Ecology and Behaviour of Urban Stone Martens (*Martes foina*) in Luxembourg

by
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Declaration

I hereby declare that this thesis has not been submitted in whole or in part, either in the same or different form, for a degree or diploma or any other qualification at this or any other university. All the work described in this thesis was carried out by me at the field study sites in Luxembourg. Where other sources are referred to this is indicated.

Signature

Jan Herr

To my parents

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SUMMARY

The stone marten (*Martes foina*) is common throughout continental Europe where it often occurs in urban environments. Conflicts between humans and martens arise when the animals den under the roofs of inhabited buildings or damage car engine components. The aims of my study were (a) to provide a general description of the ecology and behaviour of urban stone martens and (b) to formulate management recommendations based on these data.

I radio tracked 13 stone martens in two towns in southern Luxembourg. Individuals were followed at night to provide information about ranging and territorial behaviour, and fixes were taken during the day to provide information about den sites. I also radio tracked five translocated martens in order to assess the usefulness of translocation as a management tool.

The socio-spatial organisation of urban martens was based on clear intrasexual territoriality. Territories were generally smaller than those previously recorded in rural areas and activities were almost entirely restricted to urban habitat. Urban martens were completely nocturnal and their activity rhythms were adapted to achieve temporal avoidance of humans and traffic.

Martens denned almost exclusively in buildings. Most denning was in uninhabited buildings during summer, autumn and spring but there was a marked shift towards inhabited buildings in winter. There was also a clear seasonal pattern in martens' use of roads and cars. This, together with observations of scent marking of cars, suggests that car damage is linked to the species' territorial behaviour.

A wild-caught adult urban stone marten that was translocated to forested habitat returned rapidly to urban habitat but died soon afterwards. Translocated captive-reared juveniles remained in rural habitat and survived for longer.

I review possible explanations for my results and conclude that in most respects martens are typical 'urban adapters'. I suggest various recommendations for human-marten conflict management in light of my findings.

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ÖKOLOGIE UND VERHALTEN URBANER STEINMARDER (*Martes foina*) IN LUXEMBURG

ZUSAMMENFASSUNG

Steinmarder (*Martes foina*) sind in Europa weit verbreitet und kommen häufig in urbanen Lebensräumen vor. Konflikte können entstehen, wenn sie ihre Tagesschlafplätze unter Hausdächern einnehmen oder Autos beschädigen. Die Zielsetzung meiner Studie war (a) eine allgemeine Beschreibung der Verhaltensökologie von urbanen Steinmardern vorzulegen und (b) diese zu nutzen um Vorschläge für das Management dieser Art zu machen.

Ich telemetrierte 13 Steinmarder in zwei Kleinstädten im Süden Luxemburgs. Dabei folgte ich den Tieren nachts um Daten über ihre Raumnutzung und Territorialität zu gewinnen. Tagsüber lokalisierte ich sie um ihre Tagesschlafplätze bestimmen zu können. Des Weiteren wurden fünf umgesiedelte Marder telemetriert um so den Nutzen von Umsiedelungen im Rahmen des Konfliktmanagements zu bewerten.

Die räumliche und soziale Organisation urbaner Steinmarder basierte auf intrasexueller Territorialität. Die Reviere waren allgemein kleiner als die aus anderen Studien bekannten Reviere in ländlichen Gebieten. Die Aktivitäten der Marder begrenzten sich fast ausschließlich auf urbane Lebensräume. Die Tiere waren nur nachtaktiv und passten ihre Aktivitätsmuster so an, dass Menschen und Verkehr größtenteils gemieden wurden.

Tagesverstecke wurden fast komplett in Gebäuden eingenommen. Unbewohnte Gebäude wurden hauptsächlich im Sommer, Herbst und Frühjahr genutzt. Im Winter dagegen bevorzugten sie Tagesschlafplätze in bewohnten Gebäuden. Auch die Nutzung von Straßen und Autos unterlag jahreszeitlichen Schwankungen. Zusammen mit Beobachtungen von Mardern, die gezielt Duftmarken an Autos anbrachten, deutet dies darauf hin, dass der Revierverteidigung eine wichtige Rolle bei den von Mardern verursachten Autoschäden zugeteilt werden muss.

Ein adulter, urbaner Marder, der in ein Waldgebiet umgesiedelt wurde, kehrte schnell wieder in ein besiedeltes Gebiet zurück, starb aber wenig später. Ausgesetzte Handaufzuchten hingegen verweilten in ländlichen Lebensräumen und überlebten länger.

Ich liefere veschiedene Erklärungsansätze für meine Ergebnisse und schlussfolgere, dass Steinmarder größtenteils als typische „urbane Anpasser“ (‘urban adapters’) angesehen werden können. Auf der Basis meiner Daten mache ich verschiedene Vorschläge zum Management von Marder-Mensch Konflikten.

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ECO-ETHOLOGIE DE LA FOUINE (*Martes foina*) EN MILIEU URBAIN AU LUXEMBOURG

RESUME

La fouine (*Martes foina*) est très répandue à travers l'Europe continentale où elle fréquente souvent les milieux urbains. Des conflits entre humains et fouines peuvent se manifester quand les animaux gîtent en dessous des toits de bâtiments habités ou endommagent des voitures. Les objectifs de mon étude étaient (a) de produire une description générale de l'écologie et du comportement de la fouine en milieu urbain et, en se basant sur ces données, (b) de formuler des recommandations pour la gestion de ces conflits.

J'ai suivi 13 fouines par radiotélémétrie dans deux petites villes du sud du Grand-Duché de Luxembourg. Le suivi des fouines se faisait la nuit en vue d'étudier leur utilisation de l'espace et leur comportement territorial. Des localisations diurnes étaient effectuées afin d'étudier la sélection de leurs gîtes. J'ai aussi suivi cinq fouines transférées pour évaluer l'utilité de cette méthode en tant qu'outil de gestion de conflits.

L'organisation spatiale et sociale des fouines urbaines se basait sur la territorialité intrasexuelle. En général les territoires étaient plus petits que ceux connus des zones rurales et les activités se limitaient presque exclusivement sur les zones urbaines. Les fouines urbaines étaient complètement nocturnes et elles adaptaient leur rythme d'activité de façon à éviter les humains et le trafic routier.

Les fouines passaient presque toutes les journées à l'intérieur de bâtiments. En été, en automne et en printemps elles gîtaient de préférence dans des bâtiments non-habités, tandis qu'en hiver dans des bâtiments habités. Je constatais aussi des variations saisonnières dans leur fréquentation des rues et des voitures. Ceci indique, ensemble avec des observations de fouines qui marquaient des voitures de leur urine, que les dégâts aux voitures sont liés au comportement territorial de l'espèce.

Une fouine adulte urbaine qui était transférée et lâchée en milieu boisé retournait rapidement vers une zone urbaine mais était morte peu après. Par contre des fouines jeunes élevées en captivité restaient en milieu rural après avoir été lâchées, et survivaient plus longtemps.

Je passe en revue des explications potentielles pour mes résultats et peux conclure que les fouines sont à considérer comme des «adaptateurs urbains» ('urban adapters') typiques. J'énumère par la suite certaines propositions concernant la gestion des conflits entre humains et fouines en me basant sur les données de cette étude.

Chapter 1: General Introduction

1.1. Urbanisation and its effects

1.1.1. Global trends in urbanisation

Urbanisation refers to the transition from a rural to an urban human population, reflecting a net increase in the proportion of the population residing in areas classified as urban (United Nations Population Fund 2007). The year 2008 is projected to be the first year ever when more than half the world's population will be living in urban environments. Currently, approximately 70 to 75% and 80% of humans are already living in urbanised areas in Europe and North America, respectively. By 2030, urban populations worldwide are expected to have grown by an additional 1.6 billion people, with most of this growth taking place in smaller cities with less than 500000 inhabitants (United Nations Population Fund 2007).

1.1.2. 'Urban' – Definitions

Finding a definition for 'urban' is not straightforward and the meaning often depends on the context in which the term is used. Generally, social scientists use urban to refer to areas with high human densities, while ecologists use the term more widely to refer to areas under human influence (McIntyre *et al.* 2000). The United Nations define the word 'urban' as settlements or localities that are classed as urban by national statistical agencies (United Nations Population Fund 2007). However, these definitions vary widely and are often arbitrary. Thus the US Census Bureau defines urban areas as having population densities of > 620 inhabitants$\cdot$km^{-2} (US Census Bureau 2002), while in the UK an urban area is considered to be any settlement with > 10000 inhabitants (UK Office for National Statistics 2004). In Luxembourg, urban units are defined as continuous built-up areas with buildings being separated by less than 200 m and a core area containing at least 3000 inhabitants or a residential density of > 300 inhabitats$\cdot$km^{-2} (Sohn 2006). Urban areas have also simply been defined as areas dominated by built structures (> 10 buildings$\cdot$ha^{-1}) (Shochat *et al.* 2006).

McIntyre *et al.* (2000) recognised the difficulties of agreeing on a single definition of 'urban' and suggested that a working definition of urban environment should be used instead. Such a definition should include as much information as possible on demography and physical geography, providing a benchmark with which to compare other studies (McIntyre *et al.* 2000). I have included such data in the description of my study areas in Chapter 2.

1.1.3. Biotic homogenisation

With the current trend towards urban sprawl one would expect repercussions on biodiversity. A number of papers have recently dealt with this issue (e.g., McKinney 2002; McKinney 2006; Shochat *et al.* 2006; Turner *et al.* 2004). They view urban growth as a large-scale disturbance that generally destroys habitat of native species thus leading to considerable loss in biodiversity. This trend is often paralleled by an increase in non-native species (due to accidental importation or importation of species for cultivation, pets and other uses) that are able to thrive in urban areas. Overall these changes lead to biotic homogenisation of urban ecosystems (Clergeau *et al.* 2006a; McKinney 2002, 2006), so that cities across the globe are often a lot more similar to each other in terms of animal and plant communities than to the natural environments surrounding them (McKinney 2006).

However, these changes are often complex and may vary along the rural-urban gradient. Thus, diversity may peak at intermediate levels of urbanisation (e.g., in suburban or residential areas) due to an increase in structural diversity in vegetation and buildings with an associated increase in diversity and abundance of resources (Blair 1996; McKinney 2002). In fact, domestic gardens, typically associated with residential areas, can make up a considerable proportion of urban green spaces and provide habitats for a range of plants and animals (Gaston *et al.* 2005). Extreme development, with increasing proportions of paved and built-up surfaces, should, however, decrease these factors (Blair 1996). Consequently, at a landscape level, the number of species of breeding birds and mammals tend to decrease from low to high levels of urbanisation (Clergeau *et al.* 2006b).

1.2. Urban mammals

1.2.1. Responses to urbanisation

Because urban systems are maintained outside a natural equilibrium, they tend to need a huge input of resources and management. A consequence of this is often that temporal changes in resource (e.g., food, water) availability are considerably dampened (McKinney 2006; Shochat *et al.* 2006). Not all organisms, however, can take advantage of these conditions (e.g., Crooks 2002). For example, VanDruff and Rowse (1986) showed that urban mammal communities are impoverished, consisting mostly of generalists that are able to use a matrix of different habitats. Blair (1996) applied a three-way classification for birds (later extended to other organisms by McKinney 2002, 2006) describing their responses to urbanisation. In what follows I will limit my discussion to mammals and will concentrate on carnivores.

i) *Urban avoiders* are very sensitive to human development and are generally the first to disappear because they are directly persecuted, relatively rare or have low reproductive rates. They generally rely on natural resources and include mammals such as large predators and large herbivores (Crooks 2002; McKinney 2002).

ii) *Urban adapters* are typically able to use human-subsidised foods such as cultivated plants or garbage, as well as natural resources (McKinney 2002). They usually reach their highest densities in low to moderate levels of urbanisation and are often natives that immigrate into human-created habitats from surrounding areas (McKinney 2006). They include mammals with burrowing habits, medium-sized omnivores and carnivores that consume a wide variety of foods (McKinney 2002).

iii) *Urban exploiters* are highly or even fully dependent on human resources. They often live mainly inside buildings and reach their highest densities in the urban core. They are also often non-natives that leapfrog from one urban area to another. Typical representatives among mammals are house mice (*Mus musculus*) and brown rats (*Rattus norvegicus*) (McKinney 2002, 2006).

1.2.2. Human-wildlife conflict

The biotic homogenisation that results from urbanisation may cause urban human residents to become increasingly disconnected from nature (Miller 2005; Turner *et al.*

2004). Thus, the presence of wildlife in urban or suburban areas can provide a variety of benefits or positive values. These can range from an animal's aesthetic or historic value to scientific and educational benefits that keep urban residents in touch with nature. Furthermore, humans may gain enjoyment from the presence of wild animals through recreational activities such as wildlife watching, photography or hunting (Adams *et al.* 2006; Conover 2002). In Germany, for example, many residents of towns with high raccoon (*Procyon lotor*) densities classified them as cute, probably getting enjoyment out of watching the animals in their backyards (Hohmann *et al.* 2001).

Unfortunately, however, where humans and wildlife co-exist in close proximity, conflicts are often unavoidable. These human-wildlife conflicts can go in both directions such that the animals' activities adversely affect humans and their property, or certain human activities may have negative impacts on wildlife (Conover 2002). Mammals are particularly often involved in these actual or perceived conflicts. In the USA, eight groups of mammals figured among the top ten species responsible for most recorded damage incidents between 1994 and 2003, including (in decreasing order) raccoons, coyotes (*Canis latrans*), skunks (Mephitidae), beaver (*Castor canadensis*), deer (Cervidae), squirrels (Sciuridae), opossums (*Didelphis virginiana*) and foxes (various genera) (Adams *et al.* 2006). Many of these can be seen as typical urban adapters. The conflicts that they cause range from disease transmission, through damage to property, to nuisance behaviour and compromised human safety.

Disease

Bradley and Altizer (2007) have reviewed the effects of urbanisation on wildlife disease ecology. The environmental changes accompanying urbanisation can potentially affect the biology of pathogens, vectors and hosts. Increased and clumped food resources may result in higher wildlife densities, thus increasing contact rates and disease transmission between infected and susceptible animals. Furthermore, anthropogenic stressors may increase the susceptibility of wildlife to various diseases. Also, urban environments may favour the survival, reproduction and activity of arthropod vectors that transmit diseases (Bradley and Altizer 2007).

Research has mostly focused on the ecology of wildlife reservoirs that directly carry zoonoses or otherwise play a vital role in the life cycle of a disease that can potentially affect humans. In Europe, the role of urban red foxes (*Vulpes vulpes*) in spreading the tapeworm *Echinococcus multilocularis*, which causes liver disease in humans, is currently a focus of attention (Brochier *et al.* 2007; Gloor 2002; Hegglin *et al.* 2007; Schweiger *et al.* 2007). Raccoon roundworm *Baylisascaris procyonis* infections have been found to be common in some North American and German raccoon populations. This parasite can have fatal consequences when ingested by humans, especially children (Hohmann and Bartussek 2001; Sorvillo *et al.* 2002). In North America, raccoons, striped skunks (*Mephitis mephitis*) and red foxes are studied to actively halt the spread of rabies in urban areas (Guerra *et al.* 2003; Rosatte *et al.* 2007), while in Europe urban red foxes have been studied to gain insights into their potential role in future rabies outbreaks and to develop possible management strategies (Hegglin *et al.* 2004; Saunders *et al.* 1997; White *et al.* 1995).

Unlike the previous examples, the white-tailed deer (*Odocoileus virginianus*) is a mammal that is common in urban areas and plays an important role in the prevalence of a disease (Lyme disease) without, however, directly transmitting the disease itself. Rather, deer act as host for the vector (ticks) responsible for transmitting the disease. Hence, high urban deer densities may increase the risk that humans will contract Lyme disease in these areas (Adams *et al.* 2006).

Damage to property and other nuisance behaviour

Certain mammals can cause considerable damage to private property. In the USA, most damage to households in metropolitan areas is caused by mice, followed by squirrels, raccoons and moles (Talpidae) (Conover 2002). In some German towns where raccoons occur at high densities, residents report them raiding their fruit trees and ravaging garden ponds (Hohmann *et al.* 2001; Michler *et al.* 2004). Raccoons may also damage roof insulation when using attics as den or cub-rearing sites. Similar denning-related problems have been reported from urban brushtail possums (*Trichosurus vulpecula*) in Australia. Urban white-tailed deer may damage ornamental garden plants (Jones and Witham 1990) and Eurasian badgers (*Meles meles*) can cause damage to fences, lawns, plants and dustbins. Substantial damage can result from the burrowing activities of badgers in gardens or beneath buildings (Davison 2007). Some urban predators (e.g., coyotes and red foxes) have been shown to occasionally attack or prey on pets including small dogs (*Canis lupus familiaris*), cats (*Felis catus*), rabbits (*Oryctolagus cuniculus*) or guinea pigs (*Cavia porcellus*) (Harris 1981b; Timm *et al.* 2004).

Other forms of nuisance may relate to noise or odours resulting from the animals' activities. Skunks may be considered a nuisance due to the strong-smelling musk that they spray when threatened (Gehrt 2004). Activity of raccoons, brushtail possums or squirrels (e.g., *Sciurus carolinensis*) in attics or roof voids can cause considerable disturbance to house owners, and their faeces and urine may result in odours and staining of ceilings (e.g., Matthews *et al.* 2004).

Human safety

Human safety can be compromised through the presence of wild animals in urban environments. Direct attacks on humans are a concern to many residents living in proximity to larger predators like coyotes: coyote attacks on children or even adults do occasionally take place in urban areas and in some areas they seem to be becoming more frequent (Timm *et al.* 2004). Cougars, on the other hand, do not generally occur in urban or suburban areas, though Beckmann and Berger (2003b) suggest that increasing deer populations in suburban areas may also alter the distribution of cougars and there have been some attacks on humans close to human settlements (Maehr 2004). Although such cases are very rare, the media attention that they get may increase perceived threat levels among suburban residents living alongside predators.

Deer can also pose a direct threat to humans. In the USA, up to 200 human fatalities and many more injuries occur per year as a result of deer-car collisions (Adams *et al.* 2006). Although these statistics are not restricted to urban areas, they nevertheless underline the fact that car collisions with wildlife may warrant serious considerations in urbanised ecosystems (Nielsen *et al.* 2003). Collisions with larger cervids such as moose (*Alces alces*) may pose even more serious risks (Garrett and Conway 1999).

1.2.3. Urban carnivores

Large carnivores generally respond negatively to increasing urbanisation and are thus among the first to disappear. Hence, they can be classed as typical urban avoiders (Crooks 2002; McKinney 2002). However, there are examples of black bears (*Ursus americanus*) having established in urban areas, even occurring at higher densities than in natural areas (Beckmann and Berger 2003a, b). The coyote is probably the largest carnivore that commonly occurs in urbanised areas or in natural habitat fragments surrounded by developed areas (e.g., Gibeau 1998; Grinder and Krausman 2001; Markovchick-Nicholls *et al.* in press; Quinn 1991; Tigas *et al.* 2002). Nevertheless, its distribution seems to remain mostly confined to the fringes of urban development (e.g., Randa and Yunger 2006). In southern California, where coyotes did occur in urban areas, their home ranges were larger than in natural areas, suggesting that developed areas were in fact less suitable for them (Riley *et al.* 2003).

Crooks (2002) showed that medium-sized carnivores (mesocarnivores or mesopredators) were generally the most successful in highly fragmented and urbanised landscapes. Domestic cats responded most positively to fragmentation (Crooks 2002). Indeed, cats are typical non-native urban exploiters that are transported by humans between urban areas (McKinney 2002), where they may either occur as pet (Kays and DeWan 2004) or feral animals (Haspel and Calhoon 1991; Schmidt *et al.* 2007). The red fox is among the most successful of non-domesticated carnivores to have established breeding populations in urban areas. The urban fox phenomenon was first extensively studied in the English cities of Bristol (Harris 1981a) and Oxford (Doncaster and Macdonald 1991) and subsequently in continental Europe (Gloor *et al.* 2001), as well as in its non-native ranges in North America (Adkins and Stott 1998) and Australia (Marks and Bloomfield 2006). Other fox species that have been occasionally recorded in urban areas include gray (*Urocyon cineroargenteus*) and San Joaquin kit foxes (*Vulpes macrotis mutica*) (Cypher and Frost 1999; Riley 2006).

The raccoon is a mesocarnivore that rivals the red fox in its adaptation to urban environments both in its native range in North America (e.g., Bozek *et al.* 2007; Hadidian *et al.* 1991; Randa and Yunger 2006) and in its introduced range in Germany (Hohmann *et al.* 2001). Striped skunks have also entered urban areas successfully (Rosatte 1991). Among the mustelids there are few urban representatives. Eurasian badgers occasionally inhabit towns and cities (Davison 2007; Harris 1982) but as of now, urban badgers seem to be mostly confined to the UK (though see Aaris-Sørensen 1987; Kaneko *et al.* 2006). Other mustelids such as otters (*Lutra* spp.) or mink (*Mustela vison*) have sporadically been recorded in urban environments but no real urban populations of these species have been studied to date (Mech 2003; Sleeman and Moore 2005).

Most of the above-mentioned species are mesocarnivores that successfully adapt to urban habitats. However, not all mesopredators show this same response to urbanisation. One factor that may allow some species to occur in urban areas could be the absence of a larger predator (Crooks and Soulé 1999). Thus in southern California gray foxes occur in urbanised environments where coyotes are absent (Riley 2006) but are rare where coyotes are common (Markovchick-Nicholls *et al.* in press). Diet seems to be another important factor. Crooks (2002) showed that some small or medium-sized carnivores such as North American badgers (*Taxidea taxus*), spotted skunks (*Spilogale gracilis*), long-tailed weasels (*Mustela frenata*) and bobcats (*Felis rufus*) were very sensitive to urbanisation. The main difference between these carnivores and comparable adapters is that urban adapters are resource generalists, while the avoiders are primarily carnivorous (Crooks 2002). Thus one key to becoming an urban adapter seems to be an ability to take advantage of anthropogenic foods such as garden fruits, garbage or deliberate supplemental feeding.

