gravelly sand lag deposit	massive	
+	5	Light-grey medium sand	faint planar bedding	
-	4	Gravelly sand lag deposit	massive	
+	3	Light-grey medium sand	laminated	
+	2	Olive-grey very fine sand	convoluted lamination and cross-lamination	
-	1	Coarse pinkish-grey sand	massive	

*The plough layer and the bioturbated layer are mechanical mixtures of several sedimentary layers. Their composition changes depending on the position. **Field estimate.

Figure 2-7. Northern part of the section (N9) with chipmunk burrow (B). Note the lower boundaries of the plough layer (Ap) and of the bioturbated layer (Bhf), and rotten roots (A).

Figure 2-8. Layer sequence in quadrat N0. See Table 2-3 for description of layers. Faults outlined in red, arrow points to clay rip-up clasts.

Figure 2-9. Outwash deposits at the bottom of quadrat 0N1, showing loading structures (A), fluidization structures (B) and clay rip-up clasts (C). See Table 2-3 for description of layers. Measuring tape attached at the depth of 160 cm.

Figure 2-10. Horizontal and vertical root features (outlined in white) in quadrat -1N0. Note the fault (red dotted line), and an erosional surface between layers 2 and 1.

Another factor in the variability of the sequence are faults, which are mostly oriented east to west and result in vertical displacements of up to 30 cm. Figure 2-10 shows layer sequences in the southernmost quadrat (0N1) separated by a large fault.

Lamination, continuousness of bedding and compactness are geologic features important for trace-fossil recognition and interpretation. Trace fossils are recognized from either grain-size, compactness and colour contrast with the matrix or from absence of bedding and lamination. Therefore, even when there is no marked grain-size difference between two layers, the mere presence or absence of a boundary enables the recognition of trace-fossils. The less extensive the sedimentary features are spatially, the more difficult it is to recognize trace-fossils. The layers in the study site are contained in five metre-scale features and are further broken up by subvertical faults. Although this spatial variability makes it more difficult to recognize burrows, it makes it possible to infer the direction of burrow fill because burrows cut across multiple layers of contrasting coloration and grain-size.

Although the process of burrow filling has not been studied, it is believed that it is influenced by the geotechnical characteristics of the matrix, and in particular, by its density (compactness). The more compact layers may be expected to be less prone to collapse than the less compact layers.

2. Bioturbated layer. Between the plough horizon and the geological layers, all features of original bedding have been obliterated by bioturbation (most likely tree uprootings) down to a depth of 50-70 cm (this is the Bhf horizon on Figure 2-7). The original composition of the upper part of the section cannot be determined since several layers have likely been mixed together, but the presence of large boulders (up to 45×35

cm) suggests glacial origin of the original deposits (Benn and Evans 1998). The colour of the bioturbated layer is brownish yellow (10YR 6/6), probably from pedogenic deposition of iron oxides. The lower boundary of the bioturbated layer is clearly apparent from the density contrast between it and the lower, more compacted undisturbed deposits below (Figure 2-7).

Trace subfossils in the section include invertebrate and vertebrate burrow casts, and root casts:

- a. Burrow casts were distinguished from other geologic features and trace-fossils based on their form, colour, and density. Invertebrate (wasp?) burrow casts appear as small (less than 2 cm in diameter) elongate features extending down from sedimentary boundaries. Vertebrate burrow casts appear on the section wall as oval to round spots 5 to 20 cm in diameter. Taken into account the burrower fauna of the study area (Table 2-1), and the known diameter ranges of their burrows and maximum depths (Elbroch 2003), constructions 5 to 7 cm in diameter were identified as chipmunk, and those 15 to 20 cm in diameter, as woodchuck.
- b. Root features are represented by four types. (1) Subhorizontal brownish yellow bodies follow some layers that are richer in dark minerals or clay (Figure 2-10). These are likely oxidation halos whose coloration is derived from deposition of iron oxides along tree roots, which are known to branch into fine rootlets within bands of more favourable soil in poor sands (Köstler et al. 1968). (2) Vertical features are distinguished from the encasing deposits by their colour; they are also less compact (Figure 2-11).

Figure 2-11. Vertical root features with infill (outlined in white) and rotten roots (outlined in black).

Figure 2-12. Hardened feature impregnated with manganese oxides.

(3) A subvertical round shape found in quadrat N5 that cuts across bedding and is dark stained and hardened (Figure 2-12), possibly by the deposition of manganese oxides (Parfenova and Iarilova 1977). (4) Smaller root traces are recognized by disturbed lamination, but do not form a density or colour contrast with the matrix.

The type of root features that can be confused with burrows are vertical root casts below the bioturbated layer (type 2 in the list above). Only trees with taproots can leave behind traces below the depth of frequent bioturbation (50-70 cm). Among these trees, fewer still can compare in diameter to woodchuck burrows below the depth of 80 cm, where most burrows were found. In the study area, only vertical pine roots fit these criteria (Köstler et al. 1968). Although these root casts can appear very similar to burrow traces on a single section, root features quickly disappear on subsequent sections, whereas burrow traces persist.

3. Anthropogenic features. The top of the section everywhere is a 15-20 cm deep featureless plough layer (Ap horizon).

Burrows

Qualitative description

Infilled burrows

Burrows were found in three parts of the excavation (Figures 2-3, 2-13). The woodchuck burrow was found in quadrats N1-N3, chipmunk burrow A in quadrat N5, and chipmunk burrow B in quadrat N8. Cross-cutting relationships indicate that construction and filling of burrows postdate the deposition of the whole sequence.

**Southwestern corner of the study site
 showing location of the sections**

Elevation in centimetres above site datum.
 The left edge of each section is labeled
 with the number of the corresponding photograph.

Figure 2-13. Close-up map of the Gatineau site showing location of sections of the woodchuck burrow.

Burrows were nowhere cut by geologic features, were found at all depths in the sequence and cut across several layers. The infill of the burrows was much less compacted than the surrounding soil. Burrows and root casts were nowhere cut by faults, supporting a younger age for burrows. Woodchuck burrows did not penetrate the plough layer; therefore, these burrows must have been excavated before the cultivation of the land started in the middle of the 19th century. On the other hand, some chipmunk burrows did penetrate the plough layer, which suggests that these have been excavated and filled in the last 60 years since the field has been abandoned in the 1940s (National and Provincial Parks Association of Canada 1972).

The reconstruction of the woodchuck burrow was based on 50 contours traced off 31 vertical sections (Figure 2-14a; see Appendix B for photographs and tracings, Appendix F for burrow reconstruction). Multiple branches were present on some sections, which explains why the number of contours was greater than the number of sections. The reconstructed woodchuck burrow system spanned a volume of about eight cubic metres. Out of the total traced length of 6 m, 5.2 m were completely filled with sediment. The filled portion of the burrow generally presented sharp contours on vertical cross-sections (Figure 2-15). On some cross-sections the burrow contour had a serrated outline (Figure 2-16). The burrow contour was often more diffuse at the top than at the base. The fill was quite homogeneous, without lenses that would originate from gradual filling.

The fill was considerably less dense than the encasing substrate and is permeated by fine roots. Depending on the depth, it is possible to identify the source layer of the fill.

Figure 2-14. Three-dimensional models of infilled burrows from the Gatineau site. A- segment of woodchuck burrow; B - chipmunk burrow A. Scale bar 10 cm.

Figure 2-15. The chamber of a filled woodchuck burrow. Arrows point to a crescent-shaped organic layer interpreted as lining.

Figure 2-16. Woodchuck filled burrow on a vertical section (outlined). Arrows point to serrations in the outline. Grid 10 cm.

Figure 2-17 A. Multiple fills in a section of the woodchuck burrow. Original photo. Grid mesh is 10 cm.

Figure 2-17 continued. B. Multiple fills (outlined in white) in a section of the woodchuck burrow. Numbers indicate the relative age of fills interpreted from cross-cutting relationships on several consecutive sections. Note sedimentary layers (dotted lines), root features (thin white outline), and faults (outlined in red). Grid mesh is 10 cm.

In eight sections infill was from units above the unit containing the burrow, in 12 sections it was from units below the unit containing the burrow. In the other 30 cross-sections, the origin of the fill is difficult to establish. The plough layer nowhere filled the woodchuck burrows, but most other layers were represented in the burrow fill (Table 2-3). An area of cross-cutting fills was found (Figure 2-17) that probably represents a filled and re-excavated passage of the same burrow. Only the youngest fill (identified from cross-cutting relationships) was used in the reconstruction of burrow geometry.

The architectural elements recognized in this filled burrow besides the tunnels are junctions, chambers, and ramps. No steep shafts (plunge-holes), typical for woodchuck hibernation burrows, were found. Burrow junctions connected 13 segments that ran either roughly parallel or roughly perpendicular to the excavation wall (north-south or east-west). The minimum angle of junction was 118° horizontally and 132° vertically. Some chambers were almost 15 cm wider than the tunnels. The largest was 37 cm in diameter. One chamber, although a similar size to the tunnels (11.5 cm wide by 11.7 cm high), contained evidence of litter in the form of a crescent-shaped organic layer at the bottom of the feature (Figure 2-15).

Two filled chipmunk burrows were mapped during the study. The 3D reconstruction of the chipmunk burrow A was based on 18 contours from 15 sections (Figure 2-14b). It consisted mostly of a straight tunnel dipping at approximately 40° . The burrow was 45 cm long and descended from a 10 cm depth down to the depth of 35 cm. The total volume spanned by the burrow system was 0.093 m^3 . Three fills were distinguished in some cross-sections. The outer fill was dark brown, the inner fill light

Figure 2-18. Vertical section of chipmunk burrow A in quadrat N5 showing three fills.

brown. Both of these fills had oval cross-sections. The third fill was present in only three of the eighteen cross-sections, was white and had angular outlines (Figure 2-18).

Nowhere were multiple fills arranged into horizontal lenses as would be expected to result from slow passive filling.