The increased availability of food resources in urban areas has usually been taken for granted in studies on urban wildlife. However, there have also been studies that directly demonstrate the use of anthropogenic foods. Direct scavenging from garbage and compost heaps or the presence of scavenged food in the diet has been documented for feral cats (Haspel and Calhoon 1991), black bears (Beckmann and Berger 2003b), raccoons (Bozek *et al.* 2007), red foxes (Contesse *et al.* 2004; Harris 1981b), gray foxes (Harrison 1997) and coyotes (Fedriani *et al.* 2001). Deliberate feeding of Eurasian badgers and red foxes by urban residents has also been recorded (Baker *et al.* 2000; Davison 2007). However, not all urban carnivores seem able to take advantage of such anthropogenic resources to the same degree. Thus, striped skunks hardly ever forage in or near trash cans, while raccoons that live in the same area use this resource extensively (Prange and Gehrt 2004). Consequently, demographic and behavioural responses to these altered environments may differ between different urban adapters (e.g., Prange and Gehrt 2004). Nevertheless, changes in densities and socio-spatial organisation, as well as in movement and activity patterns, commonly accompany adaptation to urban systems (see Chapters 3 and 4).

1.3. General ecology of stone martens

1.3.1. Distribution and population trends

One mustelid that has adapted well to urban habitats in Europe is the stone marten (*Martes foina*, Erxleben 1777), sometimes referred to as the 'beech marten'. In what follows I will use the terms 'stone marten' and 'marten' to refer to *M. foina*. Where I refer to other marten species this will be specified.

Stone martens are widespread throughout mainland Europe, their geographic range extending from Portugal in the West to southwestern Russia and Turkey in the East. However, the species is missing from the UK, Ireland, and most of Scandinavia (Sweden, Norway, Finland). East of the Caspian Sea it occurs in discontinuous populations in, among other countries, Afghanistan, Pakistan, India, Nepal and Bhutan (IUCN 2007a). A small, introduced population has been reported to exist in southern Wisconsin, USA, probably resulting from animals having escaped or having been released from a fur farm sometime between the 1940s and the early 1970s (Long 1995). Throughout most of its European range (apart from parts of the Iberian Peninsula) the stone marten is sympatric with its close relative the pine marten (*Martes martes*) (IUCN 2007a, b).

Due to the stone marten's wide distribution and large population it is currently listed as a species of 'Least Concern' on the European Red List (IUCN 2007a). However, high hunting and trapping pressure depleted stone marten populations in the early 1900's. Bag statistics from several countries (including Germany, Denmark, and Switzerland) indicate that populations started to recover between the 1950s and 1970s (reviewed in Libois and Waechter 1991; Stubbe 1993). Re-colonisation of regions where the animal had completely disappeared has also been documented (e.g., in the Netherlands: Broekhuizen and Müskens 2004).

1.3.2. Morphology and reproductive cycle

The stone marten's fur consists of long brown-greyish guard hairs and grey-whitish down hairs. The appearance of the animal is characterised by a white throat/chest patch that is usually bilobed, with each lobe extending down onto a front leg. However, there may be considerable variation in the shape of this patch (Stubbe 1993). The animal is sexually dimorphic in body weight. Mean body mass of adults ranges from 1.6 to 1.7 kg for males and from 1.2 to 1.3 kg for females (Krüger 1995).

The reproductive cycle of stone martens is characterised by delayed implantation, as it is in about a third of all mustelid species (e.g., Ferguson *et al.* 2006; Thom *et al.* 2004). Early observations on captive animals established that matings took place in summer (July and August), 8.5 to 9 months before the litters were born (Schmidt 1943). However, the mechanism of delayed implantation was confirmed only much later (Canivenc *et al.* 1981). Testis development in males peaks in June (Audy 1976; Madsen and Rasmussen 1985), just prior to the onset of the mating season, which extends from July to mid August. Litters are born from early March to mid-April, with average litter sizes of around 3 young (range: 1-5) (Madsen and Rasmussen 1985; Schmidt 1943). Young martens start consuming solid food at about seven weeks of age but will not leave the den until they are about 11 weeks old (i.e., late May to early June: Skirnisson 1986). Dispersal may occur from August onwards. However, it is not known if there is a typical dispersal period (Herrmann 2004). Stubbe (1993) and Libois and Waechter (1991) provide more detailed reviews of the reproductive cycle.

1.3.3. General diet

The feeding ecology of the stone marten has been the subject of numerous studies, all of which agree that this mustelid is a particularly opportunistic feeder. This conclusion seems independent of the habitat that the study animals are living in. While few authors have investigated feeding habits in predominantly wooded environments (e.g., Genovesi *et al.* 1996), many have concentrated on rural settings with villages surrounded by pastures, agriculture and wooded areas (e.g., Baghli *et al.* 2002; Brangi 1995; Lachat Feller 1993b; Lanszki *et al.* 1999; Lanszki 2003; Lodé 1994; Skirnisson 1986).

The two major food groups consumed by martens are fruits and small mammals (Baghli *et al.* 2002; Brangi 1995; Genovesi *et al.* 1996; Lachat Feller 1993b; Lanszki 2003; Lodé 1994). Where feeding patterns have been analysed over all seasons, fruits and berries constitute a major component of the marten’s summer and autumn diet, while they are less represented during winter and spring (Baghli *et al.* 2002; Genovesi *et al.* 1996; Lanszki *et al.* 1999; Lodé 1994). In some areas fruit is also consumed heavily in winter (e.g., Lachat Feller 1993b). Overall fruit is consumed heavily whenever it is present in the marten’s environment (Genovesi *et al.* 1996; Rödel and Stubbe 2006). Conversely, mammalian prey makes up a higher proportion of the diet in winter and spring (Baghli *et al.* 2002; Genovesi *et al.* 1996; Lanszki *et al.* 1999; Lodé 1994). Among mammals, voles and mice are by far the most common prey, followed by insectivores (Baghli *et al.* 2002; Genovesi *et al.* 1996; Lachat Feller 1993b; Lanszki 2003; Lodé 1994). Larger mammals, such as roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) or domestic cats are presumably only consumed as carrion (Baghli *et al.* 2002; Brangi 1995; Genovesi *et al.* 1996; Lanszki 2003; Prigioni and Sommariva 1997).

Birds are eaten throughout the year, although less frequently than mammals and fruits. Peaks in bird consumption vary between different studies (Genovesi *et al.* 1996; Skirnisson 1986). The most commonly encountered remnants in faeces are from passerines (Baghli *et al.* 2002; Genovesi *et al.* 1996; Lanszki 2003), although some studies have found domestic chickens to be frequently consumed (Lachat Feller 1993b). Eggs are eaten when they are available but their consumption is probably under-represented in faeces because martens tend not to consume the shells (Baghli *et al.* 2002; Genovesi *et al.* 1996; Lachat Feller 1993b). Interestingly, amphibians and reptiles are consumed only very rarely (Brangi 1995; Lanszki *et al.* 1999). Insects are found in all studies and can make up a considerable proportion of the entire diet, especially in summer (Brangi 1995; Genovesi *et al.* 1996; Lachat Feller 1993b; Lodé 1994). Those studies that specifically looked for earthworm chaetae found earthworms to be an important constituent of the stone marten’s diet (Rödel and Stubbe 2006; Skirnisson 1986).

While martens living in agricultural environments consume mainly wild prey, those living in villages often rely on species typically associated with human settlements (e.g., house mouse, house sparrow *Passer domesticus*, domesticated animals) (Lanszki 2003). Furthermore, indigestible substances (mainly pieces of rubber) are found more frequently in scats from individuals living in villages (Lanszki 2003). However, such items may also be swallowed in forested or rural environments (Genovesi *et al.* 1996; Lachat Feller 1993b). In Skirnisson’s (1986) study, village martens consumed more fruit and organic household waste than rural martens, while mammals and birds were consumed in similar proportions. Fruit was also the major constituent of the diet in a locality in the Italian Alps (Prigioni and Sommariva 1997). The diet of martens in specifically urban environments is considered below (section 1.4.2.).

1.3.4. Habitat use

The stone marten is very adaptable and can be encountered in a variety of different habitats. In central Europe it is generally regarded as a synanthropic species. This has been well documented by studies on various aspects of the animal's ecology in rural villages in France (Waechter 1975), Germany (Herrmann 2004; Skirnisson 1986) and Hungary (Lanszki 2003). However, martens can also establish home ranges in mostly agricultural areas outside of rural villages. Such individuals have been studied in Switzerland (Lachat Feller 1993b), the Netherlands (Broekhuizen 1983) and Germany (Herrmann 2004).

With most work having been carried out in these environments it is sometimes forgotten that the stone marten may also occur in predominantly forested habitats. Simon and Lang (2007) radio tracked three martens in Germany whose home ranges were completely contained within a large 30-km^2 forested area. However, most work on stone martens in predominantly forested environments comes from the Mediterranean region (e.g., Delibes 1983; Genovesi *et al.* 1997). In Spain, stone martens seem to occur mostly in forests, showing a preference for higher altitudes, away from human settlements (Virgos and Casanovas 1998). Where landscapes are highly fragmented due to agricultural practices, stone marten presence is associated with large fragments close to continuous forest tracts (Virgos and Garcia 2002). In similarly fragmented landscapes in Italy, home ranges were mostly centred on wood and scrub vegetation often associated with watercourses (Rondinini and Boitani 2002). Stone martens can also be found in mountainous terrain such as the Alps, although these studies often focused on their presence in high altitude villages (Föhrenbach 1987; Lucherini and Crema 1993; Prigioni and Sommariva 1997).

Stone martens have thus adapted to cope with a range of different habitats. However, it is their ability to settle in urban centres, with much denser human populations than in the rural villages described above, that has allowed them to become abundant in central Europe (see section 1.4.).

1.3.5. Socio-spatial organisation

Surprisingly few studies have taken an in-depth look at the socio-spatial organisation of the stone marten. Genovesi *et al.* (1996; 1997) provide data on the spatial arrangement of a series of directly adjacent or overlapping home ranges from a predominantly forested habitat. Their data strongly suggest that home ranges of adult martens of the same sex hardly overlap while those of males overlap extensively with those of females. Although based on less extensive datasets, studies by Lachat Feller (1993), Skirnisson (1986) and Herrmann (2004) provide evidence for the same kind of spatial organisation in rural and village habitats. Although there is no direct evidence that home ranges are defended, the fact that there is little or no overlap between the ranges of same-sex individuals suggests a pattern of intrasexual territoriality. In addition, martens do engage in scent-marking behaviour of various kinds (Grünwald 1990; Ludwig 1995) and it seems likely that this functions at least partly for purposes of territory defence (Große-Johannböcke 1995). For present purposes, therefore, I will assume, as other authors have done, that martens are territorial and that home ranges and territories amount, in spatial terms, to the same thing.

Where same-sex home range overlaps have been documented these were either between an adult and a subadult (e.g., two males: Müskens *et al.* 1989) or between a mother and her young (Herrmann 2004; Skirnisson 1986). The existence of social groups or of overlapping home ranges, as can be seen in foxes and badgers or raccoons, respectively, has to date not been documented in stone martens or any other marten species. However, the possibility of this happening under certain environmental circumstances cannot be excluded (Powell 1994).

Stone marten territory sizes can be quite variable, ranging from around 15 ha (Rödel and Stubbe 2006) to over 800 ha (Genovesi *et al.* 1997; Simon and Lang 2007). Generally, territory size depends on the sex of the marten and the habitat that it inhabits. As males usually overlap with one or more females their territories tend to be larger than those of females (Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986), although two Italian studies found no significant differences between sexes (Genovesi *et al.* 1997; Rondinini and Boitani 2002). Another trend is for territories to be generally largest in forested (Genovesi *et al.* 1997; Simon and Lang 2007), intermediate in rural (Herrmann 2004; Lachat Feller 1993b; Rondinini and Boitani 2002) and smallest in village habitat (Herrmann 2004; Skirnisson 1986). The availability of key resources such as food and cover are thought to drive the variation in home range size between different environments (Genovesi *et al.* 1997; Herrmann 2004; Skirnisson 1986). Further details on the stone marten's socio-spatial organisation are presented and discussed in Chapters 3 and 8.

1.3.6. Activity patterns

The stone marten is typically considered to be crepuscular and nocturnal (Broekhuizen 1983; Genovesi 1993; Herrmann 2004; Lachat Feller 1993b; Posillico *et al.* 1995; Skirnisson 1986). In rural areas the start of activities outside the den seems to be more tightly linked to the time of sunset than the end is linked to the time of sunrise (Broekhuizen 1983). Consequently, martens leave their den earlier and return to their den later during long winter nights than during shorter summer nights. However, during winter, bouts of activity alternate with resting periods, while in summer martens are generally active throughout the night (Skirnisson 1986). The distances that martens cover during their active period typically differ between both sexes. Skirnisson (1986) found males to travel almost twice as far as females per night and Genovesi *et al.* (1997) reported males to move on average 5.3 km while females moved only 1.5 km. Although Lachat Feller (1993) found a similar trend, the difference here was not significant (males: 3.2 km; females: 2.1 km).

There seems to be a trend for village martens to be less active than forest inhabiting individuals (Herrmann 2004; Skirnisson 1986). Skirnisson (1986) attributed this lower activity in the village to a higher and more reliable food supply. Furthermore, village martens spend more time inside or close to their den sites. Both Skrinisson (1986) and Herrmann (2004) found evidence that village martens delay the start of their outside-the-den activity compared to martens living in habitats undisturbed by humans.

1.4. Stone martens in urban environments

The phenomenon of urban martens is not necessarily a recent one. Nicht (1969) documented the presence of stone martens in the city of Magdeburg in Germany as early as 1967. Furthermore, he referred to accounts of stone martens in the cities of Bern and Berlin in 1949 and 1961, respectively. The phenomenon of urban stone martens has now been reported from many parts of Europe including the cities of Brno (Czech Republic: Holišová and Obrtel 1982), Basel (Switzerland: Tester 1986), Nijmegen (the Netherlands: Broekhuizen *et al.* 1989), Siena (Italy: Cavallini 1992), Budapest (Hungary: Tóth Apáthy 1998), Nantes (France: Le Lay and Lodé 2004), Liège (Belgium: Lambinet 2006), Krakow (Poland: Eskreys-Wójcik and Wierzbowska 2007) and others. On the Iberian Peninsula, however, stone martens have not been reported in urban areas yet (Spain: Virgos and Garcia 1998; Portugal: M. Santos-Reis, personal communication).

1.4.1. Conflicts

Poultry depredation

Wherever stone martens occur in close proximity to humans a range of conflict situations may arise. In rural villages martens sometimes cause depredation of poultry. They visit hen houses primarily to remove eggs but such visits may occasionally result in the killing of a large number of chickens, without, however, eating or removing them. These attacks are probably caused by panicking chickens that trigger the marten's hunting instinct. They can be prevented by locking chickens up at night in a marten-secure shed (Ludwig 1999).

Gardens

There are anecdotal reports about dug-up and destroyed flower or vegetable beds, which are rightly or wrongly attributed to marten activity by affected residents (personal observation). Although it is difficult to say how often such events occur and whether stone martens are always to blame for the damage, it could be the result of martens digging for earthworms.

Cats

Some people worry about marten attacks on pet cats although these fears are probably unfounded. According to Lachat Feller (1993b), martens and cats mostly ignore each other. In the present study I observed 63 marten-cat encounters, in which on 25 occasions the cat briefly followed or stalked the marten, keeping some distance between them. Twenty-four encounters involved the cat chasing after the marten, and on 13 occasions the two species ignored each other. Chasing martens seemed to be more like play than aggressive behaviour to the cats. I never observed physical contact between the two species and only once did a marten approach a cat with a threatening posture, before running away from it.

Car damage

In central Europe stone martens are well-known for damaging cars by biting through ignition leads, vacuum hoses and coolant hoses, or tearing up noise and heat insulation mats under car bonnets. The phenomenon was first reported from Switzerland in the late 1970's (see Kugelschafter *et al.* 1984/85) but has now spread through most of Central Europe. In 1998 marten-related car damage was estimated to be worth around 20 million € with an estimated 160000 cars being damaged in Germany alone (Langwieder and Höpfl 2000). Due to the high value that European societies put in their cars, combined with the (usually unfounded) concern that martens may damage brake hoses (see Kugelschafter *et al.* 1984/85; Langwieder and Höpfl 2000), the animals are often perceived as a nuisance, especially among affected car owners (personal observation). A detailed discussion of the reasons for this behaviour is presented in Chapter 6.

Denning in buildings

Another common and real conflict situation is generated by stone martens that den in inhabited buildings (Ludwig 1999). Martens are very good climbers and usually find their way into an inhabited house through small openings in the roof. They then den in an empty roof void or in the attic. Specific conflicts that ensue from such close cohabitation between martens and humans are very similar to the ones described for pine martens in Scotland (Brown and Birks 2006). However, while this is very rare in pine martens, it is a very common conflict with stone martens in central Europe. Hygiene concerns arise from urine and faeces being deposited at latrine sites, where they accumulate and may develop odours or soak through the ceiling. Occasionally, maggots have been reported to drop from the ceiling, probably due to the remains of a dead marten or a prey animal (personal observation). These problems are usually confined to houses where the martens den in roof spaces that are inaccessible to humans. Martens can also cause more substantial and expensive damage by tearing down the roof insulation. However, by far the most frequent complaints refer to the noise that the animals make at night when active just above bedroom ceilings, especially in spring when several young may be reared for weeks in the same den. Although this conflict is commonly acknowledged, the importance of inhabited houses in the marten’s denning behaviour remains thus far unknown (see Chapter 5 for further discussion).

Disease

Disease is often a focus of attention in urban mammals (see above). As already noted, stone martens often live in close proximity to humans when denning in roof spaces or attics of inhabited buildings. These may also become contaminated with faeces or urine, which could potentially be a concern for disease transmission. Mayer (1988) reviewed the role of stone martens in the epidemiology of zoonoses and concluded that they carry and transmit very few diseases or parasites of importance to humans, rabies being considered the only potential concern. However, during a fox rabies epizootic in Switzerland, the virus was identified in only 2.6% of stone martens, with prevalence in foxes being as high as 76.6% (Steck and Wandeler 1980). Echinococcosis, which is monitored in urban foxes (see section 1.2.2.), has not yet been identified in stone martens (Libois and Waechter 1991; Mayer 1988). The relatively little research that has been carried out on the ecology of stone martens in urban areas may indeed be the result of them being generally considered of low importance in the epidemiology of zoonoses (Mayer 1988).

1.4.2. Diet

Data on the stone marten’s diet in urban environments are available from Holišová and Obrtel (1982), Lucherini and Crema (1993), Tóth Apáthy (1998), Tester (1986), Eskreys-Wójcik and Wierzbowska (2007) and Lambinet (2006). The latter four studies include data from the highly urbanised cities of Budapest (N scats = 87), Basel (N = 407), Krakow (N = 400) and Liège (N = 62), respectively. Samples from Budapest and Liège were all collected at a single den site and would thus just represent prey taken in a single territory.

Overall there seems to be a trend for birds to play a more important role in the marten’s diet in urban than in rural environments. Birds were the most common type of food item in Krakow centre and the Italian town of Pragelato (Eskreys-Wójcik and Wierzbowska 2007; Lucherini and Crema 1993), and the second most common item in Basel and Budapest (Tester 1986; Tóth Apáthy 1998). In three of these studies pigeons (*Columba livia*) were one of the dominant prey items (see also Prigioni and Sommariva 1997).

Nevertheless, fruit (often *Prunus* spp. or yew berries, *Taxus baccata*) was still the most frequently found type of food in marten scats from the outskirts of Krakow, Basel and Budapest. In terms of frequency of occurrence, mammals were only found to be in third place behind birds and fruits in Pragelato, Basel and Budapest. They were ranked second in Krakow and only fourth in Liège. Interestingly, in Liège insects were a very common prey of martens, partly due to a high prevalence of Lepidoptera larvae in scats (Lambinet 2006). Between 9 and 17% of scats from urban areas contained indigestible items such as rubber, plastic or aluminium foil (Eskreys-Wójcik and Wierzbowska 2007; Lucherini and Crema 1993; Tester 1986; Tóth Apáthy 1998).

These data suggest that there are some differences in the diet between rural and urban areas, specifically relating to the importance of birds and mammals. Although the species consumed by urban martens may be typical representatives of anthropogenic environments (not necessarily found in rural areas), urban stone martens nevertheless largely rely on free-ranging animals and free-growing plants rather than on garbage or food deliberately put out by humans (e.g., Tester 1986).

1.4.3. Telemetry studies in human-dominated environments

Compared to urban mesocarnivores such as red foxes, raccoons or coyotes, very little telemetry work has been carried out on urban stone martens. And where such work has been done it is usually not widely available in the scientific literature. Thus the current knowledge of urban stone marten behaviour and ecology is mostly derived from a very limited set of studies, many of which have worked with a rather small number of martens.

In Germany, Skirnisson (1986) followed one female in a small rural village (17 family homes; 5 farms) and one male in a somewhat larger locality (1000 inhabitants, 15 farms). In the mid 1980s Herrmann (2004) radio tracked eight martens that, for at least part of their tracking period, resided in rural villages (500 - 3000 inhabitants). Only two of these martens were adults, the rest being subadults or juveniles. Both these studies found differences in the ecology of village and rural martens. These differences mostly related to smaller home ranges, shorter activity periods and evidence of temporal avoidance of human activities in village habitat (see Chapters 3 and 4). In the Italian Alps, three martens (presumably subadults, according to their low weights) were followed in a small ski resort (3700 inhabitants) (Prigioni and Sommariva 1997). The authors reported very small home ranges (around 3 ha) for these martens. However, these estimates were based on the average nightly range rather than on accumulated areas over several nights. Based on these results they estimated a very, and almost certainly unrealistically, high marten density for this town (see Chapter 3).

Most telemetry work on urban stone martens, however, comes from the Netherlands. In the late 1980s several martens (at least eight) were radio tagged in the city of Nijmegen (150000 inhabitants). Home ranges in this city were relatively small, ranging between 15 and 55 ha for females and between 30 and 80 ha for males (Bissonette and Broekhuizen 1995). The animals mostly denned on the ground in uninsulated sites in summer but chose well-insulated sites in winter (van Bostelen and Verhoog 1992). Another key finding was that reproductive rate in this environment was relatively low (Lammertsma *et al.* 1994). Other, more specific findings from this Dutch study will be mentioned throughout the following chapters. In a later study, Müskens and Broekhuizen (2005) tracked four martens (3 females, 1 male) in a Dutch village (< 2000 inhabitants), which, however, was located in a densely urbanised landscape. They found female martens to occupy small territories (9 to 31 ha) and confirmed the intrasexual territoriality model that had been described for stone martens in other habitats. This is also the only study that has looked at the spatial distribution of car damage in relation to known marten territories (see Chapter 6).

1.5. Stone martens in Luxembourg

Baghli *et al.* (1998) used a questionnaire survey, distributed among hunters and forest wardens, to gather information on the distribution of mustelids across Luxembourg. Of hunters who responded to the survey (N = 196; 32.3%), 91.8% reported stone martens to be present in their hunting areas and the animals were considered a nuisance by 50.5% of respondents. Among forest wardens (N = 48; 78.7%), 97.9% reported stone martens to occur in their forestry units and 27.1% considered the animals to be a nuisance. Baghli *et al.* (1998) thus showed that the stone marten occurred throughout Luxembourg and was the most common of all seven native mustelids (i.e., *Martes foina, Martes martes, Mustela putorius, Mustela erminea, Mustela nivalis, Meles meles, Lutra*

lutra). Due to a variety of conflicts (see section 1.4.1.) it was also the species that was most often considered a nuisance.

F. Wolff (unpublished data) used camera traps to survey a 5 by 5 km grid for mesocarnivores across Luxembourg. He evaluated habitat suitability of focal species with spatially explicit distribution models, based on ecogeographical variables that quantitatively described landscape composition and structure. Habitat suitability for stone martens was predicted to be high across most of the country, with stone martens being more influenced by landscape structure than by landscape composition (Fig. 1.1).

Until 31st of July 2007 the stone marten was a hunted species in Luxembourg, with an open season between 15th of October and 28th of February. From 1st of August 2007 the hunting season was closed year-round, following a policy of closing hunting seasons for all native carnivores apart from the red fox. However, the stone marten is still classified as a nuisance species, and can thus be legally live-trapped and euthanased at any time of the year by private persons if they encounter marten-related problems on their own property (Code de l'Environnement, 2002, Vol. 1, p.3). This may, however, be changed in 2008 or 2009 in the context of a general revision of Luxembourg's hunting laws.

1.6. Summary

Urbanisation of the human population is an increasingly important factor with important ecological implications. Consequently, the ecological impact that the expansion of urban environments has on relevant animals and plants needs to be understood in order to be able to effectively conserve dwindling species, and manage overabundant, populations. Based on the responses that organisms show in the face of urbanisation, they can roughly be divided into urban avoiders, adapters and exploiters. Among mammals, urban adapters are often charismatic species such as raccoons, foxes, badgers or squirrels that are often welcomed by suburban or urban residents although in some cases they may also cause conflict. Studies have shown that their ecology and behaviour in urban areas may be quite different from that of more natural or rural populations.

In continental Europe the stone marten has adapted well to urban environments and now occurs in many towns and cities across the continent. This sharing of a common habitat

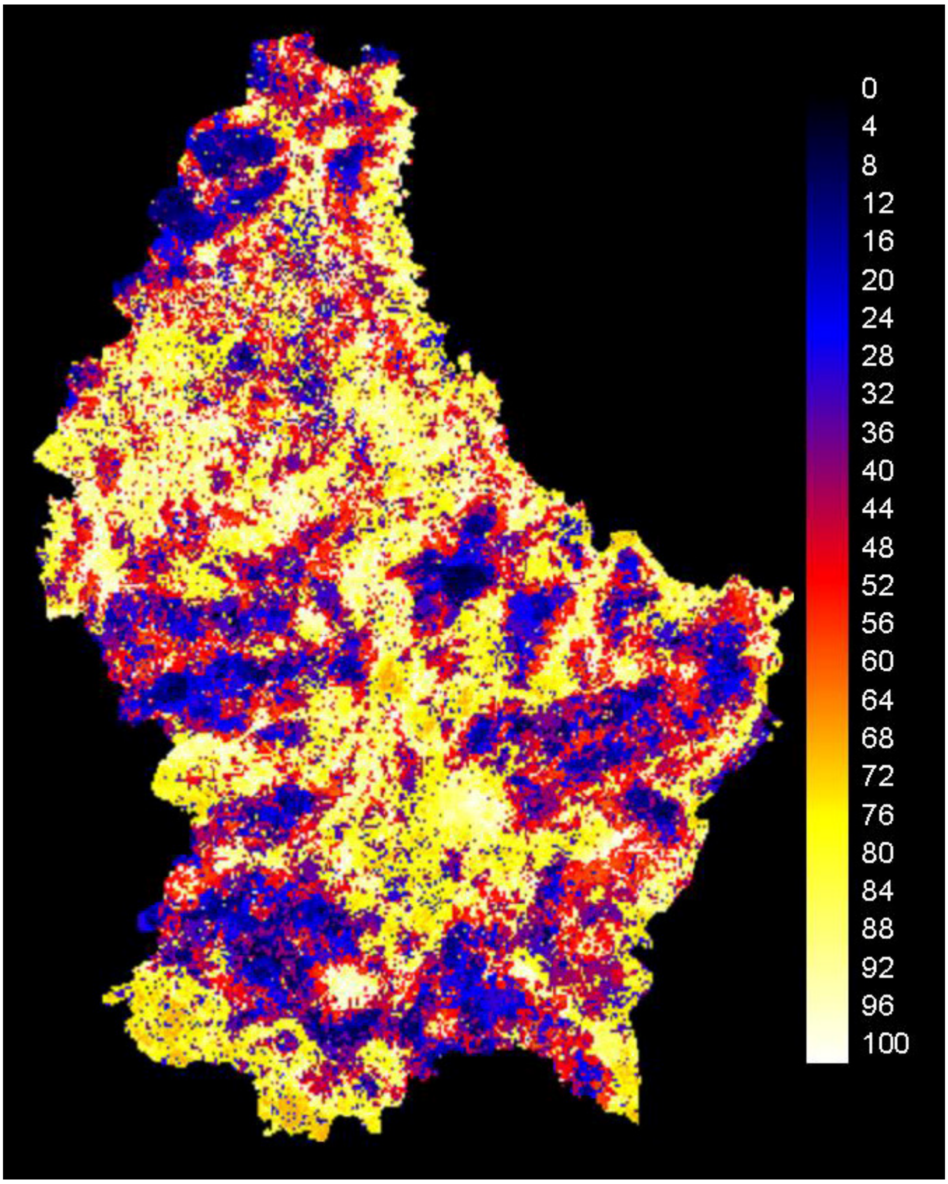

Fig. 1.1: Habitat suitability for stone martens in Luxembourg as predicted by ecological niche factor analysis. The model was based on ecogeographical variables quantitatively describing landscape structure and composition. Habitat suitability varies between 0 (not suitable) and 100 (highly suitable) (F. Wolff, unpublished data). Reproduced with the permission of F. Wolff.

between humans and stone martens has led to a number of conflicts, the commonest being their denning in inhabited houses and their damaging of car engine components. However, as relatively little is known about the behaviour and ecology of stone martens in urban habitats, the structure of such urban populations and how best to manage human-marten conflict are still unclear.

1.7. Aims

1.7.1. General aims

In order to be able to take informed decisions about how to deal with the presence of stone martens in urban areas, as well as with the resultant conflicts, it is necessary to have a good understanding of the species' behaviour in this habitat. Hence, the overall aims of the present study were to provide a thorough description of the general behaviour of urban stone martens and, more specifically, to address the behaviour patterns that are most likely to result in actual or perceived conflicts (i.e., denning behaviour and car use).

1.7.2. Contents of the thesis

- Chapter 2 gives a description of the study areas and provides an outline of the general methods that were employed in the present study.
- In Chapter 3, I analyse the spatial arrangement of marten home ranges and quantify the extent to which martens focus their year-round activity on urban habitat. I use this information to make predictions on marten densities in this type of habitat.
- Chapter 4 addresses the general activity and movement patterns of urban stone martens. These are compared to non-urban parameters in order to find out how martens have adjusted their behaviour in response to greater human presence and activity within their home ranges.
- Chapter 5 provides a general description of the stone martens' den selection and den use in a human-dominated environment. More specifically, I focus on the importance of human-inhabited buildings in den selection, as denning in such buildings is likely to generate the highest potential for conflict.
- In Chapter 6, I deal with the commonly observed phenomenon of martens damaging cars. I examine the extent to which martens made use of cars during their nightly activities and look at seasonal variations in road use. I use these data to test

hypotheses dealing with the reasons why martens associate with cars in the first place. I also examine the spatio-temporal distribution of car damage within the study towns in order to quantify the frequency with which cars were damaged.

- In Chapter 7, I present case studies that deal with the fate of one translocated adult and five captive-reared juvenile stone martens. I discuss the outcomes of these relocations in the context of management options that are often resorted to when dealing with problem martens.
- Finally, in Chapter 8 I summarise the main findings of the present study. I also revisit the stone marten's socio-spatial organisation to explore explanations for the patterns observed in Chapter 3. Furthermore I discuss the animal's urban ecology in the context of urban adapter and exploiter species as they were defined in Chapter 1. Finally, the challenges in dealing with human-marten conflicts are presented and some management recommendations are made based on knowledge from the present and other studies on stone marten behavioural ecology.

Chapter 2: General Methods

2.1. Study sites

The study was conducted in the south of Luxembourg (Fig. 2.1), in the towns of Bettembourg (49° 31' N; 6° 6' E) and Dudelange (49° 28' N; 6° 5' E; Fig. 2.2). Bettembourg is located at an altitude of 279 m and had a human population of about 7500 inhabitants (November 2006) (Commune de Bettembourg 2007). The urbanised part of the town (i.e., area delimited by urban perimeter; Fig. 2.2) covered roughly 160 ha and thus had an estimated human density of around 4600 inhabitants·km^{-2}. Buildings (excluding sheds) covered 16.8% of the urban area. The older part of town (the western part) used to have a number of farm buildings. However, at the time of the study there was only one active farm left. Other farm buildings (farm house, barns, stables etc) had been converted to family homes, offices, or storage facilities. The eastern part of town consisted exclusively of residential areas. The town was surrounded by agricultural land in the north, south and west, and orchards and a forested area in the east (Fig. 2.2).

Dudelange is located about 2 km south of Bettembourg. The area between the two towns was mostly industrial. Dudelange is located at an altitude of 286 m and, with a human population of 18300 inhabitants, was larger than Bettembourg (December 2006) (Ville de Dudelange 2007). The urbanised area covered approximately 500 ha and had a human density of around 3600 inhabitants·km^{-2}. Buildings (not including sheds) made up 16.4% of the urban area. There were some active farms in the northwestern (Burange) and northeastern (Boudersberg) parts of the town. However, the majority of the town was of residential character with a small commercial district in the centre. Dudelange was surrounded by a patchwork of forested and agricultural areas (Fig. 2.2).

Residential areas in both towns consisted mostly of family homes (1-3 storeys, terraced and/or detached), private gardens and a dense road network. There were many pet cats that spent the nights outside. Pet dogs were rarely seen outside at night without their owners and there appeared to be no stray dogs or cats. Potential food resources for martens included small mammals, birds, insects and seasonally available berries and fruits like cherries (*Prunus avium*), plums (*P. domestica*), and apples (*Malus domestica*)

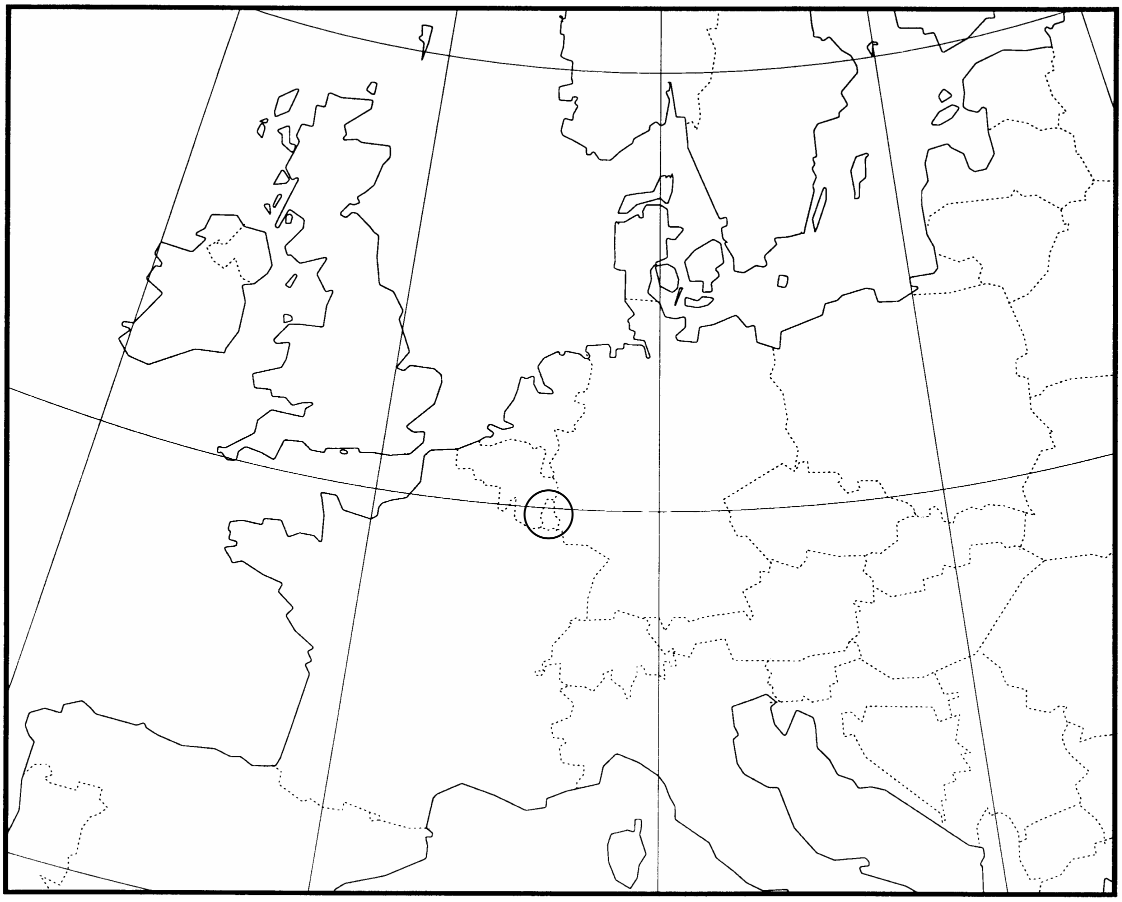

Fig. 2.1: Location of Luxembourg within Europe.

Courtesy of P. Diederich, Luxembourg.

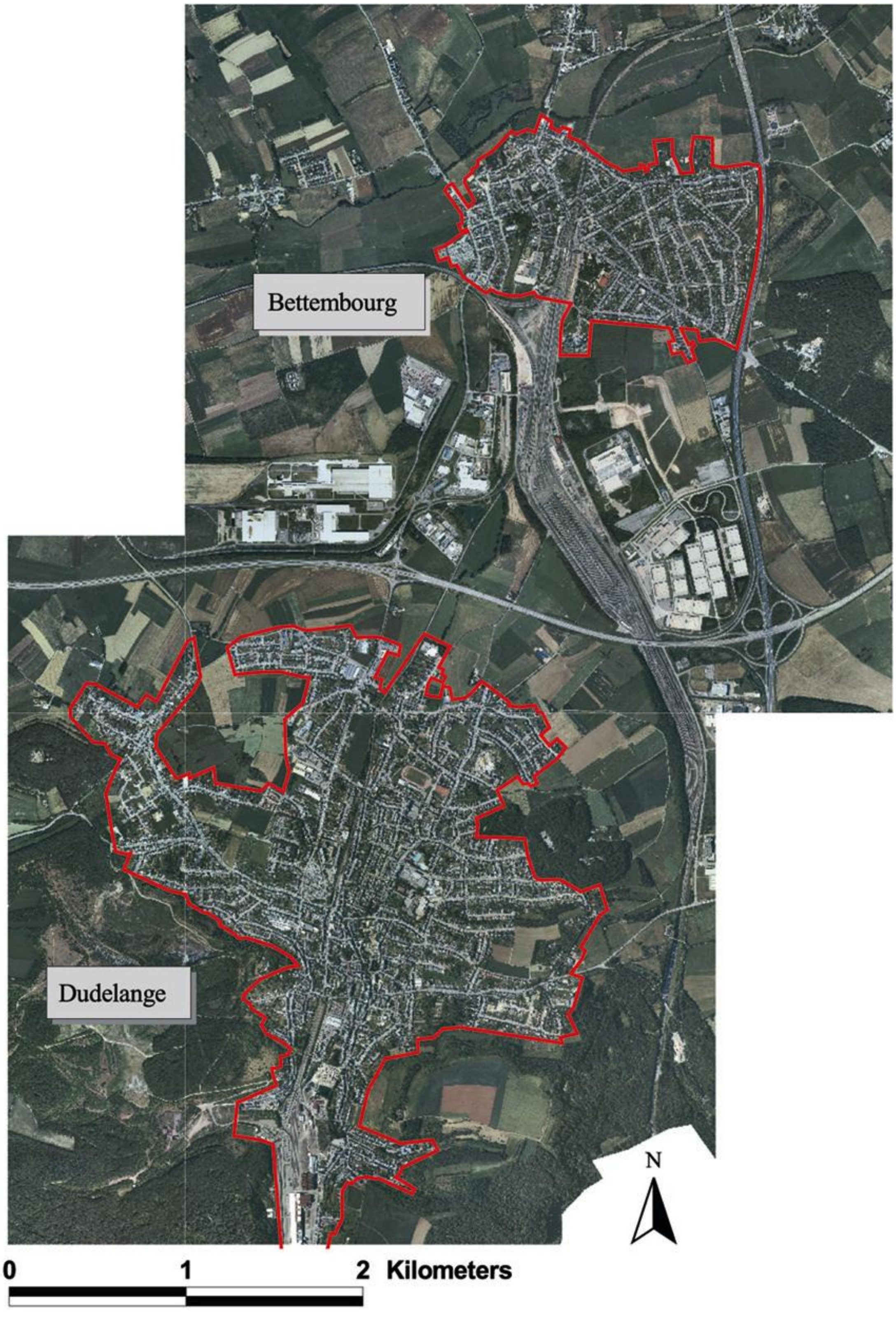

Fig. 2.2: Orthophoto showing the two study towns, Bettembourg and Dudelange, located in the south of Luxembourg. The red line delineates the urban perimeter of both towns. © Orthophoto (2004): Origin - *Administration du Cadastre et de la Topographie*. Authorisation for publication of 14th January 2008.

from trees which occurred in private gardens scattered throughout both towns. While compost heaps may have been available in some gardens, the bulk of the organic household waste was disposed of in special wheelie bins, which were emptied weekly. Other household trash was also disposed of and collected in wheelie bins and thus was not directly available to martens. However, individual scavengeable food items would have been available throughout both towns. House owners generally did not deliberately put out food for stone martens (personal observation).

Road density in both towns was similar with around 13 km of roads·km^{-2}. At both study sites there was a steady flow of traffic throughout the day, peaking during morning and afternoon rush hours on the main roads. Traffic was low on peripheral roads and at night. Dudelange was generally busier with cars and people throughout the day than Bettembourg, but at night traffic and human activity were similar in both towns. All roads were artificially lit during nighttime hours.

Two major motorways ran through the study area. The north-south motorway directly bordered the eastern part of Bettembourg and passed within 1 km of eastern Dudelange. The east-west motorway passed between both towns, about 300-400 m north of Dudelange. Bettembourg was also bisected by a major railway line (Fig. 2.2).

2.2. Climate

Meteorological summary data for the years 1971-2000 were available from the Findel meteorological station (49° 37' 0" N; 6° 12' 0" E; altitude: 376 m) (Administration de l'Aéroport 2007; Pfister *et al.* 2005), which was situated about 15 km northeast of the study sites. Mean monthly rainfall over this period was lowest in April (56 mm) and highest in December (85 mm). Mean monthly temperatures ranged from 0.6 °C in January to 17.5 °C in July (Administration de l'Aéroport 2007). Since the late 1980s the number of days with snow on the ground has always been less than 30 per year (Pfister *et al.* 2005).

During the study period (June 2005 - May 2007) monthly precipitation ranged between a minimum of 17.4 mm (September 2006) and a maximum of 174.8 mm (August 2006). Monthly mean temperatures ranged between -1.0 °C (January 2006) and 23.5 °C (July

2006). During the winter of 2005/2006 there were 34 days with snow on the ground; during the winter of 2006/2007 only five (Administration de l'Aéroport 2007).

2.3. Seasons

I divided the year into four biologically relevant seasons, based on resource abundance and the marten's reproductive biology (see references in Chapter 1, section 1.3.2.). Summer (June-August) is the season when juveniles start accompanying their mother on her nightly excursions and when mating takes place in adults. Autumn (September-November) is a transition period where few challenges seem to affect martens (i.e., generally high food abundance, little territoriality, no mating and no pregnancy costs), whereas winter (December-February) is a period of potentially restricted food abundance, possible cold stress and female pregnancy. Spring (March-May) is characterised by the birth of young, lactation and heightened territoriality.

2.4. Fieldwork

2.4.1. Trapping

At the time of the study the stone marten was classified in Luxembourg as a nuisance species that could be legally trapped at any time to prevent damage or disturbance (Code de l'Environnement, 2002, Vol. 1, p.3). Hence, no trapping license had to be obtained. In order to ensure that the study only included martens that had at least one part of their home range within a built-up area, I exclusively trapped within the urban perimeter of the study towns (Fig. 2.2). Through the use of newspaper articles and information leaflets I located suitable trap sites by identifying residents that had recently observed martens in or around their houses. I started placing traps in Bettembourg in May 2005, while in Dudelange the first traps were placed in February 2006. I employed four different kinds of live-traps. All of these traps had been successful in trapping stone or pine martens in previous research, either as target or non-target species.

i) Type 1 traps (N = 10) were foldable wire cage live-traps (model 203, 61x15x15 cm, Tomahawk Live Trap Co., Wisconsin, USA) (Baghli 2003).

ii) Type 2 traps (N = 10) were identical in design but larger than trap type 1 (model 206, 81x23x23 cm, Tomahawk Live Trap Co., Wisconsin, USA) (Balharry 1993; Lachat Feller 1993b).

iii) Type 3 traps (N = 2) were steel meshed box traps larger than the previous two types (150x40x30 cm) (Schley 2000).

iv) The Type 4 trap (N = 1) was a wooden box trap (150x32x30 cm) (Simon and Lang 2007).

All traps had a trigger plate in the middle that was activated when an animal stepped on it. I covered all wire cage traps with self-built wooden trap covers. In September 2005 I abandoned the use of type 1 and type 3 traps, as the former were too small, especially for trapping males, and the latter too large for transporting or leaving in private gardens for several months.