Chipmunk burrow B was much more loosely filled than burrow A so that the fill could easily be removed from the burrow. The burrow system consisted of several segments oriented predominantly in the long-wall direction (north-south) and dipping at 45°. The total volume spanned by the burrow was 0.072 m³. This burrow was partially excavated into root casts and rotten roots. The plough layer material was present in the fill, judging from its colour.

The orientation of burrows in plan view varied little. Chipmunk burrow A mostly ran perpendicular to the face, while chipmunk burrow B was predominantly oriented parallel to the face. Because of the small length of chipmunk burrow B and its orientation parallel to the section wall, only burrow A has been used for 3D modelling.

Open burrows (Ottawa and Prince Edward Island sites)

The woodchuck open burrow examined from the Ottawa site occurred in the following sequence of layers, in ascending order:

- 1) medium sand with pebbles (130–160 cm);
- 2) compacted anthropogenic construction mix consisting of gravel (120-130 cm);
- 3) anthropogenic construction mix consisting of medium sand with pebbles (30–120 cm);
- 4) anthropogenic turf layer and a humus horizon developed over it (top 30 cm).

The burrow was 6.2 m long and, about half of it was built in unit 1 about 10 cm beneath the construction mix (unit 2). The burrow consisted of a primary tunnel ending in a chamber. Three side tunnels were observed during the excavation, but only one could be cast with plaster. The other two were partially or entirely blocked off with earth plugs or litter (twigs, cones and shredded plastic bags). The cross-sectional shape of the burrow roof was round along most of the burrow cast, while the shape of the floor was variable but generally flat. Claw marks were present on the sides of the burrow and sometimes on the roof, but never on the floor of the burrow.

Three chipmunk burrows from the Ottawa site were 100 cm, 70 cm, and 80 cm long, respectively. The first two were tunnels without branching, and the third one contained a steep ramp that branched at the bottom into three short tunnels ending in earth plugs approximately 20 cm from the junction.

Partially filled burrows (all sites)

A 0.8 m segment of the woodchuck burrow system at the Gatineau Park site (located in the easternmost part of the section) was found to be only partially filled. It is a tunnel leading into a chamber. The shape of the hollow portion of the burrow was studied from a plaster cast. It is semi-elliptical in cross-section, with a flat bottom and an arched top. The width exceeds the height almost twofold. The sides of the empty tunnel show surface relief from claw marks. The filled portion was studied from vertical sections. All of the filled portion was found below the hollow part of the burrow. The fill was homogeneous, without lamination (Figure 2-19). Some vertical sections exposing partial fill were made during the excavation of the plaster cast at the Ottawa site. Within a metre

Figure 2-19. Open burrow segments from the Gatineau site: chamber (A) and tunnel (B). The hollow space is filled with white plaster; the burrow fill below it is outlined.

Figure 2-20. Fills of different age within a single burrow. A-C. Filled and open portions of a woodchuck burrow from the Ottawa site. Note the proportion occupied by open space (filled with plaster, outlined in white) and filled portion below it (outlined in black). D. Two distinct fills in a filled woodchuck burrow from quadrat -1N1 in the Gatineau site. Note the shape and color contrast similar to photo C.

Figure 2-21. Evidence of multiple episodes of fill and re-excavation in a chipmunk burrow at the P.E.I. site. Numbers indicate relative age inferred from cross-cutting relationships.

of the entrance of the burrow, the fill below the plaster cast was thickly stratified in some places (Figure 2-20).

The occupied burrow studied at the Prince Edward Island site was 1.5 m long. The hollow burrow was semi-elliptical in cross-section, had an arched bottom and top. The height exceeded the width. Evidence of multiple fill was found during excavation at numerous points along the burrow. Two types of fill were found, an inorganic fill possibly due to collapse and an organic fill (nut shells) deposited by the animal (Figure 2-21). Filled tunnels were found below and beside the hollow tunnel.

Quantitative description

Woodchuck burrows

Tables 2-4 shows mean and median values, as well as standard deviations for the measured woodchuck burrows (See Appendix C for raw data). Figure 2-22a shows the distribution of widths in the infilled woodchuck tunnels from the Gatineau Park site, measured at 29 perpendicular sections of the reconstructed model. The widths vary from 13.4 to 25 cm. Figure 2-22b shows the distribution of heights in the infilled woodchuck burrow. The distribution is slightly skewed to the right (towards higher numbers), but has a single peak at 18.5 cm. Figure 2-22c shows the distribution of widths in the open (plaster-cast) woodchuck burrow. The height distribution of open burrows (Figure 2-22d) has two peaks, a main peak at 11 and a smaller one at 17 cm.

Chipmunk burrows

Figure 2-23a shows the distribution of widths in the filled chipmunk burrow A, measured at 12 perpendicular sections of the model. The distribution is strongly skewed to the right. Median width is 4.75 cm. The height distribution (Figure 2-22b) has three

Table 2-4. Results of statistical comparisons between cross-sectional measurements of filled and open woodchuck burrows.

	Width				Height			
	n	Median (cm)	Mean (cm)	Standard deviation	n	Median (cm)	Mean (cm)	Standard deviation
Woodchuck filled	29	17	17.6	4.96	32	19.4	20.2	2.81
Woodchuck open	47	17.4	18.0	3.68	47	11.5	11.8	3.38
Mann- Whitney U significance	0.455				0.088

Figure 2-22. Distribution of width and height in filled (A, B) and open (C, D) woodchuck burrows. The normal curve is superimposed on the histogram. The number in the upper right corner shows the significance level for the Kolmogorov-Smirnov goodness-of-fit test.

Figure 2-23. Distribution of width and height in filled (A, B) and open (C, D) chipmunk burrows.

peaks at 5 cm, 6 cm and 7.75 cm. Figures 2-23c and 2-23d show the distribution of widths and heights in the open (plaster-cast) chipmunk burrow. Unlike the filled burrow, the median width (6 cm) is greater than the median height (4.8 cm). Furthermore, median values are close to those in the filled burrows, if one compares widths with heights. It appears that the two burrows being compared have different cross-sectional shape but similar cross-sectional area. This may be due to original differences, rather than taphonomic ones.

Statistical analysis

Woodchuck burrows

The Shapiro-Wilk statistic shows the distributions of open burrow width and open burrow height to be strongly non-normal ($P=0.029$ and $P=0.02$, respectively). The open burrow height distribution has a pronounced peak at 11.75 cm that comprises more than 25% of all cases. The distribution of filled burrow height is normal ($P=0.336$). The distribution of filled burrow width is close to normal according to the Shapiro-Wilk statistic ($P=0.095$) but strongly skewed to the right (skewness 0.933).

Because of non-normality and a comparatively small sample size, open and filled burrow dimensions were compared using the nonparametric Mann-Whitney U-test. The results are shown in Table 2-4. Values below 0.05 indicate that the samples come from two populations with different medians. In filled burrows, height is significantly greater than burrow width ($p<0.05$), while in open burrows, it is the width that is significantly greater than height ($p<0.01$).

The width medians are not significantly different between open and filled woodchuck burrows ($p>0.05$) while height medians show highly significant differences

($p < 0.01$), with the height of infilled burrows being greater than the height of open burrows. Filled burrow height is significantly greater than open burrow height ($p < 0.01$) and filled burrow width is significantly greater than open burrow height ($p < 0.01$).

Chipmunk burrows

The Shapiro-Wilk test would suggest that the height in filled burrows is normally distributed ($p = 0.2$), but the frequency graph has three peaks, so that the distribution cannot be considered normal. Widths in filled burrows have a distribution close to normal ($p = 0.13$) and a single peak, but the distribution is strongly skewed to the right (skewness 0.656). The distributions of height and width of open burrows are strongly non-normal ($p < 0.01$). The non-parametric Mann-Whitney test was therefore used to compare the burrow dimensions (Tables 2-5 and 2-6). Chipmunk filled and open burrows show a difference in widths at the 0.059 significance level, which is only slightly above the higher boundary of significance (0.05). Chipmunk filled and open burrow height shows a highly significant difference ($p < 0.01$), with height of filled burrows being significantly greater. A comparison of filled burrow height with open burrow width, as well as the comparison of filled burrow width with open burrow height did not show a significant difference ($p > 0.8$) (Table 2-6).

DISCUSSION

Previous excavations of infilled burrows (Heinrich and Jäger 1975, Burns 1996), focused on burrow assemblages as sites of exceptional preservation of fossils and examined colonial settlements with a significant time depth. In such large assemblages, the identification of tunnels belonging to a single burrow system was difficult and cross-sectional variability within one burrow could not be described. In this study, excavation

Table 2-5. Results of statistical comparisons between cross-sectional measurements of filled and open chipmunk burrows.

	Width				Height			
	n	Median (cm)	Mean (cm)	Standard deviation	n	Median (cm)	Mean (cm)	Standard deviation
Chipmunk filled	13	4.8	5.1	0.87	13	6.0	6.1	0.8
Chipmunk open	25	6.0	6.0	0.73	25	4.8	5.0	0.69
Mann- Whitney U significance	0.06				0.000			

Table 2-6. Results of Mann-Whitney comparisons of chipmunk burrow cross-sectional measurements. Values under 0.05 indicate a significant difference.

		Open	
		Width	Height
Filled	Width	0.06	0.89
	Height	0.817	0.000

by serial vertical sections and subsequent three-dimensional reconstruction of the non-colonial burrows has enabled us to separate individual burrows for measurement.

The reconstructed three-dimensional models of infilled burrows permitted the identification of previously described (Hamilton 1934, Grizzell 1955, Panuska and Wade 1956) architectural elements. Chipmunk burrows are characterized by a very steep entrance but no vertical shaft (Panuska and Wade 1956). In this study, a 40-45° ramp was found to be present in both filled chipmunk burrows and in the plaster casts of open chipmunk burrows. The architecture of open woodchuck burrows has been described in the biological literature (Hamilton 1934, Grizzell 1955). The architectural elements recognized in the filled woodchuck burrow during this study are junctions, chambers, and ramps. The absence of a plunge-hole suggests that the burrow may be of the summer shelter type, as opposed to a hibernation burrow (Grizzell 1955). The open woodchuck burrow also lacks a plunge-hole, which suggests that it belongs to the same architectural type as the infilled burrow.

The data collected during this study enable comparisons between cross-sectional characteristics of open and filled burrows. The results of the statistical analyses show that woodchuck open and filled burrow width distributions have the same median, which supports the prediction that cross-sectional width is more readily preserved than is the height. This suggests the identification of the tracemaker should be preferentially based on width rather than height of the fossil burrow cast.

The minimum widths of both filled and open burrows reflect a lower limit on burrow size (12 cm). Measurements of shoulder width on woodchuck cadavers ($\bar{X}$ = 13 cm, s.d. = 2.3, n = 8) suggest that this lower burrow width roughly corresponds to the width

of the animal. Meanwhile, the open burrow had a much smaller median height than the filled burrow. The lower values of the height distribution in open burrows are smaller than the diameter of the lying animal ($\bar{X} = 14.6$, $n=8$ cm) (this value can be estimated from measured girth ($\bar{X} = 45.8$, $s.d.=4.8$, $n=8$) and much smaller than the height of an adult free standing animal as measured on the woodchuck (*Marmota monax*) skeleton (15.5 cm). The filled burrow was found to have a median height (19.4 cm) greater than the height of a free-standing animal (15.5 cm). The width : height ratio in filled burrows is approximately the inverse of that ratio in open burrows.

Our observations on freshly excavated woodchuck burrow entrances found that the shape of freshly excavated burrows more closely corresponds to the shape of filled burrows than to that of open burrows. Although width can exceed height in some entrances below tree-roots and boulders, the tunnel itself is higher than wide. This suggests that open burrows examined in the study had been partially filled.

The recently abandoned open burrows selected for this study are close analogues of the fossil burrow casts that are filled in a single catastrophic event such as a flash-flood or an ash-fall (e.g. Martin and Bennett 1977, Smith 1987). Plaster imitates the overbank deposits or ash filling fossil burrows. When burrow casts are said to represent open burrows, these latter have been traditionally equated with fresh, active burrows.

The incremental (as opposed to single-event catastrophic) filling of the burrow can occur either through colluvial fill from the soil surface or from roof-collapse. Surface morphology of the plaster cast enables a distinction between these two possibilities. The presence of claw marks on the burrow roof was here viewed as evidence for the preservation of original roof of the tunnel. An additional indication of the burrow history

is the shape of the burrow roof. If the burrow filled mostly through roof-collapse, then the shape of the roof may be expected to be variable. However, it is the shape of the floor that was found to be most often irregular. In addition, some burrow segments preserve claw marks on the burrow roof, but burrow width at these segments still greatly exceeds the height. Therefore, although some roof-collapse may have contributed to the fill, the main mode of filling of the open woodchuck burrow is colluvial fill. This conclusion is consistent with findings of the study of subfossil badger setts by Heinrich and Jäger (1975).

Catastrophically filled burrows produce an often homogeneous fill that presents sharp boundaries and a marked grain size contrast with the encasing substrate. The burrows observed in this study present two types of fills: laminated fill and homogeneous fill. Laminated fill reflects incremental sedimentation that has been called colluvial fill (Heinrich and Jäger 1975) and was found below some portions of open woodchuck burrows (Figure 2-20C). Homogeneous fill was found in all woodchuck and chipmunk filled burrows at the Gatineau site. Homogeneous fill may be produced in flash-flood events. However, this explanation is excluded for the Gatineau site because it is located on a local high, far outside of a floodplain. A more plausible explanation for a homogeneous fill is active fill, which is produced when the animal backfills an unused portion of the burrow (backfilling is a known behaviour in woodchuck: Grizzell 1955).

Results of this study permit a re-evaluation of published interpretations of fossil burrows. The dimensions of the burrow cast are believed to correctly represent the dimensions of the tracemaker. For instance, Groenewald et al. (2001) describe in detail a fossil burrow cast attributed to *Trirachodon*, a Lower Triassic therapsid found in some of

the burrows. This cast is typical for the fossil burrows described in the literature: it is found in flood-plain deposits and is interpreted to have been formed during a flash-flood. Scratch-marks are indistinct near the entrance but are well-developed in the part of the burrow distal to the entrance. The cross-sectional shape varies from circular to oval to bilobate. The width greatly exceeds the height (more than twofold). The authors interpret the bilobate cross-sectional shape as evidence of travel by multiple individuals in opposite directions. *Trirachodon* is believed to have occupied about half the width of the burrow (Groenewald et al. 2001).

Figure 2-24 compares cross-sectional shapes of the open woodchuck burrow with shapes of the presumed *Trirachodon* fossil burrow. The data from this study suggest that the variation in cross-sectional height in the fossil burrow may be due to partial infill. If this is the case, then width but not height measurements can be used to infer the size of the tracemaker, which is then likely to have been larger than *Trirachodon*.

Very close agreement of width distributions between filled and open woodchuck burrows in our study suggests that sample size (29 and 47 sections, respectively) is sufficient for the comparison. On the other hand, chipmunk burrows seem to present cross-sectional dimensions that are strongly non-normally distributed, which may be due in part to small sample size. Similar to woodchuck burrows, the width to height ratio in filled chipmunk burrows is the inverse of that in open burrows. This suggests that such inverse relationship may be a common feature for abandoned open vs. backfilled burrows of the same species.

Collapse, inasmuch as it is considered in the literature at all, has been implicitly assumed to occur only after the abandonment of the burrow. Biological observations

Figure 2-24. Comparison of cross-sections of woodchuck open burrow from this study (A, B, C) and cross-sections of a Triassic burrow cast attributed to *Trirachodon* (D, E, F) (Groenewald et al. 2001). Cross-sections in each column represent different parts of the same burrow. The shape differences are due to differential filling of parts of the burrow prior to the formation of the cast.

suggest that it is not the case. For instance, burrow collapse is a common source of springtime mortality in ground-squirrels (P. Fargey, personal communication). Multiple fills in the chipmunk burrows observed in the Prince Edward Island site suggest that collapse occurs during the habitation of the burrow. The chipmunk constructs the new tunnel segment beside, above, and below the axis of the filled tunnel. Woodchuck also has to deal with collapse, but there is less evidence of multiple fills, which would suggest re-excavation following filling or collapse. When multiple fills are present in a woodchuck burrow, the burrow axis shifts upward and not sideways. Zoologists and trackers note that woodchuck burrows are recognized by the frequent ejection of fresh sediment onto the throwmound (Elbroch 2003). This is probably evidence of tunnel cleaning from collapsed segments. It is therefore probable that chipmunks shift the burrow when collapse occurs, whereas woodchucks mostly clean out the collapsed lumps. This would result in a vertical enlargement of a burrow that can explain a greater height in woodchuck filled burrows than would be expected from the height of the woodchuck in free standing position.

Frequency of processes such as roof collapse and colluvial fill may depend on the nature of the substrate. However, substrate does not account for the differences observed in this study. Open and filled abandoned burrows were studied at sites with a similar, sandy substrate. Observations on occupied (chipmunk) burrows were made in a more clayey substrate, loam, which could be expected to behave more plastically than sand. However, even in loam, chipmunk burrows showed evidence of multiple burrow renewal, suggesting that collapse and colluvial fill occur in clayey as well as sandy substrate and that burrow renewal behaviour is species-specific, rather than substrate-specific.

The filled burrow and the open burrow appear to represent two preservational pathways. The more time passes before the burrow becomes completely filled, the more chance there is that collapse or colluvial fill will occur. Actively filled burrows may be more faithful reproductions of original burrow dimensions than burrows passively filled in a flash-flood assuming filling occurs soon after the burrow is excavated.

SUMMARY

The following conclusions can be drawn from this study:

1. Cross-sectional shape and dimensions of abandoned open burrows differ from filled burrows of the same species.
2. For both *Marmota monax* and *Tamias striatus*, cross-sections of backfilled burrows are higher than wide, whereas abandoned open burrows are wider than high. The width : height ratio in backfilled burrows is approximately the inverse of that ratio in open burrows.
3. The results of the statistical analyses show that woodchuck open and filled burrow width distributions have the same median, whereas, the open woodchuck burrow has a much smaller median height than the filled woodchuck burrow.
4. The lower height values observed in abandoned open woodchuck and chipmunk burrows are interpreted as a result of colluvial fill.
5. Examination of plaster casts of woodchuck and chipmunk burrows revealed the presence of claw marks. Claw marks mark the intact portions of the burrow walls and roof. The presence of claw marks in woodchuck open burrow segments with a high width : height ratio indicates that burrows were filled colluvially, rather than by roof-collapse.

6. The height in filled woodchuck burrows is sometimes higher than what would be expected for the animal's size, which can be explained by roof-collapse followed by renewal during the occupation of the burrow.
7. The results of the comparison between open and filled burrows indicate that in both woodchuck and chipmunk, burrow width is less affected by taphonomic alteration than burrow height.
8. Because original dimensions of burrows become modified to different extents depending on the burrow history, fossil burrows should be studied for evidence of collapse and re-excavation in order to correctly evaluate their preservational history and identify the burrow-maker.

CHAPTER 3

Woodchuck (*Marmota monax*) claw marks as evidence of digging movements

INTRODUCTION

Vertebrate trace fossils are biogenic sedimentary structures that often preserve direct evidence of movement and are therefore an important complement to body fossils in behavioural reconstruction (Toots 1963, Hasiotis 2002). For instance, locomotor behaviour, including posture, gait, and speed, have been reconstructed from fossil vertebrate trackways consisting of footprints preserved on a bedding surface (Padian and Olsen 1989, Gatesy et al. 1999). The functional interpretation of trace fossils requires an understanding of the link with kinematics and tracemaker morphology, which can be best established by a study of modern analogues of trace fossils.