I exclusively set the traps in private gardens or in passages between houses (on the ground, next to a wall or a hedge), where I had unrestricted access to them at all times. Not more than 10 traps were operated at any given time. I prebaited the traps (for up to three months) with whole raw eggs (Lachat Feller 1993b). Other bait, like cat food, dried fruit or a mixture of oats and raspberry jam, was tried but later abandoned as it either resulted in the capture of non-target species or failed to attract animals at all. I initially placed the eggs in the trap entrance, with the trapping mechanism blocked. Once martens started removing the eggs, I gradually placed the bait further into the traps until the animals completely entered them. Only then did I activate the traps. Due to the small size of type 1 and 2 traps I always left one door shut and placed the bait right behind the closed door, forcing the martens to completely enter the trap. In type 3 and 4 traps both doors were left open and the bait was placed on the trigger plate in the middle of the trap.

No trapping was carried out on nights with low temperatures (below freezing) or in March and April when females were pregnant or could have had dependent young. Exceptions were made when it was known that the marten taking the bait was not a lactating female (e.g., through the use of camera traps, when the adult female in the territory had already being collared or when the adult female in the territory was known not to have any young). Whenever I had five martens equipped with functioning collars, I suspended trapping as this was the maximum number of individuals that could be efficiently tracked by a single person.

2.4.2. Handling procedures

Traps were checked at dawn between 0500 and 0700 h. Trapped martens were processed immediately at the site of capture. I induced anaesthesia with isoflurane gas (Potvin *et al.* 2005). For this purpose the martens were first transferred into a holding cage (61x37x30 cm), which was then placed into a transparent, plastic box (78x40x40 cm). I placed one tablespoon of isoflurane into the box and as soon as the animal was motionless, it was removed from the cage. I then injected the marten intramuscularly with a ketamine hydrochloride (100 $mg{\cdot}mL^{-1}$) (Anesketin, Eurovet), medetomidine hydrochloride (1 $mg{\cdot}mL^{-1}$) (Domitor, Pfizer) and butorphanol tartrate (10 $mg{\cdot}mL^{-1}$) (Torbugesic, Fort Dodge Animal Health) mix (ratio of 2:1:2 by volume) at a dose rate of 0.2 $mL{\cdot}kg^{-1}$ (de Leeuw *et al.* 2004). The use of the analgesic butorphanol tartrate was later stopped as it was considered to be unnecessary due to the non-invasive nature of the handling procedure (see Dzinlak *et al.* 2002).

Each marten was sexed, weighed (to the nearest 50 g), measured (nose - base of tail; tail; neck circumference; hind foot length) and aged. Age classes were defined as juvenile (< 12 months), subadult (between 12 and 24 months; living in mother's territory) and adult (> 12 months; sole owner of a territory) based on tooth wear (Habermehl and Röttcher 1967), reproductive status (developed testes, signs of lactation) and the subsequent observation of other martens in a territory. The martens were then fitted with a radio collar (Biotrack Ltd, UK; model TW-3; frequency band: 150 MHz; pulse rate: 50 $pulses{\cdot}min^{-1}$). Radio tags consisted of a braided nylon collar with an external antenna to increase signal range in the urban environment. However, signal range often suddenly deteriorated to about 50 m after six to ten months, which may have resulted from the antenna having been chewed off. In order to take advantage of the entire expected tag lifespan (16 months; Biotrack, personal communication), collars with integrated antennas may be preferable for future studies. The tag mass of 30 g was below the recommended limit of 3% of an animal's body mass (1.6% and 2.0% for tagged males and females, respectively) (Kenward 2001). As with most mustelids, the collar had to be secured fairly tightly to prevent the animal from pulling it over its head or from becoming entangled in fences or vegetation.

As I judged it unsafe for martens to be released during daylight hours because of road traffic, I did not administer a reversal drug but instead let the martens recover in a pet holding box containing a burlap sac for hiding as well as food and water. The box was kept at the site of capture, covered by a blanket and sheltered from direct sunlight until the marten was released the same evening after 2200 h when it was dark and there was less traffic.

2.4.3. Trapping success and study animals

A total of 393 trap nights resulted in 15 captures of 14 individuals, which equates to one capture per 26.2 trap nights. Seven martens were caught in Bettembourg and seven in Dudelange (Tables 2.1 and 2.2). Domestic cats (N = 12) and hedgehogs (*Erinaceus europaeus*; N = 12) were the only non-target species that were caught in the traps and they were released without harm. On 16 occasions, traps (types 1 and 2) were sprung without resulting in a capture. Trap visitation by martens usually stopped for several weeks after a trap was sprung once. Three martens had a broken canine probably resulting from biting the wire mesh of the trap. Müskens and Broekhuizen (2005) successfully used a wooden box trap (110x20x15 cm) for stone marten research in the Netherlands. This type of trap would better address animal welfare, trapping reliability and ease of transport issues, while hygiene and risk of disease transmission may be less of a problem in wire cage traps.

2.4.4. Telemetry

All radio tracking was carried out by myself. I tracked tagged martens by using a receiver with an attached foldable antenna (model RX-98 H, TVP Positioning AB, Sweden) or, when necessary, an additional three-element yagi antenna (Biotrack Ltd, UK). I tracked martens continuously throughout their principal activity period (PAP) from the time of first emergence from their daytime den until the final retreat into a daytime den in the morning (Harris *et al.* 1990; Kenward 2001). I aimed to follow each marten between six and nine nights per season (Table 2.3). During each radio tracking session I focused on one individual and took a positional fix every 15 min (i.e., full hours, quarter hours and half hours) (Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986). At each fix I noted the animal's location on a 1:5000 paper map, whether it was inside or outside the diurnal den, active or inactive, visible or out of sight, and whether there was precipitation or not. As the transmitters were not equipped with an activity sensor, I determined activity on the basis of signal strength fluctuations during a 30 s

Table 2.1: Trapping summary and radio tracking period for 14 stone martens included in the study.

ID	Sex	Age	Capture Date	Town[a]	Trap Type	1st Night[b]	Last Night[b]	Status
F1	F	Adult	10/06/05	B	3	12/06/05	12/03/06	signal life exceeded / seen alive 05/07
F2	F	Adult	15/06/05	B	1	16/06/05	14/05/06	signal life exceeded 08/06
F3	F	Adult	21/07/05	B	1	24/07/05	27/07/05	road-killed 28/07/05
F4	F	Adult	05/08/05	B	1	6/08/05	24/05/06	dead or collar shed 09/06
F5	F	Juvenile	06/08/05	B	1			died after exposure to isoflurane 06/08/05
F6	F	Subadult	03/05/06	D	2	04/05/06	06/06/06	dead or collar shed 06/06
F7	F	Adult	27/06/06	D	4	28/06/06	15/02/07	signal life exceeded 04/07
F8	F	Juvenile	31/07/06	D	2	01/08/06	22/08/06	signal lost / last contact 25/08/06
F9	F	Adult	07/08/06	D	2	20/08/06	09/05/07	alive 31/05/07
F10	F	Adult	18/08/06	D	2	21/08/06	07/05/07	signal life exceeded 05/07
F11	F	Adult	13/01/07	D	2	15/01/07	08/05/07	alive 31/05/07
M1	M	Adult	08/09/05	B	3	09/09/05	07/03/06	signal life exceeded / seen alive 03/07
M2	M	Adult	13/04/06	B	2	14/04/06	14/11/06	road-killed 04/04/07
M4	M	Adult	07/06/06 + 13/06/06	D	2	14/06/06	01/03/07	signal life exceeded 03/07

[a] B = Bettembourg; D = Dudelange

[b] Radio tracking night

Table 2.2: Morphometric measurements for 14 stone martens included in the study.

ID	Sex	Age	Weight (kg)	Body length (cm)	Tail length (cm)	Hindfoot length (cm)	Neck circumference (cm)
F1	F	Adult	1.50	50.0	26.0	8.0	16.0
F2	F	Adult	1.60	50.0	25.0	9.0	17.5
F3	F	Adult	1.40	48.0	25.0	8.0	15.5
F4	F	Adult	1.50	47.0	25.0	9.0	15.0
F5	F	Juvenile	1.40	48.0	23.0	8.5	16.5
F6	F	Subadult	1.50	52.5	25.0	7.5	16.5
F7	F	Adult	1.60	50.0	23.5	8.5	16.0
F8	F	Juvenile	1.15	45.0	24.0	8.5	16.0
F9	F	Adult	1.50	49.0	25.0	8.0	15.5
F10	F	Adult	1.60	49.0	22.0	8.5	15.5
F11	F	Adult	1.40	47.0	26.0	8.5	14.0
M1	M	Adult	2.00	51.5	25.0	9.0	17.5
M2	M	Adult	1.85	52.0	25.0	9.0	16.5
M4	M	Adult	2.20	54.0	27.0	9.5	18.5
mean ± SD	F		1.47 ± 0.13	48.7 ± 2.00	24.5 ± 1.24	8.4 ± 0.45	15.8 ± 0.90
	M		2.02 ± 0.18	52.5 ± 1.32	25.7 ± 1.15	9.2 ± 0.29	17.5 ± 1.00

Table 2.3: Seasonal telemetry summary for 13 stone martens radio tracked between June 2005 and May 2007. Each season includes data from only one year.

	Tracking nights					**All fixes (night)**					**Active fixes (night) [a]**					**Fixes (day)**				
	su	**au**	**wi**	**sp**	**tot**	**su**	**au**	**wi**	**sp**	**tot**	**su**	**au**	**wi**	**sp**	**tot**	**su**	**au**	**wi**	**sp**	**tot**
F1	15	8	6	2	31	410	295	249	79	1033	237	129	94	20	480	76	83	75	78	312
F2	14	8	6	8	36	414	278	238	273	1203	214	108	79	154	555	72	84	72	80	308
F3	4				4	90				90	62				62	6				6
F4	9	8	6	12	35	286	296	240	453	1275	157	147	96	188	588	57	80	75	80	292
F6	2			6	8	59			200	259	49			133	182	7			23	30
F7	8	7	6		21	199	270	251		720	141	123	88		352	41	65	64	22	192
F8	5				5	156				156	97				97	15				15
F9	2	7	7	9	25	69	261	298	327	955	45	155	152	241	593	8	65	66	69	208
F10	2	7	7	9	25	66	275	291	330	962	53	185	177	239	654	7	66	67	70	210
F11			7	9	16			305	342	647			160	245	405			40	69	109
M1		12	6	1	19		453	240	40	733		260	123	28	411	60	77	73	79	289
M2	8	7		9	24	236	289		314	839	202	159		224	585	61	63		41	165
M4	8	7	7	1	23	235	285	314	45	879	188	175	172	28	563	51	65	66	6	188
total	**77**	**71**	**58**	**66**	**272**	**2220**	**2702**	**2426**	**2403**	**9751**	**1445**	**1441**	**1141**	**1500**	**5527**	**461**	**648**	**598**	**617**	**2324**
mean	7.0	7.9	6.4	6.6	20.9	202	300	270	240	750	131	160	127	150	425	38	72	66	56	179
SD	4.6	1.6	0.5	3.9	10.4	130	58	32	143	378	73	45	39	94	199	28	9	11	28	110

[a] includes only fixes taken during the principal activity period where the martens were active outside the daytime den; fixes used for kernel analysis

period at fix time and inactivity on the basis of a steady signal. During visual observations I took notes on the martens' behaviour.

Inside the town, signal reflections from buildings made it impossible to use triangulation to determine a marten's position. Thus I proceeded by homing in on the focal animal (White and Garrot 1990). I initially approached the signal by car fitted with a car-mounted omnidirectional antenna (model: O-5/8M, TVP Positioning AB, Sweden). The fix was then taken on foot, usually within 50 m of the marten. Disturbance was kept to a minimum as tracking was carried out from the road while martens spent most of their time in gardens behind houses. Although care was taken not to disturb the animals, it was unavoidable that sometimes martens would emerge onto the road close to the tracker. In that case they usually turned around, only to re-emerge a couple of houses away and continue moving in their original direction. When I happened to drive past a focal marten who was active under a row of cars, the animal would usually just duck down and continue with its activity after my car had passed. When the martens left the perimeter of the town I determined their position through triangulation by taking two cross bearings (Kenward 2001).

As martens are nocturnal and show no activity outside their den sites during daytime hours (Herrmann 2004), I did not carry out any continuous tracking during the day. Instead I located each marten once per day to determine its daytime den site (Table 2.3). When there were doubts whether the signal came from inside a house or from behind a house, I contacted the owners and asked permission to get behind the house. However, when I was sure that a marten was in a specific house I avoided contacting the owners as this often sparked attempts to get rid of the animal, which would have interfered with recording natural den selection patterns. Martens that had presumably chewed off the antenna of their radio collar were still located during the day, but not tracked at night.

2.5. Data analysis

I manually inputted all telemetry fixes into a Geographical Information System (ArcView GIS 3.3, ESRI, Redlands, Ca., USA). All points were overlaid onto 1/5000 digital topographic maps of the study area (product: BD-L-TC, Administration du Cadastre et de la Topographie, Luxembourg) (Figs. 2.3, 2.4, 2.5). I used the Animal

Fig. 2.3: Telemetry fixes for four female stone martens in the town of Bettembourg.

Fig. 2.4: Telemetry fixes for two male stone martens in the town of Bettembourg.

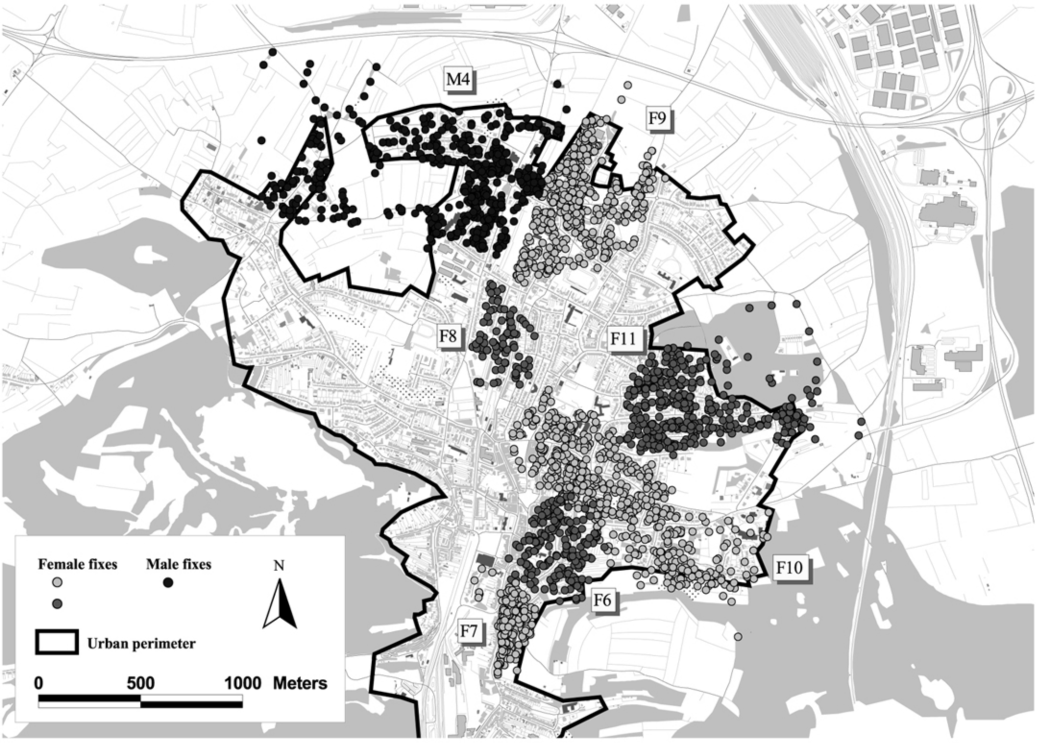

Fig. 2.5: Telemetry fixes for one male and six female stone martens in the town of Dudelange.

Movement Analysis extension to ArcView for all analyses on space use and movement patterns of the martens (Hooge and Eichenlaub 2000).

2.5.1. Autocorrelation

Animal location data is said to be autocorrelated when an animal's position at time $t + 1$ is a function of its position at time t (Swihart and Slade 1985b). There has been considerable debate about the importance of autocorrelated data in telemetry studies. Earlier studies, mostly based on simulated data, recommended collecting non-autocorrelated data (Cresswell and Smith 1992; Harris *et al.* 1990; Swihart and Slade 1985a). The rationale behind this was that autocorrelated data sets resulted in negatively biased estimates of home ranges, especially when produced by probabilistic methods (Cresswell and Smith 1992; Swihart and Slade 1985a). Swihart and Slade (1985b) introduced a test to determine the appropriate sampling interval (time-to-independence; TTI). In practice, attempts to reduce autocorrelation included the destructive subsampling of data or the arbitrary use of a time interval during which an animal was supposed to be able to cross its entire home range (Kenward 2001).

Otis and White (1999), however, pointed out a conceptual error in Swihart and Slade's (1985a) analyses, namely that they had based their estimates on equal numbers of locations spaced over unequal time periods. Real telemetry studies, by contrast, usually have a fixed time frame within which observations can be collected with a lower or higher sampling frequency. It has since been shown, using real animal data as well as simulations, that subsampling and longer sample intervals reduce the biological significance of home range and movement estimates (De Solla *et al.* 1999; Hansteen *et al.* 1997; McNay and Bunnell 1994; Reynolds and Laundre 1990; Rooney *et al.* 1998). Furthermore, for animals that move in a non-random fashion and live within well defined home ranges, successive points will never be fully independent (Rooney *et al.* 1998).

Thus the current consensus is that within a fixed study period, the number of observations should be maximised as long as the sampling interval is kept constant and each moment in time is sampled equally (De Solla *et al.* 1999; Fieberg 2007; McNay and Bunnell 1994). As the telemetry regime described above followed these recommendations I did not subsample the data and thus kept it directly comparable to those for other stone marten studies (e.g., Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986).

2.5.2. Home range estimators

Burt (1943) defined the home range as "…that area traversed by the individual in its normal activities of food gathering, mating, and caring for the young". Size, shape and structure are typically used to characterise home ranges (Kenward 2001), and the parametric minimum convex polygon (MCP) has long been the preferred estimator to this end (Harris *et al.* 1990; Mohr 1947). The MCP is constructed by connecting the outermost locational fixes by straight lines. According to Harris *et al.* (1990) the MCP is the only method that is strictly comparable between studies and should thus be included as a range estimator in any study. However, as its boundary includes all fixes, the MCP size is strongly influenced by peripheral fixes and includes areas that are seldom or never visited. There is still considerable debate about the biological relevance of MCPs. Some authors have found the method to be highly inefficient leading to considerable and unpredictable biases, and have specifically recommended that MCPs should not be used at all (Börger *et al.* 2006). Others have recommended the use of 95% MCPs in combination with other home range estimators (Wauters *et al.* 2007).

One alternative, and more advanced method of depicting an animal's home range is to define its utilisation distribution (UD), which describes the relative amount of time that the animal spends in any given place (Seaman and Powell 1996). Kernel density estimators are a commonly used nonparametric method for estimating UDs (Worton 1989). The method consists of placing a probability density (kernel) over each locational fix. A rectangular grid is then overlaid onto the animal's location fixes and a density is estimated for each grid intersection, based on the average density of kernels that overlap with it. Thus, areas with more fixes will produce higher density estimates (Seaman and Powell 1996). The distance over which a fix can affect the density at a grid intersection is determined by the smoothing parameter (bandwidth; h). Large values of h reveal the general shape of the distribution, while small values of h reveal the small-scale detail (Seaman and Powell 1996). Kernels that apply the same bandwidth across the plane are called fixed kernels. Adaptive kernels apply a higher bandwidth to areas with lower concentrations of points and vice versa (Worton 1989).

Most of the recent literature has focused and agreed on the use of fixed kernels for home range estimation (Börger *et al.* 2006; De Solla *et al.* 1999; Gitzen *et al.* 2006; Seaman and Powell 1996; Seaman *et al.* 1999; Wauters *et al.* 2007). However, there is currently considerable disagreement over which method to use to choose the appropriate value of *h*. Simulation based studies have tended to favour least-square cross-validation (LSCV) over the reference method (REF) (Gitzen *et al.* 2006; Seaman and Powell 1996; Seaman *et al.* 1999). Hemson *et al.* (2005) concluded, from a study based on real animal data, that LSCV tended to fail (i.e., the function was unable to find a local minimum at an inflection point) when applied to large data sets. This was attributed to the presence of many identical or spatially close location fixes (i.e., very dense clusters) resulting from the repeated use of areas or den sites by the animals. While other bandwidth selection methods have been suggested (Gitzen *et al.* 2006; Wauters *et al.* 2007), Börger *et al.* (2006) stressed that both LSCV and REF performed satisfactorily as long as the entire sampling regime was standardised (i.e., the number of days sampled, constant inter-fix interval). As most of the observed variation resulted from inter-animal variation rather than the kernel method, they recommended that, rather than maximising the number of fixes per animal, the number of animals included in the study should be maximised (Börger *et al.* 2006).

Kernel home ranges are usually represented as density isopleths within which an animal can be expected to spend a specified proportion of its time. Ninety five and 50% are often the standard isopleths used to delineate home range and core areas respectively (Hooge and Eichenlaub 2000). However, concerns about the reliability of the outer contours have been expressed (Seaman *et al.* 1999). Börger *et al.* (2006) recommended using isopleths between 90 and 50%.

I used 100% MCPs (MCP100) as all other stone marten studies have used the same estimator (e.g., Genovesi *et al.* 1997; Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986). Additionally, I calculated 95% MCPs (MCP95) based on the recalculated harmonic mean method (Hooge and Eichenlaub 2000). So far only Müskens and Broekhuizen (2005) have applied kernel estimators to stone marten telemetry data, although they did not specify the method they used. Preliminary analyses showed the REF and LSCV methods to produce almost identical results when applied to the current data set. As of now, LSCV is the most widely used method for choosing bandwidth and no general consensus on other methods has been reached yet. Consequently, I used fixed kernels with LSCV bandwidth selection. Following Börger *et al.* (2006) I addressed potential problems with poor performance by having standardised my sampling protocol as follows. An attempt was made to sample a similar number of nights per marten, maintain constant inter-fix durations, always sample the entire principal activity period (PAP) equally and analyse home ranges within determined time spans (i.e., seasons). In order to reduce potential problems with LSCV failure due to identical or spatially close fixes (Hemson *et al.* 2005), I eliminated all fixes from the data set where a marten was located inside the daytime den before and after the PAP, and all fixes during the PAP where a marten was outside the daytime den but was inactive (Table 2.3). I used 95% (KH95) and 50% (KH50) isopleths to delineate home range and core areas respectively. Following Börger *et al.*'s (2006) recommendations I included 90% isopleth values for future reference without, however, using them for further analyses.