For digging animals, the digging motions are reflected in the morphology of the surface marking of fossil burrows (Martin and Bennett 1977, Hasiotis 2002, Gobetz 2005, 2006). Surficial marking on burrow walls consists of furrows left by claws or incisors during the excavation of a burrow. A fossil burrow is a cast of the original burrow, on which the furrows are preserved as ridges. Because the preservation of surficial marking depends on moisture content and cohesion of soil, not all fossil burrows are found with marks (e.g., Loope 2006). Previous research on surficial marking of mammal burrows focused on the recognition of scratch-digging and incisor-digging from the occurrence of claw and incisor marks, respectively (Martin and Bennett 1977, Gobetz and Martin 2006). Incisors leave wide, flat, paired marks, whereas claws leave narrower marks that often

occur in sets corresponding to digits of the manus (Martin and Bennett 1977). Some details of digging behaviour have been reconstructed from orientation and arrangement of incisor marks in *Paleocastor* burrows (Martin and Bennett 1977) and of claw marks in fossil mylagaulid burrows (Gobetz 2005). Gobetz (2006) recognized the presence of differently oriented claw marks that she interpreted as reflections of different digging strokes. However, none of the existing studies have quantified the variation in claw mark morphology that could be related to a diversity of digging strokes.

Published descriptions of digging kinematics in extant scratch-digging mammals show that burrow excavation involves two to three stages (soil break-up, accumulation, and evacuation), each of which is typically associated with a characteristic movement (Stein 2000). Each of the broad categories of digging movements probably encompasses some variation, which can be expected to be reflected in claw mark morphology. The relationship between claw mark morphology and digging movements can be best studied in extant animals, because the tracemaker of a modern burrow is easily known. Gobetz (2005) described a single type of surficial marking on the burrow cast of the modern mole (*Scalopus aquaticus*). The absence of variation in the claw marks of the mole burrow may be explained by the mole's highly specialized humeral-rotation digging style. This paper presents an analysis of the variability of claw marks within a single burrow of a common North American burrower, the woodchuck (*Marmota monax*).

The woodchuck (*Marmota monax*) is a solitary, unspecialized burrower that constructs burrows for hibernation and shelter (Hamilton 1934). Its digging movement has not been studied in the laboratory, but field observations suggest that its unspecialized scratch-digging style can be compared to other sciurids and possibly to

other scratch-digging rodents (Hamilton 1934, Gilbert 1940). Agrawal (1967) mentions woodchucks as one of the animals that use their incisors to dig. Hamilton (1934) also reports that woodchucks use their incisors, especially when initiating a burrow. If incisor-digging is common in woodchuck, then incisor marks can be expected to be found on burrow casts.

Scratch-digging in mammals involves two stages: loosening of the soil and soil evacuation (Camín et al. 1995, Casinos et al. 1983, Giannoni et al. 1992, 1993, Laville 1989, Stein 2000). The digging sequence of woodchuck has not been studied, but is probably similar to that described for its close relative (Herron et al. 2004), the prairie dog (*Cynomys*: Stalheim-Smith 1984). Prairie dogs brace with their head against the roof of the burrow, extend the forelimbs into packed soil, pull loosened soil under the shoulder, then under the abdomen and pelvis. During scratching, the elbow first extends, then the elbow and the wrist repeatedly flex and extend as the soil is being loosened. When the animal moves loosened soil under itself, both the elbow and the wrist flex. During digging, the left and right forelimb alternate, as is the case in most scratch-digging mammals (Stalheim-Smith 1984, Nevo 1999, Stein 2000). *Marmota monax* is known to throw back soil with its hind limbs (Gilbert 1940). In summary, it is reasonable to expect in woodchuck the three types of digging movements that are found in the prairie dog and are common to several other diggers (Casinos et al. 1983, Laville 1989):

1. scratching to dislodge soil;
2. movement of loose soil under the body;
3. evacuation of soil by hind feet.

In the rest of the paper, claw mark variability is examined for evidence of morphological groups, groups are compared statistically, and the kinematics is inferred from the morphological variation using a preliminary two-dimensional model that links forelimb digging movements with claw mark shape.

STUDY SITE

The woodchuck burrow cast obtained for this study results from fieldwork conducted in the late fall of 2005. The study site is located on unoccupied lands of the Lebreton Flats in Ottawa, Ontario. It is an old embankment oriented northwest – southeast and now overgrown with pines and shrubs. To select an uninhabited burrow, a 2 mm wire was used to probe for earth plugs. By November, woodchucks go into hibernation and plug their burrows, usually within 1 m from the entrance (Hamilton 1934). The absence of an earth plug was taken as an indication that the burrow is not in use. The chosen burrow was excavated into a steep slope (10°) on the north-eastern side of the embankment. The sedimentary units exposed in the section are, in ascending order (Figure 3-1):

- 1) medium sand with pebbles (130–160 cm);
- 2) compacted anthropogenic construction mix consisting of gravel (120–130 cm);
- 3) anthropogenic construction mix consisting of medium sand with pebbles (30–120 cm);
- 4) anthropogenic turf layer with an overlying humus horizon (0–30 cm).

About half of the length of the burrow was built in unit 1 about 10 cm beneath the construction mix (unit 2). The burrow contained twigs, leaves, and plastic that had probably been brought in as bedding material by the animal.

Figure 3-1. Soil section showing layers encountered during the excavation of the burrow cast. Arrow points to a compacted layer between 120 and 130 cm. Total depth 160 cm.

METHODS

Burrow casting and imaging

Previous workers have cast burrows using clay (Panuska and Wade 1956), concrete (White 1962), and polyurethane foam (Felthausen and McInroy 1983, Hembree and Hasiotis 2004). In this study, plaster of Paris was used because it is known to preserve detailed surface structure (Gobetz 2005).

Thinly mixed quick-set plaster of Paris was poured into the burrow. The resulting cast was extracted in fifteen segments (each 20–40 cm long) that were sawed off as the excavation proceeded. Filling the burrow with plaster took approximately 10 hours over a period of three days. The excavation of the burrow cast, using both large and small hand tools, took approximately 50 hours. The casts are housed at the Canadian Museum of Nature (National Heritage Building, Aylmer, Quebec).

In order to be able to measure the curvature and to study the cross-sectional shape of the claw marks, the plaster casts were first scanned at 1 millimetre resolution using a 3D surface scanner at the Canadian Museum of Nature, courtesy of Arius 3D. The claw marks were then traced off the digital model of the burrow using Rhinoceros 3D modelling software (McNeel 2006).

Claw mark measurements

Well preserved claw marks were selected for measurement and analysis. Wherever claw marks were found in a set (interpreted to correspond to digits of the manus), only the longest claw mark was selected for measurement. This mark likely corresponds to digit III, which is the longest of the four functional manus digits (Bezuidenhout and Evans 2005). Thirteen variables were measured for statistical analysis

in order to characterize the claw marks (see Figure 3-2, A-C). The measured variables reflect, in addition to the length of forelimb segments, the geometry of the digging motion. Distance from the roof, length and orientation of the claw mark were measured in Rhinoceros 3D software (McNeel 2006). The *length* of the claw mark was measured because it relates to the angle through which the limb segments are rotated during the digging stroke. The *orientation* of the claw mark was measured in side view as the smaller angle in degrees between the chord of the claw mark (the straight line connecting the end points of the claw mark) and the long axis of the burrow (Figure 3-2A). The orientation relates to the initial position of the limb and the angle spanned by each limb segment during motion. The *distance* from the highest point of mark *to the roof* reflects the position of the forelimb at the beginning of the digging stroke. The distance from the ceiling was used instead of height above the floor because evidence of partial fill was found in many segments of the burrow (see Chapter Three). Therefore, the measurement from the floor would be affected by the amount of fill and/or roof collapse that has occurred since the excavation of the burrow. For the measurement of *curvature* in the plane of the claw mark, tracings of individual claw marks were imported into AutoCAD (Autodesk 2004) that enabled easier planar measurements. Curvature was characterized in two ways: through three radii of curvature and through seven perpendicular distances from the chord to the claw mark (Figure 3-2C). Radius of curvature reflects the length of those forelimb segments that are involved in the movement. Figure 3-2B shows how the radii of curvature were measured for each claw mark. In some claw marks, curvature is approximately constant for the entire claw mark. In that case, a single circular arc was

Figure 3-2. Claw mark measurements used in this study. A. Linear and angular measurements. B. Radius of curvature measurements. Arcs fitted to segments of the claw mark are shown. Circles mark the centre of curvature. The radius is distance from the centre of curvature to the arc. The arrow marks the interpreted movement of the centre of curvature. C. Measurements of perpendicular distance from chord to claw mark. D. Cross-sectional measurements of the claw mark ridge.

fitted to the claw mark shape and its radius of curvature measured. In other claw marks, curvature changes along the length of the mark, typically at one or two inflection points. Such claw marks were broken into parts according to the number of inflection points and circular arcs were fitted to approximate the shape of each part. The boundaries of each part were set at the inflection points. The relative as well as absolute length of each arc depended on the position of inflection points within the claw mark. For uniform description, three radii are presented for all claw marks, including simple shapes without inflection points. In these cases, the same value has been assigned to the three radii of curvature. Straight claw marks present a difficulty for the measurement of the radius of curvature because, mathematically this value is equal to infinity. For nonparametric analysis, a dummy value of 250 mm was assigned to straight claw marks. In the second method used to estimate curvature, seven distances from the chord to the claw mark were measured perpendicular to the chord (Figure 3-2C). Measurements were spaced one eighth of the chord length apart, so that the absolute spacing depended on the length of the claw mark. The chord distances were found to correlate with the claw mark length. In order to remove the size effects, chord distances were regressed against claw mark length and the geometric mean residuals were used in further analysis.

In addition to thirteen measurements described above, three further measurements were made for descriptive purposes on a limited sample of claw marks. The claw marks were selected in areas with least cross-cutting and a high relief. Claw mark width was measured at the base of the claw mark ridge (Figure 3-2, D). The width of the four widest claw mark sets was measured. The relief height of the claw mark was measured for claw marks with the highest relief.

Statistical analysis

The claw marks were grouped visually into groups and six measurements (length, roof distance, orientation, first, second, and third radii of curvature) were compared between the groups in SPSS software (SPSS Science 2006). Distributions of all measurements were tested for normality using the Shapiro-Wilk statistic and for equality of variances using Levene's test. The t-test was used in comparisons where distributions were found to be normal, whereas Mann-Whitney test was used for distributions found to be non-normal and also used for curvature measurements because they included a dummy value. Because multiple comparisons were made, the Bonferroni correction was used to reduce the probability of Type 1 errors (Miller 1981), and the significance level was lowered to 0.017.

In order to explore the variation in multiple variables, principal component analysis was performed on the data in Unscrambler software (CAMO 2007). Angle measurements were converted to radians to reduce the variance (Sokal and Rohlf 1995). Correlation matrix was used because the data comprised angle and linear measurements. Ten variables were used: length, orientation, roof distance, and six chord distances. The variables were weighted inversely to their variance.

Cadaver and osteological measurements

Interpretation of the claw marks required the collection of gross morphometric data on both cadavers and the osteological material. Six adult woodchuck cadavers were obtained from a local trapper in order to measure the articulated manus. Although males are known to be slightly larger than females in woodchucks (Barash 1989), the measurements were pooled because of the small sample size, so that six values were

obtained for both the manus length and the manus width. The manus length was measured using a Gneupel calliper from the centre of the wrist on the level of the medial styloid process to the tip of the third digit. The manus width was measured at the base of the claw on digit V.

In addition to measurements on cadavers, the length of long bones was measured on seven specimens in the collection of the Canadian Museum of Nature (Osteology collection numbers Z729, 75548, 41083, 75403, 75033, 41019, 75141). The total length of humerus and the functional length of ulna (total length minus olecranon length: Duerst 1930) were measured using a Gneupel calliper. The claw width was measured off the third manual digit of four collection specimens at the base of the keratin claw (CMN 41619, 73194, 75403, Z-161).

RESULTS

Distribution of claw marks

The studied burrow system was 6.2 m long and included straight tunnels, three turns, two junctions, one blind pocket, and a chamber (Figure 3-3). The burrow had a single entrance. Out of the fifteen segments into which the burrow was sawed during excavation, twelve contained more than one claw mark set. Claw marks were mostly found on the sides of the burrow cast, although on three segments claw marks were preserved extensively on the roof of the burrow, whereas no claw marks were preserved on the floor of the burrow. The floor of the burrow showed evidence of colluvial fill (See Chapter 2 of this thesis). A blind side tunnel was covered with claw marks running from ceiling to side walls. On the blind tunnel, the claw marks were convex towards the

Figure 3-3. Plan view of the excavated woodchuck burrow. Scanned parts of the burrow in blue. Arrow points to burrow entrance.

terminus. In other parts of the burrow, claw marks were mostly concave towards the entrance. The claw marks were unequally distributed along the burrow and their density per 50 cm long segment varied from 28 to 77. No claw marks were found in the 20 cm adjacent to the entrance. In some areas of the burrow, claw marks were widely spaced out, while in other areas claw marks cross-cut densely, forming a network of pits and ridges (Figure 3-4).

Claw marks were often found in sets of two to four parallel marks. The average width of a claw mark was 5.3 mm ($n=12$, $s.d.=1.16$). The average width of a claw mark set was 3.6 cm ($n=16$, $s.d.=6.3$). On three segments, claw marks occurred in offset pairs on either side of the tunnel (Figure 3-5). One of the burrow segments contains three sets of straight claw marks arranged on the same side of the burrow behind each other along a straight line (Figure 3-6).

Several burrow segments contained knobs (Figure 3-7), 4.5–7.3 cm in diameter. The knobs were covered with claw mark ridges of about the same length as the diameter of the knob.

Claw mark morphology

Out of the total of 554 claw marks traced on the burrow, 46 claw marks were measured (See Appendix E for raw data). Many claw marks were partially obliterated by their dense cross-cutting. The claw marks selected for measurement were those found in claw mark sets. Partially obliterated claw marks were thus excluded. The average maximum height of the claw mark ridge in relief was found to be 3.3 mm ($n=10$, $s.d.=1.12$) and up to 5 mm (Figure 3-8). Claw mark length ranged from 26 mm to 164

Figure 3-4. Density of claw marks on different portions of the scanned burrow (lateral view). A. Widely spaced claw marks. B. Network of pits and ridges from cross-cutting claw marks. Scale bar 5 cm.

Figure 3-5. Top view of scanned burrow cast segment 10 showing claw mark sets on either side of the tunnel (traced in different colours) meeting at the crest of the burrow. Scale bar 10 cm.

Figure 3-6. Side view of a scanned burrow segment 3. Arrows point to parallel sets of claw marks arranged en echelon. Scale bar 10 cm.

Figure 3-7. Knob on the ceiling of the scanned burrow cast (arrow). A. top view. Note claw marks on the knob. B. Cross-section of the knob showing asymmetry.

Figure 3-8. Claw mark ridges in relief. A. Oblique view of the plaster cast. Section A-A' outlined in green. B. Cross-sectional view across three claw marks (arrows). C. Oblique view of three cross-sections of a claw mark (claw mark traced in red)

mm (Table 3-1). Although care was taken to only select claw marks with unobscured ends, it is likely that some claw marks are shorter due to overprinting by later claw marks. The orientation of the whole claw mark varied from parallel to the long axis of the burrow (2°) to nearly perpendicular (78°).

Three shapes of claw marks are distinguished visually in the studied data (Figure 3-9). The first type (type 1) comprises straight ridges often running close to the burrow floor nearly parallel to the axis of the burrow. This type is the least common on the studied burrow. The next, the most common type (type 2) includes long ridges often curved near their top, running perpendicular or at a sharp angle to the axis of the burrow. The final group (type 3) comprises short ridges with a radius of curvature comparable to their length. The three types of claw marks occur throughout the burrow.

The curvature changes along the length of the claw mark. Usually, the top end of the claw mark has a smaller radius of curvature than the lower part. The cross-sectional height of the claw-mark ridge (relief height) varies between claw marks and also along the length of a single claw mark (Figure 3-8). In the claw marks that are curved near the top, the top part often has higher relief.

Statistical grouping of claw mark types

Table 3-1 presents the characteristics of statistical distributions for measured parameters of claw marks. With the exception of orientation measurements, distributions of measured variables were found to be non-normal by the Wilk-Shapiro test and their variances unequal by the Levene's test; therefore, a non-parametric Mann-Whitney test was used to compare the groups.

Table 3-1. Some characteristics of the three claw mark types (average values and standard deviations). Orientation angle is given in degrees and radians. Linear measurements are in millimetres. See Figure 3-2 for explanation of terms.

n		Type 1 9	Type 2 21	Type 3 16
Length	Mean	72.76	84.6	38.93
	Median	50.46	77.94	39.92
Orientation	Mean	27.16° (0.47 rad)	59.51° (1.06 rad)	57.71° (1.04 rad)
	Standard deviation*	10.87° (0.19 rad)	10.87° (0.39 rad)	21.39° (0.34 rad)
	Median	28.18° (0.49 rad)	58.13° (1.06 rad)	55.78° (1.07 rad)
Distance from the roof	Mean	53.68	24.60	42.33
	Median	57.13	12.39	37.13
Radius1	Mean	N/A***	26.48	16.98
	Median		35.80	10.80
Radius2	Mean	N/A***	101.27	26.17
	Median		68.70	23.40
Radius3	Mean	N/A***	101.42	27.05
	Median		68.70	23.40

* Standard deviation given only for normally distributed variables.

** Angle in radians

***Radius of curvature not defined for straight marks.

Figure 3-9. Three types of claw marks on the burrow cast. A. Example of Type 1 claw marks (lateral view). B. Examples of type 2 and 3 claw marks (lateral view). C. Schematic drawing of three types of claw marks recognized in this study. Scale bar 5 cm.

Table 3-2. Pairwise comparisons for six measured variables (using the Mann-Whitney test). Significant differences (after correction for multiple hypothesis testing: Verhoeven et al. 2005) shown in red italics.

Length		1	2	3
	1		0.295	0.009
	2			<0.001
	3			
Distance from the roof		1	2	3
	1		0.015	0.808
	2			0.008
	3			
Orientation		1	2	3
	1		<0.001	0.001
	2			0.899
	3			
Radius 1		1	2	3
	1		0.137	0.008
	2			0.029
	3			
Radius 2		1	2	3
	1		0.18	<0.001
	2			<0.001
	3			
Radius 3		1	2	3
	1		0.002	<0.001
	2			<0.001
	3			

Table 3-2 shows the results of pairwise nonparametric comparisons between the three groups. Types 1 and 2 are significantly different in distance from the roof, orientation, and third radius of curvature. Types 2 and 3 are significantly different in length, distance from the roof, first, second, and third radius of curvature. Types 1 and 3 are significantly different in length, orientation, first, second, and third radii of curvature.

Principal Component Analysis

Figure 3-10 show the results of the principal component analysis performed on ten measurements: length, orientation, minimum distance from the roof, and the six length-normalized chord distances (Figure 3-2). The first two principal components explain 75% and 13% of the data, respectively. The first principal component mostly reflects shape variables (residuals of chord distances) and length (Table 3-3). The second principal component mostly reflects distance from the roof and orientation. The first principal component mostly separates type 3 from types 1 and 2, and the second principal component separates type 1 from types 2 and 3 (Figure 3-10). The PCA graph shows type 1 claw marks as lower on the burrow (i.e. greater distance from the roof) and oriented at a sharper angle to the axis of the burrow (i.e. high angle values). Type 2 claw marks are high on the burrow (low distance from the roof values) and are oriented closer to parallel on the burrow (low angle values). Type 3 claw marks are short (low length value) and curved (low chord distance residuals).

Figure 3-10. Principal component analysis of morphological data from woodchuck (*Marmota monax*) claw marks.