2.5.3. Den selection

When diurnal locations from a specific marten were available for the same season in two consecutive years I only included the most complete season in the analysis in order to avoid pseudoreplication. Den selection was analysed at four different levels (Table 2.4). The classification was designed to best reflect the anthropogenic nature of the environment and thus identify the potential for human-marten conflicts related to denning behaviour. As it was usually impossible to gain direct access to the den inside a building I limited myself to identifying the type of building that housed the den. Thus I did not differentiate between, for example, attics, roof voids, or any kind of objects/materials stored inside a building.

2.6. Statistical analysis

Averages are presented throughout as mean ± SD. Data sets were tested for normality and homogeneity of variance using the Anderson Darling and Levene's tests respectively (Dytham 2003). When the assumptions were met, parametric tests were used; otherwise, nonparametric equivalents were employed (Sokal and Rohlf 1995). The significance level was always set at 0.05 and all tests were two-tailed. All statistical analyses were carried out in MINITAB$^{®}$ version 14 (Minitab Inc. 2004).

Table 2.4: Classification of den sites used by stone martens in urban habitat.

Level 1	**Level 2**	**Level 3**	**Level 4**
Anthropogenic	buildings	inhabited	family home, apartment block
			business, public building
		uninhabited	empty/ruined house
			warehouse
			garage
			shed (wood and stone)
			farm building (active and inactive)
			other/unknown uninhabited building
		unknown	building of unknown inhabitation status
	other structures		culvert
			car
			noise protection wall along motorway
			pile of steel girders
			firewood pile
			other/unknown
Natural			bramble
			hedge row
			tree
			dense brush
			underground animal burrow
Unknown			unidentified den

Chapter 3: Socio-spatial Organisation

3.1. Introduction

The typical spacing pattern observed in mustelids is based on intrasexual territoriality (Powell 1979). While females defend territories against other females and males against other males, male and female territories overlap extensively (Balharry 1993; Powell 1979). Female territoriality is thought to be driven mainly by the need for securing exclusive access to enough resources (principally food) for themselves and their offspring. Males are mostly concerned with securing exclusive access to females, which they can achieve by maintaining territories that entirely overlap with those of one or more females (Sandell 1989). Wherever marten (*Martes* spp.) spacing patterns have been studied they have typically conformed to this pattern of intrasexual territoriality (Balharry 1993; Powell 1994).

However, there is ample evidence that the socio-spatial organisation of carnivore populations can be shaped by the environment they inhabit. In particular, urban habitat can have various impacts on carnivore spacing patterns and social organisation. Urban red foxes, for example, tend to live in larger social groups than their rural counterparts (e.g., Baker *et al.* 2000; Gloor 2002) and may in some places exhibit a pattern of drifting territoriality (Doncaster and Macdonald 1991). Furthermore, compared to rural sites, urban raccoons have smaller home ranges and occur at extremely high densities (Hohmann *et al.* 2001; Michler *et al.* 2004; Prange *et al.* 2004), while urban badgers can also achieve unusually high densities (Huck *et al.* in press) and can have smaller social group territories (Davison 2007). Powell (1994) predicted that marten (*Martes* spp.) spacing patterns should change from transient to exclusive territories, to intrasexual territories, and finally to overlapping home ranges along a spectrum from low to very high prey or resource densities (and, consequently, from low to high population densities). Urban habitats are often considered as resource rich and may support high population densities. Hence urban stone marten populations could be expected to figure among the overlapping-ranges end of Powell's (1994) continuum.

Although stone martens are known to commonly live in urban habitats, their socio-spatial organisation has been mostly studied in forested or rural environments (e.g., Genovesi *et al.* 1997; Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986). Where martens have been radio tracked in human settlements these were usually so small that a single territory covered the entire village (Herrmann 2004; Skirnisson 1986). Thus, little is known about the dynamics of stone marten spacing patterns in urbanised areas large enough to potentially accommodate a number of territories (but see Bissonette and Broekhuizen 1995; Müskens and Broekhuizen 2005).

The aim of this chapter is to investigate the socio-spatial organisation of stone marten populations in two urban areas, each large enough to harbour a number of marten home ranges. Specifically, I determined home range areas, seasonal home range stability, extent of mutual home range overlap and the degree of urban habitat use. Based on results from other urban carnivore studies I predicted that urban stone martens might display more extensive territory overlap, smaller home ranges and higher densities than have been found in other environments.

3.2. Methods

The study area, telemetry procedures and home range estimators were described in detail in Chapter 2. I determined whether home range asymptotes were reached for seasonal home ranges by plotting the accumulated MCP100 area against the number of radio tracking nights (Balharry 1993), rather than against the number of fixes (Harris *et al.* 1990), because the data were collected during all-night continuous tracking sessions rather than as a series of independent fixes. I subjectively defined the point at which an asymptote was reached as the night after which only minor increases in accumulated home range area were observed. For the purpose of the analyses presented here I did not differentiate between the adult females and the two subadults (F6 and F8), since young martens have been shown to use the same ranges as their mothers (Herrmann 2004).

3.2.1. Home range fidelity

I assessed site fidelity by calculating home range shift distances and overlaps between successive seasons. Following White *et al.* (1996) and Henry *et al.* (2005), I calculated for each seasonal home range the arithmetic mean of all active fixes (i.e., fixes where a marten was outside the daytime den and was not inactive). Home range shift distance was then expressed as the straight-line distance between the arithmetic means from consecutive seasons.

In order to determine to what degree an individual marten's home ranges from consecutive seasons overlapped, I employed an index of overlap (I_{Ov}) adapted from Sørensen's similarity coefficient (see Dekker *et al.* 2001; Henry *et al.* 2005):

$$I_{Ov} = 2HR_{Ov} / (HR_t + HR_{t+1}),$$

where HR_t and HR_{t+1} are the areas of two home ranges from two consecutive seasons. HR_{Ov} represents the area by which both home ranges overlapped. I_{Ov} is dimensionless and can vary between 0 (no overlap) and 1 (complete overlap). A value of 1 would indicate that the home range remained identical in area, shape and location from one season to the next.

3.2.2. Mutual home range overlap

Mutual home range overlaps were assessed for two types of marten dyads: i) same-sex (intrasexual) and ii) opposite-sex (intersexual). In an ideal situation, all martens would have been tracked simultaneously over the same time periods. However, this was not always possible and some martens were tracked for unequal time periods, or only after their respective neighbours or mates had already been tracked. However, evidence from rural and village martens suggests that inter-individual relationships remain essentially stable across consecutive seasons and years and that vacated home ranges would be reoccupied without major spatial rearrangements (Herrmann 2004). Therefore, I used total home ranges (i.e., with data from different seasons combined) to assess home range overlaps, even in dyads where both martens were not tracked simultaneously. However, when calculating seasonal home range overlaps, I only considered marten dyads where both members were tracked during the same season in the same year.

Home range overlaps were calculated using the same index (I_{Ov}) as was described above:

$$I_{Ov} = 2HR_{Ov} / (HR_1 + HR_2),$$

where HR_1 and HR_2 are the home range areas of both martens making up a dyad. HR_{Ov} represents the area of overlap between the two home ranges.

3.2.3. Urban overlap

I defined urban habitat as any area located within the urban perimeter (see Chapter 2, Fig. 2.2), which was defined as the line following the properties of buildings at the periphery of the relevant towns (Gloor 2002). I also included other habitats that were located in the periphery and were directly associated with human activities (e.g., allotments, cemeteries), as well as fields or pastures that were completely surrounded by housing, as lying within the town borders. The martens' overlap with urban habitat was estimated as i) the percentage of the home range that overlapped with the urban area and ii) the percentage of active fixes that were located within the urban perimeter.

3.2.4. Urban marten densities

Urban marten densities were deduced from the mean home range sizes and the mean percentage overlap of home ranges with urban habitat. The calculation was based on two assumptions: i) absence of overlap between adult martens of the same sex, and ii) absence of long-term unoccupied areas within the urban perimeter. The latter assumption was based on direct observations of martens, bait removal at traps and reports of den sites and car damage (see Chapter 6) in areas where no martens were radio tracked in both study towns. I restricted the calculation of densities to adult martens as I did not have reliable data on the presence of juveniles or subadults.

3.2.5. Statistical analysis

Averages are presented throughout as mean ± SD. Data sets were tested for normality and homogeneity of variance using the Anderson Darling and Levene's tests respectively (Dytham 2003). When the assumptions were met, parametric tests were used (i.e., univariate GLM, one-way ANOVA, paired t-test); otherwise, nonparametric equivalents were employed (i.e., Kruskal-Wallis test, Wilcoxon signed ranks test) (Sokal and Rohlf 1995). When testing for seasonal differences in home range size, individual martens were used as a blocking factor to control for inter-individual variation. The significance level was always set at 0.05.

3.3. Results

3.3.1. Home range and core area size

The choice of home range estimator (see Chapter 2) had a significant impact on total home range area (Table 3.1). MCP100 produced consistently larger home range values than MCP95 (Figs. 3.1 and 3.2) (Wilcoxon signed ranks test: W = 91.0; N = 13; $p < 0.01$) and KH95 (Figs. 3.3, 3.4 and 3.5) (W = 88.0; N = 13; $p < 0.01$). The removal of the peripheral 5% of active fixes resulted in a decrease in area (MCP100 vs. MCP95) by on average 24.8 ± 14.4% (range: 3.2% - 52.4%). However, MCP95 and KH95 produced similar home range estimates (W = 37.0; N = 13; $p = 0.576$) (Table 3.1). KH50 core areas made up on average 11.3% (range: 3.6% - 27.9%) of the total KH95 home range (Figs. 3.3, 3.4 and 3.5).

MCP100, MCP95 and KH95 home range estimates were all significantly influenced by sex, with male ranges being larger than female ranges (Tables 3.1 and 3.2), but not by town. There was no significant interaction between these two factors (Table 3.2). Hence, for all subsequent analyses data from both study towns were combined.

Seasonal home range asymptotes were reached on average after about 5 ± 2, 4 ± 1, 3 ± 1 and 5 ± 2 tracking nights in summer, autumn, winter and spring, respectively (Fig. 3.6). Late home range increases as seen for M1 in autumn or M2 in spring can be attributed to exceptional forays outside the area usually used. No asymptote was reached for F3 in summer when this female was killed on the road after four nights; and none for F1 in winter, whose range further increased on nights 5 and 6 after having been stable beforehand.

There was no clear effect of season on female home range size. Mean female home range size was found to be largest in spring for MCP100, MCP95 and KH95 (Tables 3.3 and 3.4). However, a significant effect of season was only confirmed for MCP100 and MCP95, not for KH95 (Table 3.5). Post hoc comparisons (least significant difference: LSD) for MCP100 found spring to be significantly different from both summer and autumn, but not from winter, while winter did not differ from summer or autumn. However, LSD failed to pinpoint significant seasonal differences for MCP95. Using individual martens as a blocking factor showed that indeed most of the observed

Table 3.1: Total home range and core area estimates (ha) for 13 stone martens as determined by different home range estimators. The estimates are based on all active fixes that were collected irrespective of season.

Marten	MCP100	MCP95	KH95	KH90	KH50
F1	58.3	53.6	51.3	41.9	4.8
F2	22.8	20.9	16.5	9.7	0.6
F3	39.6	27.8	33.2	24.2	4.0
F4	38.3	24.3	26.9	21.2	2.1
F6	17.0	14.1	20.0	17.1	2.8
F7	9.5	4.5	4.0	2.6	0.4
F8	10.5	10.2	13.0	10.6	1.6
F9	39.6	31.7	29.4	20.4	1.0
F10	73.5	53.5	66.0	51.1	12.4
F11	60.9	36.7	41.5	34.2	11.6
M1	135.8	85.3	94.0	73.8	16.1
M2	86.4	63.9	48.2	30.1	1.7
M4	115.6	95.5	79.6	59.2	10.4
mean ± SD					
females	37.0 ± 22.2	27.7 ± 16.7	30.2 ± 18.7	23.3 ± 15.1	4.1 ± 4.4
males	112.6 ± 24.8	81.6 ± 16.1	73.9 ± 23.4	54.4 ± 22.2	9.4 ± 7.2

Fig. 3.1: Total 95% MCP home ranges for six stone martens in the town of Bettembourg.

Fig. 3.2: Total 95% MCP home ranges for seven stone martens in the town of Dudelange.

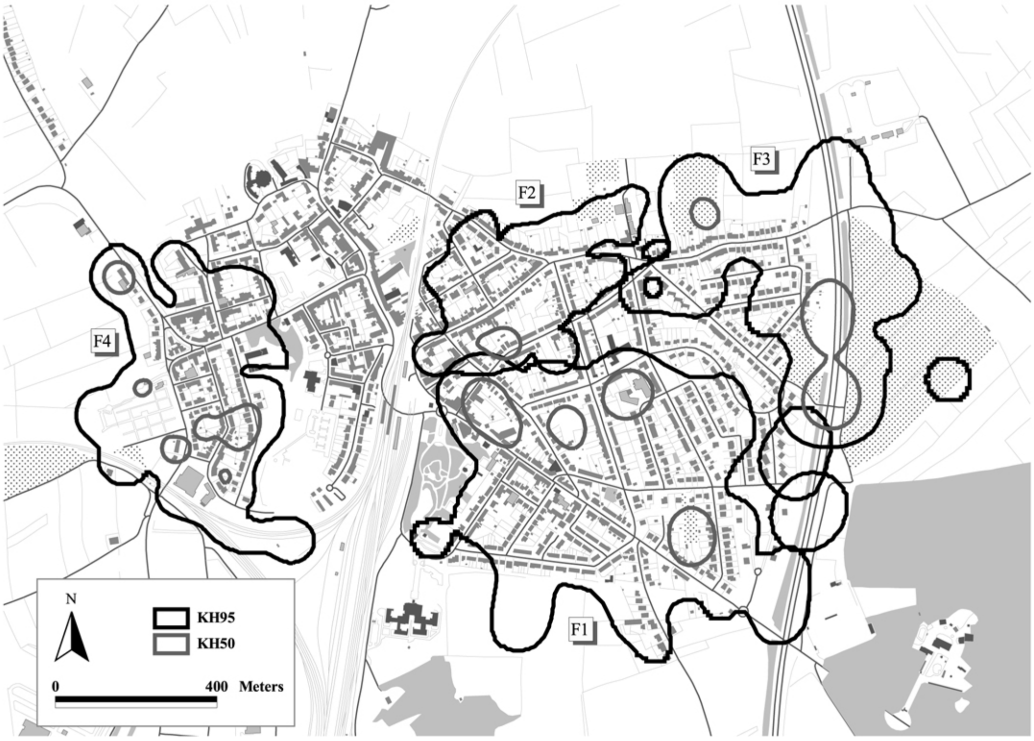

Fig. 3.3: Total 95% fixed kernel home ranges and 50 % kernel core areas for four female stone martens in the town of Bettembourg.

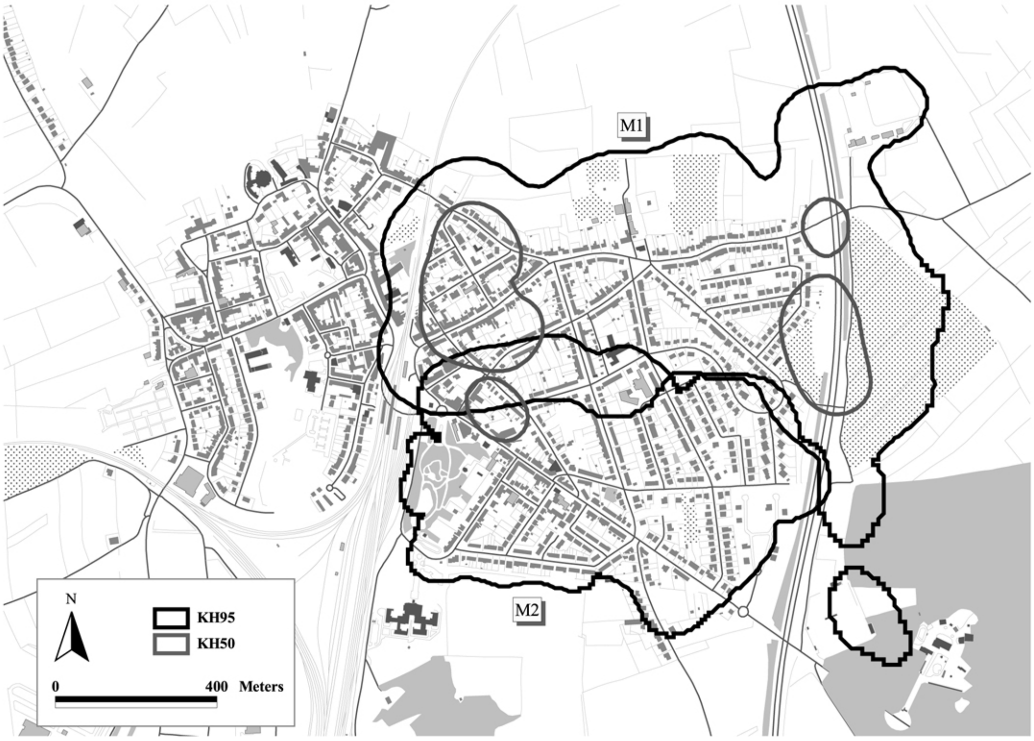

Fig. 3.4: Total 95% fixed kernel home ranges and 50 % kernel core areas for two male stone martens in the town of Bettembourg.

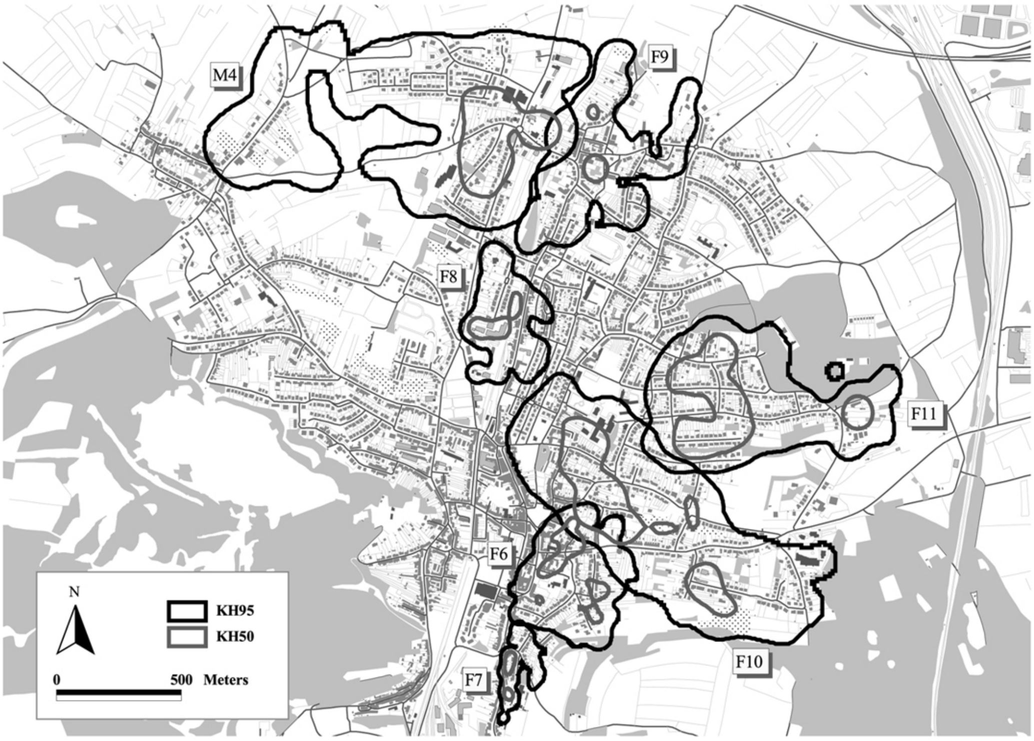

Fig. 3.5: Total 95% fixed kernel home ranges and 50% kernel core areas for seven stone martens in the town of Dudelange.

Table 3.2: Univariate GLM to investigate the effects of sex and town on total home range size for 13 stone martens. Significant p values are given in bold.