Osteological and cadaver measurements

The average humerus total length in woodchuck was found to be 6.00 cm ($n=7$, $s.d.=0.36$). For the same specimens, the average ulna functional length was 4.74 cm ($s.d.=0.33$) and the average length of articulated manus was 2.4 cm ($s.d.=0.27$). The average measured claw width was 1.99 mm ($n=4$, $s.d.=0.22$) (See Appendix D for raw data).

DISCUSSION

The diameter and architectural morphology of the burrow described in the previous chapter are comparable to those described for woodchuck summer shelter burrows, which, unlike the hibernation burrows, are known to lack a vertical tunnel (Hamilton 1934).

The distribution and arrangement of surficial markings, which was described qualitatively in this study, enables some interpretations of general digging style in woodchuck. Several authors have reported incisor-digging in woodchuck (Hamilton 1934, Agrawal 1967). Incisors are believed to be used by woodchucks during burrow initiation, and can therefore be expected to be found immediately near the entrance. No marks were found close to the entrance, so the possibility that woodchuck uses incisors to initiate the burrow could not be investigated here.

In *Marmota monax* the manus has four functional digits (II-V), of which digit V is by far the shortest (Figure 3-11). Manus digits II-IV are of a similar length, digit III being the longest. The pes has five functional digits, of which digits II-IV are much longer than digits I and V (Bezuidenhout and Evans 2005). Claw marks on the burrow walls mostly occur in sets of three, sometimes one, or two, rarely four marks, which agrees with the

Figure 3-11. Woodchuck manus. A. Cadaver. B. Skeleton (after Bezuidenhout and Evans 2005).

morphology of the manus. The widest claw marks are up to 2.5 times wider than the keratin claws of the forelimb. The discrepancy between the width of claws and the width of claw marks may be explained by the fact that the claw approaches the wall of the burrow during a digging stroke at an angle. The further this angle is from ninety degrees, the wider the claw mark can be expected to be. Since no three-dimensional accounts of digging kinematics have been published, this suggestion remains to be tested. However, this consideration has to be taken into account when identifying the tracemaker from the width of the claw marks.

The direction of digging can be interpreted from the arrangement of claw marks at the terminus of a blind-tunnel (Figure 3-5), because the animal must have been facing the terminus at the time of its excavation. The claw marks were found to be convex towards the terminus, so that direction of digging could be interpreted for other curved marks. Claw marks were occasionally found on the same part of the burrow running in opposite directions (Figure 3-12), suggesting that multiple episodes of excavation in both directions are recorded on the walls of the burrow.

Scratch diggers, including the prairie dog (*Cynomys*), excavate the burrow with alternating strokes of the forelimbs (Stalheim-Smith 1984, Nevo 1999, Stein 2000). The studied burrow demonstrates sections with slightly offset type 2 claw marks on either side of the tunnel roof (Figure 3-7). The claw marks overlap near the centre line of the burrow. Similar arrangement of claw marks in a Miocene mylagaulid burrow was interpreted by Gobetz (2006) as evidence for alternate motions of the two forelimbs.

One of the burrow segments contains three sets of type 1 claw marks arranged behind each other along a straight line (Figure 3-6). The interruptions in the claw path

Figure 3-12. A side view of a burrow cast segment showing claw marks going in opposite directions. Scale bar 10 cm.

may be explained by the inequalities of the soil. Another explanation is that these claw marks represent a digging movement not recognized in other parts of the burrow. The knobs found on the ceiling of the woodchuck burrow cast are similar to the ones reported by Gobetz (2006) for fossil mylagaulid burrows. The knobs on casts correspond to cavities on the original burrow. Gobetz (2006) interpreted such knobs as traces of either a dislodged stone or a clawed out tuber. At least in the studied burrow, the knobs cannot be explained as tuber marks, because tubers do not occur at the depths where knobs are found, so the knobs are more probably places where the digger encountered stones.

In some areas of the burrow, especially close to the entrance, claw marks were incomplete or missing, perhaps due to wear on the walls, collapse, or overcutting. Multiple passages cause material to be brushed off the walls of the burrow. This wear during habitation has been assumed to account for lack of claw marks in some areas of fossil burrows (Smith 1987, Groenewald et al. 2001). Given that claw marks are initially furrows, a large volume of substrate would have to be eroded off the burrow wall in order for the claw mark to be eliminated. In the studied burrow, claw mark ridges are up to half a centimetre high. For another mammal, Gobetz (2006) reports even more prominent claw mark ridges (up to one centimetre). Erosion from wear may account for the absence of claw marks on the studied burrow in the vicinity of the entrance. Roof-collapse is excluded as a mechanism for claw mark obliteration at least in some segments of the studied burrow, because their cross-sectional shape is smooth and round near the top. The absence of claw marks on the roof of the burrow may be explained by wear or head tapping of the roof during excavation, a behaviour described for other species of marmots (Bibikov 1967).

Analysis of claw mark measurements shows three morphological groups which are not directly associated with the three types of movements predicted from published descriptions of digging in the introduction to this chapter. Among the three phases of the digging cycle, only evacuation is believed to be produced by the hindlimbs in woodchuck. For *Pitymys duodecimcostatus*, Casinos et al. (1983) show the movement of the hindlimb extremity directed backwards, parallel to the floor of the burrow and slightly concave upwards during the digging stroke (Fig. 3 in Casinos et al. 1983), and indicate that successive movements tend to increase in amplitude. Jarvis and Sale (1971) found *Bathyergus suillus* and *Tachyoryctes splendens* kicking dirt backwards with a simultaneous motion of the hindlimbs. Gobetz (2006) interpreted longitudinal and angled straight marks near the floor of the fossil mylagaulid burrow as traces of a hindlimb evacuation movement.

The hindlimb claw marks can be expected to occur in pairs on either side of the burrow, be longer than the forelimb claw marks (as the hindlimbs are longer than the frontlimbs), and possibly contain more claw marks in a set, since the pes has one functional digit more than the manus (Bezuidenhout and Evans 2005). Type 1 marks are the most likely candidate for being an evacuation mark. However, none of the claw mark sets observed on the burrow cast contained five claw marks, low angle (type 1) claw marks were not significantly longer than high angle (type 2) marks, and there is no evidence that any of the claw marks were produced by a simultaneous movement of the limbs. It is therefore likely that all three types of claw marks observed in this study are produced by the forelimbs.

In order to relate the three observed claw mark types to the two forelimb digging movements, a preliminary model of claw mark production was developed. During the digging stroke, the claw marks are produced by the distalmost point on the limb. In the model, the two-dimensional trace of the distalmost point on the limb was taken as the synthetic claw mark. The forelimb was modelled as three segments connected at three joints. The segments of the forelimb represent the arm (brachium), forearm (antebrachium), and manus. The lengths of the segments were taken from average measurements of the woodchuck humerus, ulna, and manus (See Appendix D for raw data used). The three modelled joints represented the shoulder, elbow, and wrist joints. The digging stroke was parameterized in terms of changes in joint angles connecting forelimb segments. The elbow and wrist angles were taken between the segments they joined, and the shoulder angle was taken with the horizontal (as used in Fig. 2, Laville 1989).

Limb movements in the model were derived from published graphs of angle change and drawings (in side view) of initial and final positions of the forelimb during a given stroke. The modelled movement was then adjusted within the effective joint ranges of motion of *Cynomys* (Stalheim-Smith 1984) to produce synthetic claw marks that approximate the average length, orientation and curvature of each of the three claw mark types observed on the burrow cast (Table 3-1). Effective range of motion for a joint was taken as the range of joint angles at which digging forces are produced. Movement of loose soil under the body (shoulder adduction, elbow and wrist flexion) was modelled from Figure 7 C and D in Stalheim-Smith (1984), and Figure 5 in Laville (1989). The movement produces slightly curved, low angle claw marks with the leading edge lower

Figure 3-13. Synthetic claw mark (red line) corresponding to type 1. A. Movement path of claw tip. Initial position of limb segments in brown, final position in black. Movement is upwards. B. Angle change in degrees at three forelimb joints through the digging stroke. C. Radius of curvature of the claw mark in centimetres. Time units arbitrary.

than the trailing edge, comparable to type 1 claw marks but curved upwards. Figure 3-13 shows the adjusted movement reproducing straight type 1 claw marks.

Scratching to dislodge soil was modelled as simultaneous elbow extension and wrist flexion with angles for the beginning and end of stroke taken from Figure 7 B and C in Stalheim-Smith (1984). The movement produces curved claw marks that run at a high angle to the sagittal axis of the animal and are concave downwards and forwards, with the leading edge higher above the burrow floor than the trailing edge. The synthetic claw mark for the scratching movement is comparable to both type 2 (long curved) and type 3 (short curved) claw marks observed on the burrow cast. Short curved claw marks (type 3) differ from the synthesized claw mark in having a small radius of curvature which is close to the length of the manus. When the movement was adjusted by flexing the wrist joint only, the shape and size of the resulting synthetic claw mark approximated claw mark type 3 (Figure 3-14). Wrist-only movements are not specially described in the literature on other scratch-diggers, including the prairie-dog. Wrist-only digging may be a behaviour specific to *Marmota* or a more general behaviour overlooked in the literature.

The long curved claw marks of type 2 differ from the synthetic claw mark in having a smaller radius of curvature near the top of the mark. Such shape may be the result of wrist flexion only occurring at the beginning of the stroke. Indeed, when the scratching movement is modulated so that wrist flexion occurs in the first tenth of the digging stroke cycle, the resulting synthetic claw mark shape and size closely resemble those of claw mark type 2 (Figure 3-15). The similarity between synthetic and observed claw marks suggests that even a simple two-dimensional model of claw mark production can be successfully used to interpret digging strokes from claw marks. The main

Figure 3-14. Synthetic claw mark (red line) corresponding to type 3. A. Movement path of claw tip. Movement is downwards. B. Angle change in degrees at the wrist joint through the digging stroke. Elbow and shoulder joint remain fixed. C. Radius of curvature of the claw mark in centimetres. Time units arbitrary.