Home range estimator	Source	d.f.	SS	MS	F value	p value
MCP100	Sex	1	13189.3	12019.9	19.31	**< 0.01**
	Town	1	20.9	0.0	0.00	0.998
	Sex * Town	1	43.0	43.0	0.07	0.798
	Error	9	5602.3	622.5		
	Total	12	18855.5			
MCP95	Sex	1	6688.6	6701.4	22.78	**< 0.01**
	Town	1	1.0	107.7	0.37	0.560
	Sex * Town	1	392.7	392.7	1.33	0.278
	Error	9	2647.0	294.1		
	Total	12	9729.5			
KH95	Sex	1	4417.7	4201.9	9.05	**< 0.05**
	Town	1	0.7	15.8	0.03	0.858
	Sex * Town	1	68.9	68.9	0.15	0.709
	Error	9	4176.4	464.0		
	Total	12	8663.8			

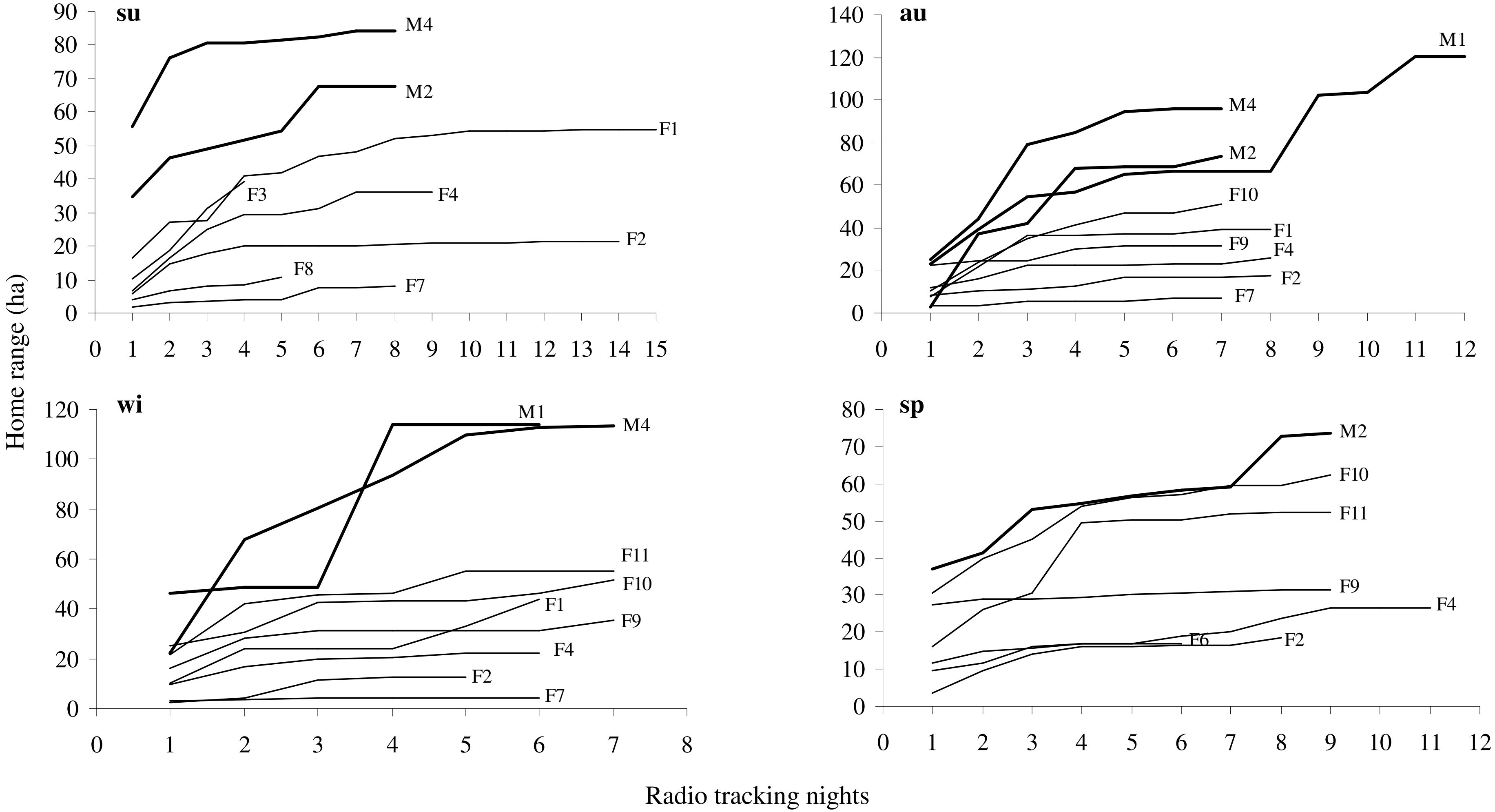

Fig. 3.6: Home range asymptotes showing accumulated home range area (100% MCP) plotted against sequential radio tracking nights for male (thick line) and female (thin line) stone martens. (su) summer; (au) autumn; (wi) winter; (sp) spring.

Table 3.3: Seasonal home range estimates (ha) for 13 stone martens based on the 100% and 95% MCP methods.

Marten	**Summer**		**Autumn**		**Winter**		**Spring**	
	MCP100	**MCP95**	**MCP100**	**MCP95**	**MCP100**	**MCP95**	**MCP100**	**MCP95**
F1	54.9	52.8	41.1	33.6	43.6	33.2		
F2	21.7	20.5	17.2	14.3	12.9	9.8	18.4	14.2
F3	39.6	27.8						
F4	36.3	30.9	25.8	21.7	22.2	16.0	26.9	21.7
F6							16.9	14.7
F7	7.9	4.3	7.3	3.6	4.5	3.9		
F8	10.5	10.2						
F9			31.4	29.5	35.2	29.5	31.3	27.4
F10			51.7	43.7	51.6	39.0	62.3	50.1
F11					55.2	33.2	52.3	33.8
M1			120.6	73.6	114.0	74.1		
M2	67.9	45.8	73.3	63.1			73.7	52.7
M4	84.8	67.8	95.8	73.5	113.5	80.9		
mean ± SD								
females	28.5 ± 18.3	24.4 ± 17.2	29.1 ± 16.0	24.4 ± 14.3	32.2 ± 19.5	23.5 ± 13.5	34.7 ± 18.6	27.0 ±13.6
males	76.3 ± 11.9	56.8 ± 15.6	96.6 ± 23.6	70.1 ± 6.0	113.7 ± 0.3	77.5 ± 4.8	73.7	52.7

Table 3.4: Seasonal home range and core area estimates (ha) for 13 stone martens based on the 95% and 50% fixed kernel methods, respectively.

Marten	**Summer**		**Autumn**		**Winter**		**Spring**	
	KH95	**KH50**	**KH95**	**KH50**	**KH95**	**KH50**	**KH95**	**KH50**
F1	47.9	2.1	51.3	7.9	40.5	2.7		
F2	21.1	0.9	18.9	1.7	2.0	0.2	17.1	1.1
F3	33.2	4.0						
F4	37.2	4.8	28.5	3.4	20.3	1.3	24.5	3.8
F6							20.3	2.3
F7	3.0	0.4	5.2	0.7	4.6	0.5		
F8	13.0	1.6						
F9			25.4	1.1	30.7	1.5	33.1	5.5
F10			62.7	9.1	58.2	9.3	66.9	10.1
F11					39.5	8.3	39.1	10.5
M1			83.3	7.6	93.1	6.6		
M2	54.5	2.0	60.1	2.6			48.6	2.0
M4	75.6	10.8	83.2	10.4	86.8	12.4		
mean ± SD								
females	25.9 ± 16.6	2.3 ± 1.7	32.0 ± 21.3	4.0 ± 3.6	28.0 ± 20.4	3.4 ± 3.8	33.5 ± 18.3	5.5 ± 4.0
males	65.1 ± 14.9	6.4 ± 6.2	75.5 ± 13.4	6.9 ± 3.9	89.9 ± 4.45	9.5 ± 4.1	48.6	2.0

Table 3.5: Univariate GLM to investigate the effects of season (using individual martens as blocking factor) on home range and core area size for ten female stone martens. Significant p values for season are given in bold.

Home range estimator	**Source**	**d.f.**	**SS**	**MS**	**F value**	**p value**
MCP100	Season	3	150.50	65.78	5.09	**< 0.05**
	Marten (block)	9	6818.74	757.64	58.58	< 0.001
	Error	12	155.20	12.93		
	Total	24	7124.44			
MCP95	Season	3	42.00	100.68	6.48	**< 0.01**
	Marten (block)	9	4335.53	481.73	30.99	< 0.001
	Error	12	186.54	15.54		
	Total	24	4564.07			
KH95	Season	3	225.82	70.32	2.78	0.086
	Marten (block)	9	7498.34	833.15	32.99	< 0.001
	Error	12	303.09	25.26		
	Total	24	8027.25			
KH50	Season	3	33.20	4.65	1.93	0.179
	Marten (block)	9	217.11	24.12	10.01	< 0.001
	Error	12	28.92	2.41		
	Total	24	279.22			

variation in seasonal home range size could be attributed to differences between martens rather than between seasons (Table 3.5). For the two females that were radio tracked over all four seasons (F2 and F4) there seemed to be a trend for home range size to decrease from summer to winter with a subsequent increase in spring. This trend was also partially observed in F1 and F10, who were tracked for only three seasons. Other females (e.g., F7, F9, F11) showed little variation in home range size (MCP95 and KH95; Tables 3.3 and 3.4).

Due to the small sample size I did not use statistics to analyse seasonal home range size variation in males. M1 used very similar areas in autumn and winter. The large difference between MCP100, by comparison with MCP95 and KH95, resulted from two 1-2 h long excursions (one in each season) by M1 into a forested area southeast of his normal range. M2’s autumn range was larger than his spring and summer ranges, due to the exploitation of an area with hedges and scrub in the southwest of his normal range. M4’s increase of home range from summer to winter was mostly due to a small number of fixes in the northern part of the range.

Female core areas (KH50) did not differ significantly between the different seasons (Table 3.5), although they were on average largest in spring and smallest in summer (Table 3.4). As was the case with home ranges, observed variation in core areas could mostly be attributed to inter-individual variation.

Due to the large influence of outliers on the MCP100 area I did not use this estimator in any subsequent analyses. I focused instead on the MCP95 and KH95 methods.

3.3.2. Home range fidelity

Shift distances

Home range location was generally stable from season to season. The arithmetic centres of seasonal home ranges shifted on average by only 70 ± 26 m (N = 6) from summer to autumn, 80 ± 50 m (N = 8) from autumn to winter and 37 ± 27 m (N = 5) from winter to spring. The home range shift distances for these three seasonal transitions were found not to be significantly different from one another (one-way ANOVA: F = 1.91; d.f. = 2,16; p = 0.181). Only one shift distance was available for the spring-summer transition (M2: 13 m). The shortest distance (5 m) was observed for F9 from winter to spring and the longest (143 m) for F2 from autumn to winter. The martens' mean seasonal shift distance made up on average 6 and 8% of the greatest diagonal of their MCP100 and MCP95 home ranges, respectively. Shifts in home range centres showed no consistency in direction within a given seasonal transition (Fig. 3.7). Also, for martens that were tracked for at least three seasons, the mean seasonal shift distance and the distance between the arithmetic centre of the first and last season was found not to be significantly different (Paired t-test: $t = -0.79$; $N = 8$; $p = 0.456$). Thus arithmetic home range centres did not shift in a net direction in subsequent seasons.

Overlaps

Because of the small sample size for male seasonal home range overlaps, I analysed male and female data together. M2 was the only marten that was tracked in spring and the subsequent summer. Hence, only one overlap estimate was available for the spring-summer dyad (I_{Ov}: 0.89 and 0.85 for MCP95 and KH95 home ranges respectively), which was omitted in the following analyses. Overall, I_{Ov} was high across all seasons and sexes. This was reflected by mean seasonal values ranging between 0.72 and 0.86 depending on the type of home range estimator used (Table 3.6). The lowest I_{Ov} values (0.15 and 0.21) were recorded for F2. These resulted from a very small KH95 home range in winter that was preceded in autumn and followed in spring by much larger home ranges (Table 3.4). Thus F2's low KH95 I_{Ov} s were the result of a home range contraction and a subsequent expansion rather than a net shift in location. All other 18 calculated overlaps were above or equal to 0.70. There were no significant differences in I_{Ov} between different season dyads (Kruskal-Wallis test: MCP95: $H = 3.94$; d.f. = 2; $p = 0.140$; KH95: $H = 0.65$; d.f. = 2; $p = 0.722$).

The only KH50 core area I_{Ov} calculated for the spring-summer period came from M2 (0.89) and was ignored in what follows. There was much variation in core area overlap across seasons and individual martens. I_{Ov} values ranged from a low of 0.04 to a high of 0.89 (Table 3.6). There was no evidence for differences in overlap between different season dyads (Kruskal-Wallis test: $H = 0.46$; d.f. = 2; $P = 0.796$). When compared to KH95 home range overlaps, core area overlaps were found to be significantly lower (Paired t-test: $t = 5.13$; $N = 19$; $p < 0.001$). These generally low overlaps between subsequent seasons were often caused by the break-up of one or two core areas into several cores that were located in different parts of an overall similar home range. This

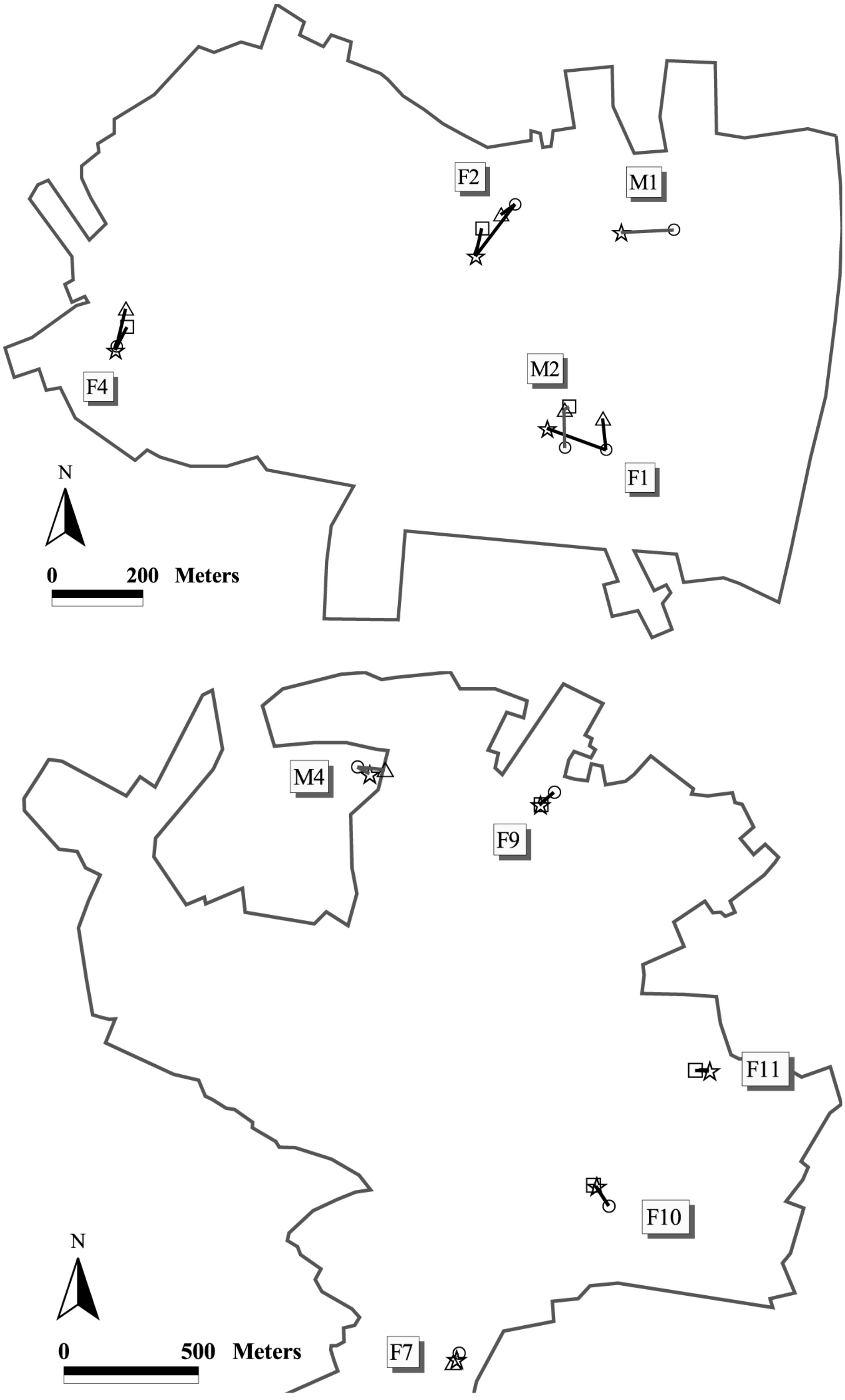

Fig. 3.7: Seasonal arithmetic home range centres and shift directions for martens in Bettembourg (top) and Dudelange (bottom). Triangle = summer; circle = autumn; star = winter; rectangle = spring.

Table 3.6: Seasonal index of overlap (I_{Ov}) values for home ranges and core areas.

	MCP95			**KH95**			**KH50**		
	su-au	**au-wi**	**wi-sp**	**su-au**	**au-wi**	**wi-sp**	**su-au**	**au-wi**	**wi-sp**
F1	0.78	0.79		0.86	0.75		0.13	0.26	
F2	0.82	0.73	0.82	0.87	0.15	0.21	0.10	0.04	0.33
F4	0.82	0.83	0.84	0.84	0.79	0.80	0.09	0.49	0.50
F7	0.81	0.94		0.70	0.84		0.63	0.35	
F9		0.88	0.95		0.73	0.89		0.69	0.37
F10		0.92	0.83		0.87	0.85		0.22	0.51
F11			0.87			0.83			0.53
M1		0.88			0.83			0.17	
M2	0.75			0.77			0.65		
M4	0.87	0.85		0.79	0.83		0.89	0.75	
mean	0.81	0.85	0.86	0.80	0.72	0.72	0.41	0.37	0.45
SD	0.04	0.07	0.05	0.03	0.24	0.30	0.35	0.25	0.35

was most striking for the females F1, F2, F4, and F10. Male core areas, especially those of M2 and M4, seemed to be more stable in both location and numbers (Figs. 3.8, 3.9 and 3.10).

3.3.3. Mutual home range overlap

Analysis of home range overlap depends on the assumption that inter-individual relationships remain stable across consecutive seasons and years (see section 3.2.2. above). The above results concerning seasonal shift distances and inter-seasonal home range (MCP95 and KH95) overlaps were consistent with this assumption. Also, observations confirmed that some martens (e.g., F1 and M1) had remained in their home ranges long after their radio tags stopped functioning. The assumption that the vacating of a home range would not result in significant changes in neighbouring ranges was supported by the fact that neither F1 nor F2 shifted their home range borders after the death of their neighbour (F3).

Overlap values within the intersexual dyads revealed the presence of two distinctive groups of dyads, those with extensive overlap (‘overlapping’) and those with essentially no overlap (‘non-overlapping’) (Table 3.7). There was a significant difference between I_{Ov} values from the three types of marten dyads considered (Kruskal-Wallis test: MCP95: $H = 8.02$; d.f. = 2; $p < 0.05$; KH95: $H = 8.12$; d.f. = 2; $p < 0.05$), with ‘overlapping’ intersexual pairs having higher overlap than intrasexual pairs or intersexual ‘non-overlapping’ pairs (Table 3.7). In fact, intrasexual overlap between neighbours was either non-existent or very small. The only male-male dyad (M1-M2) yielded a somewhat higher overlap value than the female dyads. This, however, was an artefact of the home range estimators. Close examination of the fixes within the overlap area revealed that the area was regularly used by M2 but hardly ever by M1 (Fig. 2.4). Overlap values were very similar in intrasexual and intersexual ‘non-overlapping’ dyads (Table 3.7). The slightly higher value for the M1-F1 dyad showed the same underlying cause as described for M1-M2. In the case of intersexual ‘overlapping’ dyads, M2 overlapped with only one female (F1), their home ranges being almost identical, while M1 overlapped with two females (F2 and F3). As the female home ranges were small compared to M1’s range, the calculated I_{Ov} values were much lower than for the M2-F1 dyad (Table 3.7). Nevertheless, F2 and F3’s home ranges were essentially entirely contained within the boundaries of M1’s home range (Fig. 3.1).

Fig. 3.8: Seasonal 50% fixed kernel core areas for four female stone martens in the town of Bettembourg.

Fig. 3.9: Seasonal 50% fixed kernel core areas for two male stone martens in the town of Bettembourg.

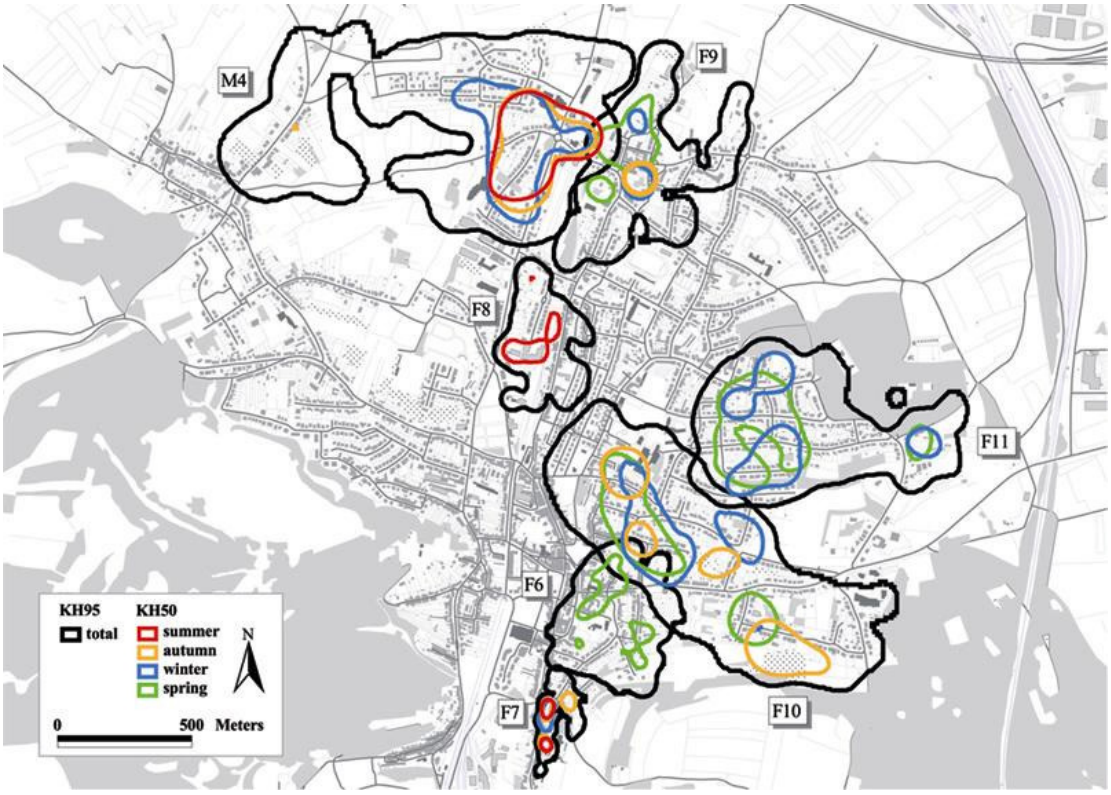

Fig. 3.10: Seasonal 50% fixed kernel core areas for one male and six female stone martens in the town of Dudelange.

Table 3.7: Index of overlap (I_{Ov}) values for intra- and intersexual marten home range dyads. Home ranges were based on all active fixes with seasons not being considered.

Marten 1	Marten 2	MCP95	KH95
Intrasexual			
F1	F2	0.01	0.02
F1	F3	0.00	0.03
F2	F3	0.00	0.01
F6[a]	F7	0.00	0.00
F6[a]	F10	0.07	0.10
F8	F9	0.00	0.00
F8	F10	0.00	0.00
F10	F11	0.00	0.03
M1	M2	0.24	0.12
	mean:	**0.04**	**0.03**
Intersexual			
'overlapping'			
M1	F2	0.39	0.30
M1	F3[b]	0.49	0.48
M2	F1	0.91	0.84
	mean:	**0.60**	**0.54**
'non-overlapping'			
M1	F1	0.21	0.11
M2	F2	0.02	0.04
M2	F3[b]	0.00	0.02
M4	F9	0.00	0.04
	mean:	**0.06**	**0.05**

[a] not known if F6 was still alive when F7 and F10 were tracked

[b] F3 was dead by the time M1 and M2 were tracked

Due to the small number of neighbouring or mated martens that were tracked during any one season it was impossible to test for seasonal differences in overlap. However, for those seasonal dyads that were calculated (Table 3.8), a similar pattern emerged as for the combined data. Intrasexual overlap was minimal or non-existent, irrespective of the season that was considered. The same was true for intersexual 'non-overlapping' dyads. During both autumn and winter, F2's home range was completely contained within M1's home range: the low KH95 winter I_{Ov} for these two martens resulted from the tiny female range in relation to the male's.

3.3.4. Urban overlap

The vast majority of the martens' activities took place within the urban perimeter of both towns (Table 3.9). However, only one marten's (F8) home range was completely surrounded by urban habitat (Fig. 3.2): the home ranges of all other 12 martens bordered on at least one side with rural or forested areas outside the urban perimeter line (Figs. 3.1 and 3.2). Nevertheless, on average 83.0 ± 16.8% of the area of MCP95 home ranges and 83.3 ± 16.4% of the area of KH95 home ranges overlapped with urban habitat. An even larger proportion of all active fixes (91.5 ± 9.8%) were located in urban habitat. M4 was the only marten to have more than 50% of its home range (MCP95) located in rural habitat but the high proportion of active fixes (87%) within urban habitat clearly demonstrates the urban character of M4's ranging behaviour.

3.3.5. Urban marten densities

Both assumptions stated in relation to the calculation of marten densities were fulfilled. Firstly, home range overlap analyses (see above) showed there to be no or little overlap between same sex neighbours. Secondly, all areas within both towns, even those where no martens were captured and tracked, appeared to be occupied by martens, as was shown by a combination of reports of marten-related car damage (see Chapter 6), martens denning in houses, marten sightings and visits to prebaited traps.

Based on mean male and female home range sizes, I calculated adult densities of 4.8 martens·km^{-2} (3.6 females, 1.2 males: based on MCP95) and 4.7 martens·km^{-2} (3.3 females, 1.4 males; based on KH95). In reality, however, only about 83% of the observed home range areas were located inside urban habitat. Consequently, I recalculated urban densities based upon mean home range size that was 83% of the

Table 3.8: Index of overlap (I_{Ov}) values for intra- and intersexual seasonal marten home range dyads. I_{Ov} was only calculated when two martens were tracked during the same season in the same year.

Marten 1	Marten 2	Season	MCP95	KH95
Intrasexual				
F1	F2	su	0.01	0.04
F1	F2	au	0.00	0.05
F1	F2	wi	0.00	0.00
F1	F3	su	0.00	0.05
F2	F3	su	0.00	0.03
F10	F11	wi	0.00	0.03
F10	F11	sp	0.00	0.03
		mean:	**0.00**	**0.03**
Intersexual				
'overlapping'				
M1	F2	au	0.32	0.37
M1	F2	wi	0.23	0.04
		mean:	**0.28**	**0.20**
'non-overlapping'				
M1	F1	au	0.07	0.07
M1	F1	wi	0.11	0.12
M2	F2	sp	0.00	0.05
M4	F9	au	0.00	0.05
M4	F9	wi	0.00	0.08
		mean:	**0.04**	**0.07**

Table 3.9: Percentages of total home range area and active locational fixes of 13 stone martens contained within the urban perimeters of the towns of Bettembourg and Dudelange.

Marten	**MCP95**	**KH95**	**Active fixes**
F1	87.3	90.0	96.3
F2	94.4	96.5	98.9
F3	56.6	50.9	66.1
F4	77.4	72.7	90.6
F6	99.7	95.6	97.3
F7	99.5	98.7	99.7
F8	100.0	100.0	100.0
F9	88.1	90.4	95.8
F10	95.2	90.6	94.3
F11	78.8	79.1	91.9
M1	69.3	58.5	77.4
M2	86.0	94.4	94.4
M4	47.1	65.7	86.9
mean ± SD	83.0 ± 16.8	83.3 ± 16.4	91.5 ± 9.8

actual mean home range sizes. This translated into densities of 5.8 (4.3 females, 1.5 males: based on MCP95) and 5.6 adult martens·km^{-2} (4.0 females, 1.6 males; based on KH95).

The above range of density estimates would predict a population of between 7.5 and 9.3 adult martens for Bettembourg (1.6 km^{2}). Five home ranges were actually mapped in the eastern part and one in the western part. Additionally there was room for one male and one or two females in the western part, bringing the predicted marten population in Bettembourg to eight or nine adults. The predicted population for Dudelange (5.0 km^{2}) was 23.3 to 29.1 adult martens. Due to the small number of martens that were tracked in relation to the true number of martens in Dudelange it was impossible to deduce the actual population size from the monitored martens, as was the case in Bettembourg.

3.3.6. Reproduction

Overall, reproduction levels in both study towns seemed to be rather low. Among the eight adult females only three reproductive events were recorded between 2005 and 2007 (Table 3.10). F1 showed signs of lactation when she was caught in June 2005 and two to three young were later observed in her territory. One of those (F5) was caught later. In spring 2007, reports of persistent nightly noise from several martens indicated the presence of a maternal den under the roof of an apartment house in F1's home range. Although her radio signal had long faded, her identity was confirmed by directly observing a collared marten leave the den (the only other collared marten (M2) in that area was dead by then). In spring 2007, F10 remained in the same den from March to at least the end of May, when her signal faded. She frequently visited the den at night and was observed carrying food items into it, and a juvenile was observed at the den on the morning of 20/05/07.

On three occasions a definite change in denning behaviour (same den on consecutive days) and ranging behaviour (visits to den during the principal activity period (PAP: see section 2.4.4.)) in March suggested that parturition might have taken place (Table 3.10). However, these three females (F1 and F4 in 2006; F7 in 2007) had resumed normal denning behaviour by early April (Chapter 5). No other females showed signs either of having lactated when captured or of having reproduced while being tracked (Table 3.10).

Table 3.10: Reproduction in adult female stone martens in the towns of Bettembourg and Dudelange. Reproduction having preceded capture was assessed based on signs of lactation at capture and the subsequent observation of young during the summer. Reproductive events during radio tracking were assessed based on denning and nightly ranging behaviour in spring.

Marten	**2005**	**2006**	**2007**
F1	+	–[a]	+[b]
F2	–	–	
F3	–		
F4	–	–[a]	
F7		–	–[a]
F9		–	–
F10		–	+
F11			–

[a] possible parturition with premature death of young
[b] based on reports of a maternal den in an inhabited building (see text)

3.3.7. Non-focal martens

During continuous tracking, 134 observations of non-focal martens were recorded (Table 3.11). However, it was generally difficult to judge the size (and, hence, the age and sex) of these animals as most observations were brief glimpses of a marten crossing a road or moving under a row of cars. A special case was a tailless marten that was observed 12 times in F1's territory between 11/06/05 and 10/01/06 (Fig. 3.11). During the next 10 months this marten was never seen again. During summer 2006, F1 was seen together with at least two (presumed) juveniles on a few occasions. In the same territory one marten was reported, with several months delay, to have been killed on the road in July 2005 and F5 died in August 2005. After 17/08/05 no observations of 'tailed' martens were made until a much bigger marten was seen in March 2006 and later caught in April (M2).

An interesting trend in these observations was that, when tracking females, other martens were seen regularly, but when tracking males, few observations of other martens were made. Whenever a male and a female were tracked in the same territory, observations of a non-focal marten were usually confirmed to be of the known mate.

3.4. Discussion

3.4.1. Spacing system

A territory can be conceptually defined as an area of exclusive use, which, in practice, may be recognised by a lack of home range overlap between neighbouring individuals (Maher and Lott 1995). According to this definition the present study revealed strong signs of territoriality between martens of the same sex. This was particularly apparent for the females, whose ranges in many cases did not overlap at all with those of their female neighbours. This very closely resembled the pattern of distinct adjacent female territories in the village of Borgharen in the Netherlands (Müskens and Broekhuizen 2005). In the present study, clear territorial borders, which were often located along roads, became quickly apparent after only a few nights of continuous tracking. This was also confirmed by observations of chases at territorial borders between neighbouring radio-tagged females (F1-F2; F10-F11). In Bettembourg, however, the ranges of both males overlapped with those of either one or two females. This system was in accordance with the intrasexual territoriality pattern that has been described for

Table 3.11. Record of visual observations of non-focal martens made during continuous radio tracking sessions of focal martens. Non-focal martens were tentatively classed into martens of 1) unknown size, 2) similar size to focal marten, or 3) definitely bigger (presumably adult male) or smaller (presumably female or young male) in size than focal marten. If known, the identity of non-focal martens, and other comments, are given in brackets.

Focal	**Non-focal**		
	unknown	**similar**	**bigger**
F1	13	12 (tailless)	3
F2	11	2 (F1)	9 (8 x M1)
F3			
F4	6		3
F6	7	1	5
F7	11	1 (roadkill)[a]	6
F8	1	2 (siblings)	
F9	7	1	12
F10	5	2 (1 x F11)	
F11	4 (1 chase)[b]	2 (1 chase)[b]	1
			smaller
M1	1		1 (CRF0)[c]
M2	1		4 (2 x F1)
M4	1		

[a] presumably a subadult
[b] between focal and non-focal marten
[c] probably a captive-reared marten (see Chapter 7)

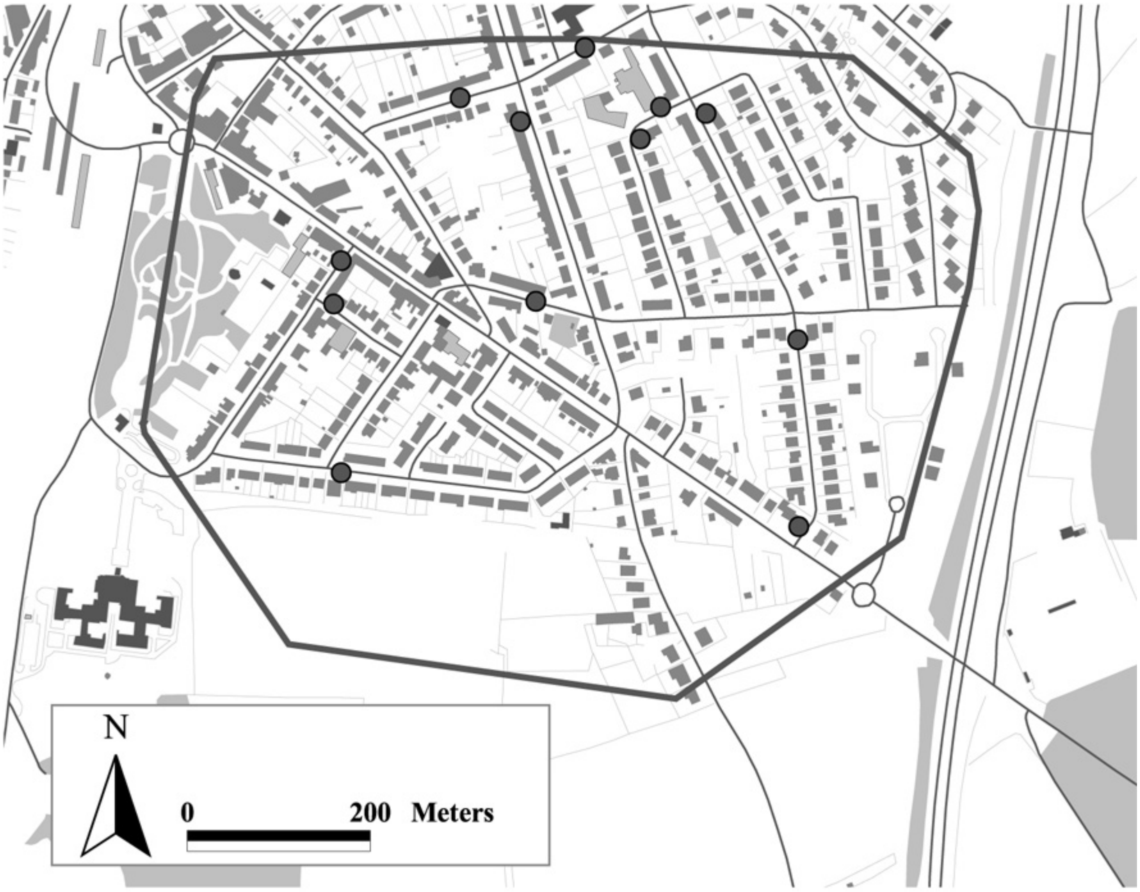

Fig. 3.11: Visual observations of a tailless marten within F1's 95% MCP home range between June 2005 and January 2006 in the town of Bettembourg.

mustelids in general (Powell 1979) and martens (*Martes* spp.) in particular (Balharry 1993; Bissonette and Broekhuizen 1995; Powell 1994; Zalewski and Jędrzejewski 2006). While female dispersion is thought to be governed by the availability of food, males adapt their territories to their respective mates' borders. Thus by completely incorporating these ranges into their own, they maintain exclusive access over their mates (Sandell 1989). This complete monopolisation of females by males was further highlighted here by the lack of significant overlap between neighbouring male and female ranges.

The observations of non-focal martens are difficult to interpret. However, it seemed that males were a lot more visible than females (see also Chapters 4 and 6). The majority of observations made while tracking females could thus likely be attributed to the resident male. In the case of F1, many of these observations were due to the presence of young. The disappearance of the tailless marten in January could also be related to a dispersal event. Overall, there were few indications that territories would have been occupied permanently by more than one pair of adults.

Thus, while urban habitat has led some carnivores to adapt their social system by forming social groups (e.g., red foxes: Baker *et al.* 2000; Gloor 2002; feral cats: Liberg *et al.* 2000) or aggregating without the formation of groups (e.g., raccoons: Michler *et al.* 2004; Prange *et al.* 2004), my data suggest that it has had no such effect on the social organisation of female stone martens. This also seemed to be the case for males, though in this case my data were limited in terms of sample size. Similar spacing patterns as in the present study have been documented in forested (Genovesi and Boitani 1995; Genovesi *et al.* 1997), rural/village (Herrmann 2004; Skirnisson 1986) and town environments (Müskens and Broekhuizen 2005). Although a number of martens had been radio tracked in the Dutch city of Nijmegen, Bissonette and Broekhuizen (1995) did not present quantitative data on home range overlap. However, female-female territoriality and male-female overlap were recorded in this population, too. Additionally, they reported extensive overlap between the ranges of an adult and a subadult male (Müskens *et al.* 1989).

3.4.2. Home range size

While the territorial system was similar to what has been described in other studies, home range sizes (MCP100) were situated in the lower range of those reported elsewhere for stone martens. The largest home ranges can typically be encountered in forested environments: Genovesi *et al.* (1997) found forest-dwelling martens to occupy home ranges of on average 361 ha (range: 63-800 ha) while Simon and Lang (2007) tracked one male that ranged over 880 ha and two females covering 150 and 180 ha respectively. Martens inhabiting rural environments in Switzerland occupied much smaller ranges, averaging 111 ha for males and 49 ha for females (Lachat Feller 1993b). Herrmann (1994) found rural home ranges (36-211 ha) to be significantly larger than village home ranges (12-61 ha) and Skirnisson (1986) reported similar results. According to the latter study, martens that moved into villages from surrounding environments greatly reduced their home range sizes. Year-round territories, however, were large, at 116 and 276 ha for two females and 292 and 310 ha for two males.

Where urbanisation is more extreme, home range sizes have been found to be generally smaller. In the Dutch city of Nijmegen, males had home ranges of around 30 to 80 ha and females of around 15 to 55 ha (Bissonette and Broekhuizen 1995). In Borgharen, a town of 750 households, three females occupied small ranges of 31, 9.9 and 9.5 ha, with a male covering 81 ha (Müskens and Broekhuizen 2005). These values, but also those from Lachat Feller's (1993b) study in rural areas, are similar to those found in Bettembourg and Dudelange (all based on MCP100). Males, in the present study, however, seemed to range over slightly larger areas, while females occupied a wider range of home range sizes. Nevertheless, there seems to be a clear trend for smaller home ranges moving from forested into rural, and from rural into urbanised environments. The high observed variation in female home range size (7-12 fold depending on the estimator used) within a single town, in which habitat appeared to be fairly uniform, supports the idea that females tend to maintain larger territories than needed to support themselves in productive environments (Herrmann 2004). Most studies, with a couple of exceptions (Genovesi *et al.* 1997; Rondinini and Boitani 2002), found male territories to be larger than female territories, which is in line with the intrasexual territoriality model.

3.4.3. Home range fidelity and seasonal stability

The above studies have mostly reported that stone marten home ranges are very stable. However, isolated home range shifts into adjacent areas have been described by several authors (Genovesi *et al.* 1997; Herrmann 2004; Müskens *et al.* 1989; Skirnisson 1986). No such shifts were found here, even for those females that directly neighboured the vacated home range of F3. When compared to home range width, mean seasonal shift distances were similar to the yearly shifts reported for stone martens in forested environments (Genovesi *et al.* 1997), and lower than seasonal shifts in a pine marten population that was characterised by a high degree of spatial stability (Zalewski and Jędrzejewski 2006).

According to Herrmann (2004), seasonal home range size fluctuations can be considerable, with males and females occupying winter home ranges comprising 40% and 50% of the summer ranges, respectively. The more moderate seasonal fluctuations that I observed could be the result of higher population densities in urban environments (see below). Due to an increased intruder pressure a marten that further reduces an already small territory in winter, may run a higher risk of permanently losing parts of it to a neighbour. Assuming that small territories are more efficiently patrolled than large ones, seasonal variations in home range area would be more easily detected by neighbours in urban than in other environments. The slightly larger ranges in spring just reflect an increase in visits to the borders in this most territorial period of the year (Chapter 4). The pattern observed here fits well with Sandell’s (1989) prediction that exclusive mating ranges should show little seasonal variation in size. Overall, my urban populations were characterised by a remarkably stable spatial structure.

A pattern of territory drift, as was described for urban foxes in Oxford (Doncaster and Macdonald 1991, 1996), certainly did not exist in my two towns. Factors such as social instability due to high mortality, or unpredictable occurrence of scavengeable food, that were hypothesised to induce territory drift (Doncaster and Macdonald 1991), may not play a major role in the present stone marten population. In fact, mortality was low with only one confirmed death during radio tracking. There was also no indication that martens relied on food provided by house owners. Furthermore, the urban habitat considered here may simply be too small for drifting home range dynamics to develop.

Such factors may, however, play a role in larger European cities where martens are known to exist (e.g., Tester 1986; Tóth Apáthy 1998) but have not been radio tracked.

Core areas were considerably less stable than home ranges. This reflects the changing productivity of food patches within territories but also, to a lesser degree, the differential use of certain buildings, across different seasons. Similar relationships between food availability and space use have also been described for rural martens (Rödel and Stubbe 2006). The pattern of within-territory space use described here supports the notion that urban habitat can indeed be considered as patchy. However, the fact that this instability in core areas was mostly observed in females may indicate that it is more vital for females, than for males, to secure good food resources in order to meet the needs of reproduction (Sandell 1989).

3.4.4. Urban adaptation

Another indication of high spatial stability was the fact that there were no observed one-way or cyclical shifts between urban and rural environment. This year-round concentration of activities on urban areas has also been observed in three females in a Dutch town (Müskens and Broekhuizen 2005) but contrasts with a study in Siena, Italy, where martens were thought to enter the city only sporadically to take advantage of good food resources (Cavallini 1992). However, the author of the latter study did not radio track martens, relying instead on householder questionnaires. Siena is a much more built-up environment than the one considered here, which may potentially contribute to a different pattern of use of this habitat. Herrmann (2004) judged urbanised habitats to be of superior quality to rural or forested environments, in which case it could be expected that once a marten has acquired a territory inside a town there would be no need for it to move between urban and peri-urban areas. However, it takes a number of behavioural adjustments to change from a forested or rural setting into an urban one (Ditchkoff *et al.* 2006), so settlement in urban areas could be favoured by having learned such behaviours at a young age.

Interestingly, urban foxes in Zurich have been shown to be both spatially and genetically segregated from their non-urban counterparts, indicating that there is very little movement between the two types of environment (Gloor 2002; Wandeler *et al.* 2003). Whether martens raised in a specific habitat predominantly settle in that same habitat is unknown. This would need to be confirmed with data on dispersal and genetic relatedness between urban and surrounding non-urban populations.

3.4.5. Densities and reproduction

Little information on marten densities, especially from urban areas, exists. Density estimates of 0.7 to 2 martens·km^{-2} (Lachat Feller 1993b) or 2 adults plus 1.5 juveniles·km^{-2} (Herrmann 2004) have been put forward for rural and forested environments. Herrmann (2004) estimated densities in rural villages to reach 6 adults plus 12 juveniles·km^{-2}. However, he worked in small villages and, because of martens' tendency to restrict their activity to urbanised areas, territory size will likely be strongly affected by the size of the village itself. Hence, density estimates from small villages may not be readily extrapolated to larger urban areas. So far, the only estimate for a real urban environment comes from Nicht (1969), who based his estimate of 8 martens·km^{-2} on data from intensive kill trapping and snow tracking in the German city of Magdeburg. Although I did not investigate reproductive rate directly, observations suggest that it was low in my study towns. Consequently, the actual density estimate for urban areas in Luxembourg (4.7-5.8 adults·km^{-2}, not including juveniles) could indeed be close to Nicht's (1969) estimate.

A low reproductive rate in urban habitats, if confirmed in other studies, would contradict Herrmann's (2004) hypothesis that high reproduction in urban areas would provide a constant flow of juvenile dispersers responsible for continually re-occupying suboptimal 'sink' habitats in rural and forested landscapes. It is, however, in line with low reproduction rates in radio-tracked females in Nijmegen (Lammertsma *et al.* 1994). They found no evidence that the frequent skipping of reproduction was related to trapping, collaring or body condition, instead attributing it to high population densities. In fact, the examination of placental scars in a sample of road killed, uncollared martens in the same city led them to the same conclusion. In Luxembourg, urban stone marten densities are thus not expected to undergo further increases, since density-dependent decrease in reproduction in combination with strong territoriality would naturally limit densities. Prigioni and Sommariva (1997) reported very high estimates from a small town in the Italian Alps (52 martens in a 60-ha town, i.e., 86.7 martens·km^{-2}). However, this needs to be treated with caution as it was based on the radio tracking of only three juvenile females predominantly during the winter months and on nightly ranges rather than seasonal ranges.