Figure 3-15. Synthetic claw mark (red line) corresponding to type 2. A. Movement path of claw tip. Movement is downwards. B. Angle change in degrees at three forelimb joints through the digging stroke. C. Radius of curvature of the claw mark in centimetres. Time units arbitrary.

limitation of modelling claw marks is the scarcity and incompleteness of published data on digging movements in scratch-diggers in general, and a lack of published data on digging movements in woodchuck. A cineradiographic study of digging in the woodchuck may be used to test the interpretation of woodchuck movements from claw marks and inform the model. The other limitations of the model have to do with the fact that the model represents movement in a single plane. The plane of the movement was assumed to coincide with the sagittal plane of the animal and the central vertical plane of the burrow. In laboratory kinematic studies, digging strokes have also been drawn and measured in lateral view (Laville 1989, Gambaryan and Gasc 1993). Lateral projection may be an adequate approximation of movements that leave claw marks on the sides of the burrow. On the other hand, claw marks on the roof of the burrow were sometimes found oriented almost perpendicular to the long axis of the burrow so that the movement must have been mostly out of the vertical central plane. In these cases, one of the assumptions of the model is not satisfied and the measurement of claw mark orientation does not reflect the corresponding digging movement.

Further refining of the model can be accomplished by extending it to three-dimensions. Some of the characteristics of the claw mark that may be related to movement out of the central plane of the burrow are relief height and cross-sectional width of the individual claw mark ridge, which were briefly described in this study.

CONCLUSION

This study presents a quantitative assessment of the variability of claw mark morphology on the plaster cast of a modern woodchuck (*Marmota monax*) burrow. The claw marks fall into three morphological groups based on length, location below the roof,

orientation, and curvature. Excavation in generalized scratch-diggers also falls into three stages: scratching, accumulation, and evacuation. Based on the morphology of the claw marks, it is suggested that two of the observed claw marks (short and long curved marks, types 2 and 3) are produced during the scratching phase, and the other one (long straight marks, type 1), during accumulation. The difference between curved and straight claw marks relates to a basic division of the digging cycle in generalized scratch-diggers. The short, curved claw marks, interpreted as wrist-only scratching, may be typical of the woodchuck, but more plausibly represent a previously overlooked movement common to a larger group of scratch-diggers.

A two-dimensional computer model of forelimb digging movement was used to generate synthetic claw marks. By adjusting the angle between limb segments through the digging stroke it was possible to generate claw marks similar to those observed in the woodchuck burrow. The similarity between synthetic and observed claw marks suggests that even a simple model of claw mark production can successfully serve to interpret digging strokes from claw marks. In the future, the model can be extended into three-dimensions, allowing for simulation of movements out of the lateral plane. A three-dimensional model of forelimb movement could account for such characteristics of the claw marks as their relief height, base width, and cross-sectional asymmetry.

Claw marks on fossil burrows provide a snapshot of the digging movements of the tracemaker. In order to develop a method for reconstructing digging strokes from claw mark shape, it is necessary to establish the link between tracemaker morphology, kinematics, and claw mark morphology, which can be achieved by studies of the kinematics of living animals and the morphology of their claw marks.

The approach to claw mark interpretation developed in this study may be used to address two problems in palaeontology. Digging movements reflected in claw marks can be reconstructed from their morphology for a known tracemaker. Conversely, the dimensions of the tracemaker forelimb can be reconstructed from the morphology of claw mark for a known limb movement. A development and application of this approach to fossil burrows may link evidence of morphological and behavioural change through the fossil record.

CHAPTER 4

Synthesis and directions for further research

The study of modern analogues of fossil burrow casts presented in this thesis provided several insights into the interpretation of the morphology of natural burrow casts. These relate to the taphonomic considerations for the identification of the tracemaker, preservational pathways of the burrows and the reconstruction of digging movements.

The dimensions of the burrow's architect are believed to be reflected in the cross-sectional width and height of its burrow. In Chapter Two it was shown that the burrow width is less likely to change through burrow history following burrow abandonment than burrow height. Therefore, the width of the burrow cast can be taken as a faithful reflection for the original burrow width. The interpretation of burrow width is also simpler than interpretation of burrow height. The maximum width of a mammal, inasmuch as its posture isn't sprawled, is little dependent on the size and position of the limbs. Therefore, burrow width should more closely correspond to the width of the trunk. The height of a mammal, on the other hand, is primarily dependent on the posture, and is therefore more difficult to estimate from burrow height. However, the results of this thesis indicate that the height of the burrow is not a reliable predictor of the burrower's height, unless it is demonstrated that no colluvial fill or roof collapse had occurred prior to the preservation of the burrow. Published interpretations that identify the tracemaker or correct the posture of the tracemaker based on the height of the burrow can be revised based on the results of this thesis, as has been shown in Chapter Two.

Chapter Two of this thesis has identified statistical differences between cross-sectional height in filled and open burrows. In abandoned open burrows, median height was significantly smaller than in the filled burrows. In some parts of the burrow the height was so small that the animal could not have possibly passed through. This result suggests that abandoned open burrows do not necessarily represent the initial dimensions of the burrow. This is because the open space inside the burrow is reduced by the colluvial fill accumulating on the floor. The cast of such a burrow produced in a flash flood in nature (or by pouring plaster in experiments) will have a height that is smaller than the dimensions of the inhabited burrow by the thickness of colluvial fill. The filled burrows studied in this thesis are closer in height to those reported for freshly excavated burrows. Features of their morphology indicate that they are actively filled by the animal. Active fill generally occurs before the burrow has experienced much modification and therefore a burrow cast produced this way is faithful to the dimensions of the original burrow.

The interpretation of fossil burrows requires a study of taphonomic processes in burrows. This thesis has contrasted burrows representing two taphonomic pathways. Open burrows and burrows backfilled by the animal can both become preserved as trace fossils. Open abandoned burrows become preserved by rapid sedimentation, for instance during a flash flood. The greater the amount of time that has passed since abandonment of the burrow at the time of its filling, the more the cross-sectional height of the burrow cast becomes reduced by colluvial fill and possibly by roof collapse. Backfilled burrows may be better reflections of original burrow dimensions than passively filled open burrows because active fill generally occurs before the burrow has experienced much

modification. The distinction between the two types may allow better interpretation of fossil burrow morphology.

Although backfilled burrows have been studied as concentrations of skeletal remains, the morphology of burrows has been little studied in unconsolidated sediments. The method of serial sections used in this study (Chapter Two) may permit the exploration of burrow morphology of extinct Pleistocene burrowers, and of older burrows that are found in soft sediments as far back as the Cretaceous. This is especially important for animals that mostly backfill their tunnels, such as many specialized burrowers (e.g., moles, mole-rats).

While burrow width can be used to estimate the animal's girth, the surface morphology of fossil burrows can be used to infer information about the animal's digging movements. In Chapter Three, measurements of length, orientation, location relative to the roof, and curvature were used to examine the morphological variability related to different movements. A preliminary two-dimensional model of movement was proposed for reconstructing forelimb movements from the geometry of claw marks as described by the four measurements.

Surficial marking is also related to animal morphology. The curvature of claw marks may be used for identification of the dimensions of the limbs. The one limb dimension that can be directly inferred from claw mark measurements is the length of the articulated manus reflected in the smallest radius of curvature of the burrow's claw marks. Although the length of other limb segments can not be inferred directly, it is possible to use the proposed model to predict claw mark geometry for particular movements and sizes of limb segments, and compare it with observed claw marks. In the future,

cineradiography of digging movements in laboratory animals (Jarvis and Sale 1971, Gambaryan and Gasc 1993) can be combined with examination of claw marks produced on the sides of the burrow to link digging strokes with the geometry of claw marks and so test the proposed model. Modelling digging movements provides a way to test hypotheses about tracemakers from burrow casts with claw marks. This technique may prove to be particularly useful for unspecialized scratch-diggers, because on one hand, their digging behaviour can not always be inferred from their morphology, and on the other hand, since their digging behaviour is believed to be relatively uniform (), digging movements described from extant scratch-diggers can be used in modelling digging movement.

This thesis shows the potential of detailed three-dimensional study of burrows and their trace fossils in soft-sediments. Using the methods developed and applied in this study, further progress can be made towards the use of taphonomic history in identification of the tracemaker and reconstruction of behaviour from fossil burrows.

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APPENDIX A

Grain size analyses of sedimentary layers from the Gatineau Park study site

	<i>SAND</i>							<i>SILT</i>
	<i>Very coarse</i>	<i>Coarse</i>	<i>Medium</i>	<i>Medium-fine</i>	<i>Fine</i>	<i>Very fine</i>	<i>Very fine</i>	
Coarser than	2 mm	850 µm	425 µm	250 µm	150 µm	95 µm	75 µm	< 75µm
Sieve #	10	20	40	60	100	160	200	
Layer								
12	3.63	3.34	7.51	20.47	42.94	18.20	1.92	1.99
11	1.52	1.47	24.87	24.81	29.64	13.80	2.09	1.82
10	36.29	7.67	48.19	1.49	4.27	1.02	0.12	0.95
9	1.25	1.51	9.79	29.04	36.89	17.00	2.20	2.32
8	6.12	34.96	48.19	2.47	1.12	4.40	1.53	1.21
7	10.20	31.35	45.02	3.33	0.32	7.61	1.27	0.90
5	2.40	12.40	49.35	23.14	6.45	4.12	1.20	0.94
3	55	1.15	30.50	22.10	26.78	13.14	2.65	3.00
2	1.34	5.75	10.93	12.17	30.22	35.05	2.49	2.05
1	3.50	47.24	23.30	14.64	6.64	2.74	0.95	0.99

APPENDIX B

Photos of soil sections from the Gatineau Park study site

Numbers of section photos refer to map on Figure 2-13. A note on the coloring conventions. Layers are white, root casts are green, faults are brown. Woodchuck and chipmunk burrows are yellow. Multiple fills in chipmunk burrows are colored, from the outside to the inside, yellow, orange, red-orange. Wherever cross-cutting fills are present, the youngest fill is contoured solid, and the older ones are contoured dashed (smaller dash corresponds to greater relative age). Kingfisher burrows (open) in orange.

Figure B-1. Section photo #2605.

Figure B-2. Section photo #2607.

Figure B-3. Section photo #2679.

Figure B-4. Section photo #2701.

Figure B-5. Section photo #2784.

Figure B-6. Section photo #2817.

Figure B-7. Section photo #2825.

Figure B-8. Section photo #2868. Remnants of the oldest fill are contoured with a fine dash.

Figure B-9. Section photo #2872

Figure B-10. Section photo #2879.

Figure B-11. Section photo #2893.

Figure B-12. Section photo #2911.

Figure B-13. Section photo #2917.

Figure B-14. Section photo #2919.

Figure B-15. Section photo #2929.

Figure B-16. Section photo #2940.

Figure B-17. Section photo #2941.

Figure B-18. Section photo #2978.

Figure B-19. Section photo #3057.

Figure B-20. Section photo #3065.

Figure B-21. Section photo #3072.

Figure B-22. Section photo #3101.

Figure B-23. Section photo #3104.

Figure B-24. Section photo #3131.

Figure B-25. Section photo #3135.

Figure B-26. Section photo #1828.

Figure B-27. Section photo #1839.

Figure B-28. Section photo #1845.

Figure B-29. Section photo #2253.

Figure B-30. Section photo #2256.

Figure B-31. Section photo #2261.

Figure B-32. Section photo #2264.

Figure B-33. Section photo #2271.

Figure B-34. Section photo #2276.

Figure B-35. Section photo #3008.

A. Enlarged part of the photo showing the burrow. B. General view.

Figure B-36. Section photo #3021.

Figure B-37. Section photo #3039.

A. Enlarged part of the photo showing the burrow. B. General view.

APPENDIX C

Cross-sectional measurements of woodchuck and chipmunk burrows

Table C-1. Cross-sectional measurements of the reconstructed (filled) woodchuck burrow (cm). Missing width values are from parts of the burrow where width could not be estimated.

#	Width	Height	#	Width	Height	#	Width	Height	#	Width	Height
1	16.0	14.5	11	31.5	15.9	20	25.0	18.2	31	12.2	-
2	15.0	15.0	12	28.0	14.7	21	29.5	19.4	32	16.7	-
3	17.8	15.2	13	36.8	35.0	22	30.0	17.5	33	17.0	-
4	15.3	13.4	14	19.7	17.7	23	25.6	15.9			
5	15.3	9.6	15	19.1	17.5	24	27.6	18.0			
6	17.0	15.2	16	20.6	19.5	25	22.0	23.3			
7	21.1	17.0	17	25.2	16.0	26	17.8	22.2			
8	23.4	16.5	18	21.4	16.7	27	19.0	20.1			
9	24.8	17.0	19	20.3	16.0	28	18.6	14.0			
10	24.1	19.0	20	25.0	18.2	29	12.6	21.6			

Table C-2. Cross-sectional measurements of the reconstructed (filled) chipmunk burrow (burrow A).

#	<i>Height,</i> <i>cm</i>	<i>Width,</i> <i>cm</i>
1	7.2	5.7
2	5.0	6.0
3	7.2	4.4
4	5.8	5.5
5	5.5	6.5
6	6.4	4.2
7	5.1	4.6
8	5.0	4.0
9	6.0	4.7
10	7.1	4.8
11	6.7	6.6
12	6.0	4.4

Table C-3. Cross-sectional measurements of the plaster-cast of a woodchuck burrow (cm).

#	<i>Width</i>	<i>Height</i>	#	<i>Width</i>	<i>Height</i>	#	<i>Width</i>	<i>Height</i>	#	<i>Width</i>	<i>Height</i>
1	15.1	10.0	14	19.1	14.5	27	15.4	10.6	40	17.5	11.5
2	14.0	11.2	15	18.3	8.7	28	16.4	11.2	41	17.4	12.4
3	14.5	9.7	16	16.4	9.1	29	19.5	12.0	42	17.4	12.2
4	13.8	10.0	17	16.2	8.4	30	16.6	12.2	43	22.0	17.0
5	14.3	10.6	18	16.1	11.7	31	24.1	11.0	44	19.5	15.2
6	18.6	8.1	19	16.0	11.9	32	18.8	12.0	45	23.6	17.6
7	19.6	7.5	20	12.6	9.6	33	18.1	13.0	46	26.8	23.3
8	15.5	8.0	21	12.0	7.0	34	15.0	12.0	47	23.1	18.8
9	16.4	8.2	22	15.9	9.3	35	21.2	13.8	48	31.8	20.0
10	17.9	6.7	23	15.7	8.5	36	18.0	11.4			
11	18.5	13.6	24	16.6	9.0	37	17.5	10.7			
12	18.2	13.9	25	24.0	14.5	38	18.5	13.5			
13	17.2	11.2	26	14.5	11.8	39	19.1	11.7			

Table C-4. Cross-sectional measurements of the plaster-cast of a chipmunk burrow.

#	<i>Height,</i> <i>cm</i>	<i>Width,</i> <i>cm</i>
1	5.70	4.70
2	6.10	5.10
3	6.20	5.80
4	6.00	5.20
5	5.80	4.70
6	5.20	4.45
7	6.00	4.70
8	6.35	4.70
9	6.10	5.70
10	6.40	4.70
11	6.30	4.85
12	6.30	4.60
13	8.40	7.00
14	6.10	4.90
15	7.60	5.10
16	5.50	5.35
17	6.10	6.10
18	5.50	6.20
19	4.90	5.10
20	5.20	4.80
21	6.10	4.60
22	5.70	4.60
23	5.60	4.15
24	5.45	4.20
25	5.40	4.20

APPENDIX D

Osteological and cadaver measurements

Table D-1. Woodchuck Cadaver Measurements.

	<i>Shoulder breadth (cm)</i>	<i>Chest girth (cm)</i>	<i>Length of manus (cm)</i>
1	13.4	42.5	2.1
2	15.1	46.8	2.7
3	13.8	43.5	2.4
4	13.9	44.0	2.35
5	13.2	41.8	2.6
6	15.9	50.5	2.9
7	16.2	52.0	2.9
Average	14.5	45.9	2.44
Standard deviation	1.22	4.02	0.27

Table D-2. Woodchuck osteological measurements.

<i>Collection number</i>	<i>Humerus length (cm)</i>	<i>Ulna functional length (cm)</i>
Z-729	5.8	4.6
75548	6.2	5.0
41083	5.6	4.5
75403	5.9	4.7
75033	6.6	5.3
41019	6.3	4.9
75141	5.7	4.3
Mean	6.0	4.7
Standard deviation	0.36	0.33

APPENDIX E

Claw mark measurements

Table E-1. Claw mark measurements. Note: straight marks were assigned a radius of 250 mm.

#	Type	Length (mm)	Angle (degrees)	Top Height (mm)	Radius1 (mm)	Radius2 (mm)	Radius3 (mm)
1	2	92.165	42.51	133.939	15.4	25.3	28.6
2	1	108.265	28.18	133	102.9	250	250
3	2	121.765	63.54	132.681	27.8	40.8	250
4	2	72.77	28.36	72.77	33.3	250	250
5	2	63.151	59.84	109.539	5.8	46.5	250
6	2	69.241	63.16	107.294	8.1	34.8	250
7	2	54.814	74.86	66.438	7.3	250	250
8	2	72.185	49.56	105.96	15.5	93	93
9	2	93.522	74.74	101.414	37.4	250	250
10	2	96.532	58.13	107.245	9.4	250	250
11	1	139.733	78.32	96.306	13.2	250	250
15	2	153.578	41.58	104.257	42.4	250	34.3
16	3	75.164	63.37	64.368	27.5	250	250
17	3	51.727	70.47	115.379	73.2	73.2	137.9
18	3	57.411	58.9	128.539	18.5	250	250
19	3	47.724	5.93	111.824	8.8	32.3	32.3
20	3	42.072	23.51	151.619	17.3	29.9	29.9
21	1	50.236	10.34	43.692	19.7	17.7	48
22	1	41.608	32.67	60.441	250	250	250
23	1	69.094	35.48	34.245	194.1	250	250
24	1	164.343	20.19	69.133	32.36	250	250
25	3	122.173	41.7	147.544	41.3	97.6	97.6
26	3	47.244	31.97	84.635	8.1	11.7	33.6
27	3	48.588	19.92	143.794	76	76	76
28	3	49.981	2.02	139.829	8.1	24.1	24.1
29	3	41.061	14.6	36.904	250	250	250
30	3	140.794	31.94	140.472	41.6	42.4	47.6
31	2	119.167	174.65	148.981	250	250	250
32	3	30.35	32.45	98.094	10.8	14.1	14.1
33	3	34.783	57.38	65.501	5.2	23.2	23.2
34	1	57.514	17.91	101.833	35.8	250	250
35	3	39.915	36.17	105.607	22.1	41.5	41.5
36	3	26.213	14.93	90.764	9.4	15.1	15.1

Table E-2. Cross-sectional measurements of claw marks. Claw mark width.

#	<i>Claw mark width (mm)</i>
1	4.4
2	5.0
3	5.1
4	5.7
5	7.1
6	6.2
7	7.5
8	4.3
9	4.5
10	5.8
11	3.4
12	4.5
Mean	5.3
Standard deviation	1.2

Table E-3. Cross-sectional measurements of claw marks. The width of a claw mark set.

	<i>Width of claw mark set (mm)</i>
1	43.2
2	33.8
3	33.4
4	32.5
5	34.6
6	44.8
7	22.8
8	26.6
9	40.0
10	32.7
11	37.1
12	38.8
13	34.0
14	35.2
15	38.6
16	45.7
Mean	35.9
Standard deviation	6.4