Other urban carnivores with a more flexible socio-spatial organisation have the potential to reach much higher densities than stone martens. Foxes can occur at 9.8 to 11.2 adults·km^{-2} (Gloor 2002) or even 5 social groups·km^{-2} with 6.57 adults per group, i.e., 32.8 adults·km^{-2} (Baker *et al.* 2000). Urban raccoons have reached levels of up to 125 individuals·km^{-2} in North America (Riley *et al.* 1998) and around 100 raccoons·km^{-2} in Germany (Hohmann *et al.* 2001). Urban badgers can reach densities of up to 32 adults·km^{-2}, which is higher than in the vast majority of rural populations (Huck *et al.* in press).

3.4.6. Conclusion

I observed a pattern of intrasexual territoriality in martens from both towns, while spatial organisation was characterised by a high degree of stability and ranging confined to urban habitat. Although urban habitat has favoured the formation of social groups in other carnivores and may thus be expected to do the same to stone martens, this was not the case here. Hence, the switch from intrasexual territoriality to extensive home range overlap, predicted by Powell (1994), has to date not been described in any stone marten population. This lends further support to Balharry's (1993) hypothesis of a phylogenetically determined intolerance of conspecifics in martens (*Martes* spp.). A dense and evenly distributed population of females would further favour the maintenance of exclusive ranges in males (Sandell 1989).Taking the evidence as a whole, the only flexibility observed in the spacing system of stone martens seems to be a moderate adaptation of home range size, with resultant changes in population density, to the type of habitat that they live in.

Chapter 4: Activity and Movement Patterns

4.1. Introduction

Activity and movement patterns of animals are influenced by a variety of factors ranging from their evolutionary origin to the local abiotic and biotic environment that sourrounds them. Goszczynski (1986) demonstrated the importance of phylogeny in explaining movement patterns in terrestrial mammalian predators, showing that for any given body weight mustelids generally move over greater distances than canids and felids. However, there is also a great deal of intraspecific variation in activity patterns, which may result from intersexual differences based on strong sexual dimorphism in body size (e.g., Marcelli *et al.* 2003) or reproductive constraints (Kolbe and Squires 2007; Zalewski 2001). In addition, important biogeographical variation between populations may be explained by climatic conditions and differential availability of food resources (Kowalczyk *et al.* 2003; Zalewski *et al.* 2004), while at the population level meteorological factors (especially temperature) and food availability may influence the time and energy animals invest in their activities (Baghli and Verhagen 2005; Zalewski 2000; Zalewski *et al.* 2004; Zielinski *et al.* 1983).

Urban habitats often provide an abundance of food and water as well as shelters (Adams *et al.* 2006) and urban mammals can be expected to adapt their behaviour accordingly. Urban red foxes and Eurasian badgers seem to be able to fulfil their energetic needs by foraging during shorter periods and over shorter distances than rural ones (Doncaster and Macdonald 1997; Harris 1982). American black bears are 36% less active in urban than in wildland areas (Beckmann and Berger 2003b). Furthermore, territory sizes in urban areas are typically smaller than in wooded or rural areas (see Chapter 3), and as such would also presumably require less effort to be effectively patrolled. Also, it is possible that the release from intraguild predation in urban areas could influence movement and activity patterns of some mesocarnivores (Crooks and Soulé 1999; Gehrt and Prange 2007).

However, urban animals are also exposed to a variety of anthropogenic stresses, which their rural counterparts are faced with to a much lesser degree. Consequently, urban animals may also be forced to adapt their behaviour in a way that allows them to avoid or mitigate these constraints (Ditchkoff *et al.* 2006). Human activities and traffic are obvious factors that have to be coped with in order to successfully subsist in human-dominated environments. There are two possible ways for animals to adapt to humans: by becoming tolerant of human presence or by adjusting to human activity through temporal avoidance (i.e., urban animals become active when humans are not: Adams *et al.* 2006). For example, bobcats and coyotes have been shown to reduce their diurnal activity in developed and urban areas, suggesting behavioural avoidance of humans (McClennen *et al.* 2001; Riley *et al.* 2003; Tigas *et al.* 2002). Black bears living in the urban-wildland interface have shown comparable activity shifts (Beckmann and Berger 2003b). Similarly, urban red foxes show strong evidence of temporal adaptation of their movement patterns to avoid even very low levels of road traffic (Baker *et al.* 2007) and habitats with higher human presence (Gloor 2002).

Even though stone martens are commonly found in urban areas, very little is known about their activity and movement patterns within this type of habitat. Bissonette and Broekhuizen (1995) presented limited data on the areas that were covered per night by two females in the city of Nijmegen, while Skirnisson (1986) and Herrmann (2004) described activity and mobility of martens in rural villages. By contrast, the latter two studies, as well as Broekhuizen (1983), Lachat Feller (1993b), Föhrenbach (1987), Posillico *et al.* (1995) and Genovesi *et al.* (1997), have looked at these aspects of activity in stone martens inhabiting mountainous, rural and forested environments.

This chapter investigates the activity and movement patterns of stone martens in urban areas. Specifically, I determined the timing of onset and termination of their outside-the-den activities and the duration of their nightly activity period, as well as movement distances and speeds. I predicted that urban martens might shift their activities to later hours of the night by comparison with rural ones, in order to avoid human disturbance. Furthermore, they were expected to be less active and to move shorter distances than has been described in forest dwelling and rural martens.

4.2. Methods

The study area, telemetry procedures and home range estimators were described in detail in Chapter 2. Ambient temperature was measured with automatic Tinytalk temperature loggers (Gemini Data Loggers Ltd, Chichester, UK) that were programmed to take a temperature reading every 4 h. The loggers were placed at ground level (one within each study town) and nightly temperatures were calculated as the mean temperature from the readings taken at 2000 h, 0000 h, 0400 h and 0800 h.

4.2.1. Den emergence and return times

Times of emergence from a den and return to a den were estimated based on all-night tracking sessions but also occasionally on shorter observations, especially for emergence times. Emergence time was defined as the time of the first quarter-hourly fix after the marten had left the den it had spent the day in. Return time was defined as the time of the first quarter-hourly fix after the marten had finally retreated into the den that it would subsequently spend the day in. Emergence and return times were determined based on direct observation of the animal exiting or entering the den. Where direct observation was not possible, emergence and return times were based on the radio signal clearly moving away from the den or approaching it and subsequently staying there. The martens usually rapidly left the general area of the den after first emergence.

4.2.2. Principal activity period (PAP) and nightly activity (NA)

PAP (h) was only estimated for nights where both emergence and return times were known. It was defined as the time period between emergence from a den and return to a den. Thus, PAP also included bouts of inactivity that may have interrupted activity bouts during the night. NA (h) was defined as the actual time that an animal was active during its PAP. It was calculated as the product of the PAP duration and the proportion of fixes that were recorded as active during the PAP. I used data from 232 tracking nights for these analyses.

4.2.3. Activity rhythms

Nightly activity rhythms were calculated on the basis of all fixes (Kowalczyk *et al.* 2003), i.e., fixes from all collared individuals pooled, grouped into 1-h periods (e.g., the 21 h category would include fixes taken at 2100 h, 2115 h, 2130 h and 2145 h, etc).

Fixes were recorded as i) inside the den (all fixes before first emergence and after final retreat into a den); ii) outside and active (active fixes during PAP); and iii) outside and inactive (inactive fixes during PAP). I did not differentiate between locomotory and stationary activity (e.g., Lachat Feller 1993b). Activity rhythms were only established for the hours between 1900 h and 0900 h. When a tracking session started later than 1900 h but before the animal had left the den, all potential fixes between 1900 h and the actual start of the tracking were recorded as inside the den. Equally, all potential fixes between the end of the tracking period and 0900 h were recorded as inside the den. This was only done for the purpose of this specific analysis and these fixes were not included in Table 2.3. I did not attempt to represent activity and inactivity of martens inside their daytime dens, as it was not possible to get a representative sample of fixes for the hours preceding emergence and following return.

4.2.4. Movement patterns

In order to quantify movement patterns I calculated four different movement parameters, following Zalewski *et al.* (2004): i) Nightly movement distance (NMD, in km): the sum of straight line distances between consecutive fixes taken at 15-min intervals; ii) Movement speed (in $km \cdot h^{-1}$): NMD divided by NA; iii) Nightly range (NR, in ha): a 100% minimum convex polygon based on all the fixes taken during a marten's PAP; iv) Nightly range as a percentage of seasonal home range (NR/SR, in %), using MCP95 seasonal home ranges (see Table 3.3) for the calculations. I based NR on MCP100 as that measure best represented an individual night's movements. MCP95 was used for NR/SR as it better represented home range over a longer time interval (see Chapters 2 and 3). Nights that were only partially completed or where too many fixes were missed were discarded from the analyses. Eventually, 251 and 252 nights were retained for NMD and NR respectively. Speeds were calculated on the basis of 230 nights.

4.2.5. Statistical analysis

In order to avoid problems with pseudoreplication I treated each animal as a sampling unit rather than treating each individual night as an independent sample, as has often been done for activity and movement pattern analyses (e.g., Kowalczyk *et al.* 2006; Zalewski *et al.* 2004). I calculated mean seasonal values (for PAP, NA, NMD, speed, NR, NR/SR) for each marten and used a univariate general linear model (GLM) to test for seasonal effects. Individual martens were used as a blocking factor to control for inter-individual variation. Post hoc pairwise comparisons were performed with a Tukey test. Due to the small number of males these statistical analyses were only carried out for females. For individual martens, no means were calculated for seasons where they were tracked for less than four nights (and thus F3 was completely excluded from these analyses).

However, when analysing emergence and return times, activity rhythms, and correlations between NA and temperature, all data (including nights from F3 and other martens that were tracked for less than 4 nights in a specific season) were included and treated as independent samples. Chi-square tests were employed to test for differences in the distribution of hourly activity (proportion of outside/active fixes) between seasons and sexes. Z-tests were used to test for within-hour differences in proportions of active fixes between sexes. In order to test for differences in emergence and return times all quarter hour intervals between 1900 h and 0900 h (the following morning) were associated with an integral number running from 1 (1900 h) to 57 (0900 h). Non-parametric tests were then run on these substitute numbers rather than on the actual times. The significance level was always set at 0.05.

4.3. Results

4.3.1. Activity patterns

Den emergence and return times

The martens in both study towns were clearly nocturnal, emerging from their daytime dens after sunset and returning to the same or different dens before sunrise (Fig. 4.1). On only two occasions did martens (M2 and M4) retreat into their den a few minutes after official sunrise time in summer. Both emergence and return times showed significant seasonal variation (Kruskal-Wallis test: emergence: $H = 27.24$; d.f. = 3; $p < 0.001$; return: $H = 91.28$ d.f. = 3; $p < 0.001$) (Table 4.1). Overall, the martens left their den sites earliest in spring, followed by summer, autumn and winter, all seasons differing significantly from each other (Mann-Whitney U tests: $p < 0.05$), apart from summer and autumn ($p = 0.144$). Return times were earliest in summer, followed by spring, autumn and winter, with all seasons differing from each other ($p < 0.001$), apart from autumn and spring ($p = 0.114$). Although there were no overall significant

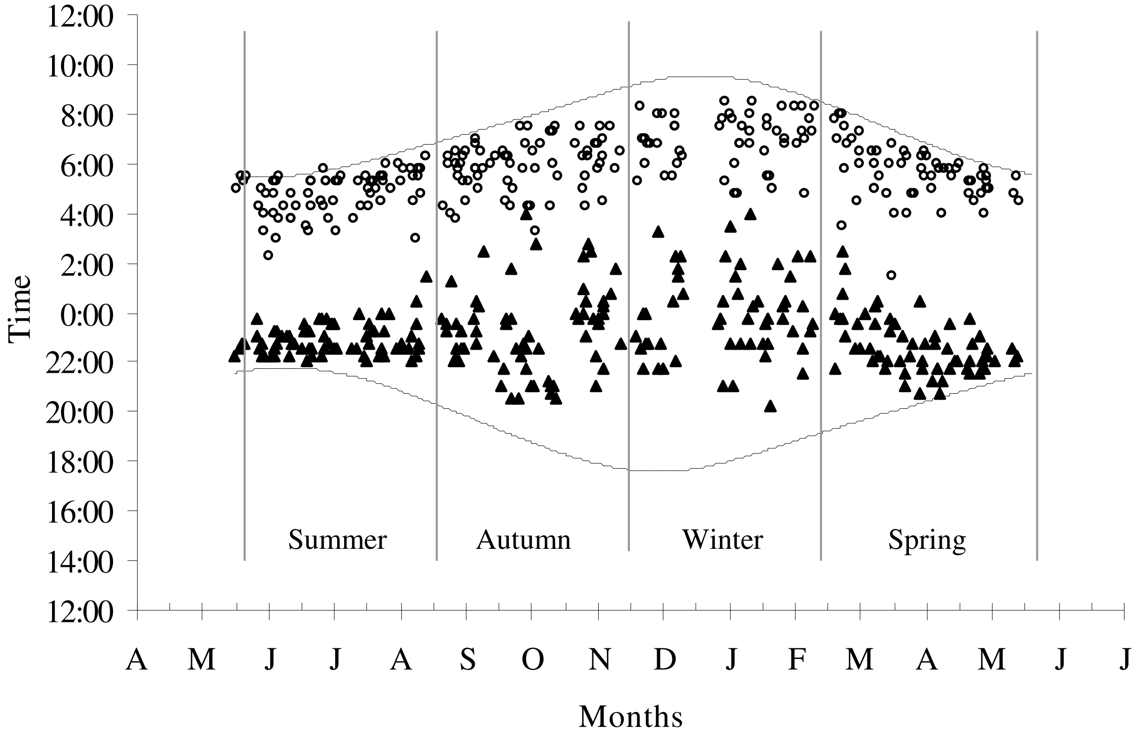

Fig. 4.1: Time (Central European Summer Time = CET + 1 h) of emergence (black triangles, N = 258) from the daytime den and return (open circles, N = 255) to the same or another daytime den by 13 radio-collared stone martens at the start and end of their principal activity period, respectively. The lower line shows the time of sunset, the upper line the time of sunrise. The area between the two lines represents night-time hours.

Table 4.1: Median time (Central European Summer Time) of first emergence from a den in the evening and final retreat into a den in the morning for both sexes separate and combined. N (emergence) = 258; N (return) = 255.

Season	**Emergence**			**Return**		
	F	**M**	**F+M**	**F**	**M**	**F+M**
su	2245	2215	2245	0445	0515	0500
au	2337	2230	2315	0545	0630	0600
wi	2337	0015	2345	0645	0815	0700
sp	2230	2200	2215	0530	0522	0545

differences in male and female emergence times (Mann-Whitney U test: W = 26218, $N_{males} = 63$, $N_{females} = 195$; $p = 0.060$), there was a trend for females to leave their dens later than males, apart from winter when males remained inside for longer (Table 4.1). Throughout the year males returned significantly later to their den sites than females (W = 22360, $N_{males} = 65$, $N_{females} = 189$; $p < 0.001$), although spring return times were similar for both sexes (Table 4.1).

Emergence times were more closely coupled to sunset in summer and spring than in autumn and winter (Fig. 4.1; Table 4.2). Although the same pattern was true for return times in relation to sunrise, it was much less pronounced. When considering only those nights where both emergence and return times were known (N = 243), it was found that in each season return times were coupled significantly closer to sunrise than emergence times were to sunset (Wilcoxon signed ranks test: (su) W = 1546.5; N = 67; $p < 0.05$; (au) W = 1894.0; N = 62; $p < 0.001$; (wi) w = 1300.0; N = 51; $p < 0.001$; (sp) W = 1503.0; N = 61; $p < 0.001$). This was most apparent in winter. Interestingly, there seemed to be a threshold at around 2100 h before which the martens hardly ever emerged from their den, even in late autumn and winter when sunset occurred much earlier. During the same period there was a threshold between 0800 h and 0830 h by which the martens had always returned to their dens, an hour before sunrise.

Principal activity period (PAP) and nightly activity (NA)

Even though night length varied from on average 8.4 h in summer to 15.0 h in winter, the martens did not adapt their PAP accordingly, although significant inter-individual differences in PAP were observed (univariate GLM: females - season: F = 0.38; d.f. = 3,12; $p = 0.767$; marten: F = 7.87; d.f. = 8,12; $p < 0.01$). During short summer nights, PAP was only about 1 h shorter than during the rest of the year where PAP remained fairly constant (Table 4.3). PAP was on average about 1 h longer for males than for females although in autumn, winter and spring there was overlap between male and female PAP values.

When considering NA (i.e., the actual time that martens were active during their PAP), significant seasonal differences became apparent for females (Table 4.4, season: F = 4.33; d.f. = 3,12; $p < 0.05$; marten: F = 16.69; d.f. = 8,12; $p < 0.001$). Females were active for significantly longer in summer than in winter (Table 4.5), though this was not

Table 4.2: Mean (± SD) time lag (h) from (a) sunset to the time of the first fix after emergence and (b) from the first fix back inside a den to sunrise. N (emergence) = 258; N (return) = 255.

Season	**Emergence after sunset**			**Return before sunrise**		
	F	**M**	**F+M**	**F**	**M**	**F+M**
su	1.6 ± 0.8	0.7 ± 0.3	1.4 ± 0.8	1.3 ± 0.8	0.4 ± 0.4	1.1 ± 0.8
au	4.6 ± 2.0	3.8 ±1.6	4.3 ± 1.9	2.3 ± 1.1	1.5 ± 0.8	2.0 ± 1.1
wi	5.9 ± 2.1	5.9 ± 1.5	5.9 ± 1.9	2.5 ± 1.1	1.6 ± 0.8	2.3 ± 1.1
sp	2.4 ± 1.6	1.7 ± 1.4	2.3 ± 1.6	1.5 ± 1.1	0.8 ± 0.5	1.4 ± 1.1

Table 4.3: Mean duration (h) of the principal activity period (PAP) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1 (12,7,5,-)[a]	5.6	4.9	5.8	
F2 (14,8,5,6)	4.5	4.2	4.1	6.0
F4 (9,7,6,11)	6.4	6.2	5.9	6.3
F6 (-,-,-,6)				6.3
F7 (4,5,5,-)	5.6	6.6	7.1	
F8 (5,-,-,-)	5.8			
F9 (-,7,7,8)		7.7	6.7	7.5
F10 (-,5,7,9)		7.7	7.6	7.5
F11 (-,-,5,9)			8.8	7.9
M1 (-,11,6,-)		7.2	6.8	
M2 (8,6,-,8)	6.8	7.2		7.8
M4 (8,7,6,-)	6.6	8.2	8.7	
mean ± SD				
females	5.6 ± 0.7	6.2 ± 1.4	6.6 ± 1.5	6.9 ± 0.8
males	6.7 ± 0.1	7.5 ± 0.6	7.8 ± 1.3	7.8

[a] number of nights considered for the su, au, wi and sp seasons, respectively

Table 4.4: Mean nightly activity (NA; h) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1 (12,7,5,-)[a]	4.3	4.2	3.6	
F2 (14,8,5,6)	4.0	3.4	3.2	5.0
F4 (9,7,6,11)	4.8	4.5	4.1	4.1
F6 (-,-,-,6)				5.7
F7 (4,5,5,-)	5.3	4.0	3.6	
F8 (5,-,-,-)	5.4			
F9 (-,7,7,8)		6.1	5.7	5.7
F10 (-,5,7,9)		7.0	6.6	7.0
F11 (-,-,5,9)			6.0	7.1
M1 (-,11,6,-)		5.2	5.2	
M2 (8,6,-,8)	6.7	5.9		6.8
M4 (8,7,6,-)	6.1	6.5	6.6	
mean ± SD				
females	4.8 ± 0.6	4.9 ± 1.4	4.7 ± 1.4	5.8 ± 1.2
males	6.4 ± 0.4	5.9 ± 0.7	5.9 ± 1.1	6.8

[a] number of nights considered for the su, au, wi and sp seasons, respectively

Table 4.5: Significant results for post hoc multiple comparisons (Tukey test) of seasonal activity and movement variables in female stone martens.

Variable	**Seasons**	**T statistic**	**p value**
NA	su-wi	3.16	< 0.05
NDM	sp-au	3.54	< 0.05
	sp-wi	4.30	< 0.01
speed	sp-au	3.42	< 0.05
	sp-wi	3.68	< 0.05
NR	sp-wi	2.98	< 0.05
NR/SR	su-au	3.65	< 0.05
	su-wi	4.64	< 0.01
	sp-wi	3.70	< 0.05

obvious from the overall seasonal mean activity values (Table 4.4). This was mostly due to F10 and F11, who exhibited generally higher activity in winter than the rest of the females but for whom summer data were missing. Male activity duration seemed to remain fairly constant across seasons and males were on average about 1 h longer active than females (Table 4.4). However, there was overlap between individual male and female NA values.

There was no overall correlation between NA and nightly temperature (Pearson product-moment correlation: $r = 0.056$; $N = 232$; $p = 0.397$). However, when seasons were considered separately, significant positive correlations were found between nightly temperature and NA in winter ($r = 0.313$; $N = 41$; $p < 0.05$) and spring ($r = 0.331$; $N = 59$; $p < 0.05$) but not in summer ($r = 0.010$; $N = 68$; $p = 0.933$) or autumn ($r = 0.072$; $N = 63$; $p = 0.574$). For each 1°C decrease in temperature martens reduced their activity by on average 7 min in winter and 12 min in spring (Fig. 4.2).

Activity rhythms

Nocturnal activity rhythms for combined sexes showed striking differences from season to season (Fig. 4.3). Summer was characterised by a rather abrupt start and end of activity outside the den with high levels above 60% throughout most of the night (2300-0400 h). In autumn, the onset of activity outside the den started a little earlier but increased more slowly than in summer. A peak of 80% activity was only reached relatively late at around 0300 h. Activity subsided gradually thereafter. In winter, the observed pattern of activity was superficially similar in shape to the one in autumn. However, there was an overall shift of activity towards the later hours of the night. A first small peak occurred around midnight at about 50%, followed by a second and higher peak four hours later (0400 h) at 72%. In the early morning hours the remaining activity outside the den ceased abruptly at 0700 h. Throughout the night the martens spent a significant proportion of their time either inside their daytime den or outside but being inactive. The spring pattern was overall similar to the summer pattern, with a more or less bell shaped appearance. By comparison with winter there was a shift of peak activity back to the more central parts of the night, with high levels being maintained throughout most of the night. At both ends of the night, activity increased and decreased less abruptly than in summer. The observed differences in nocturnal

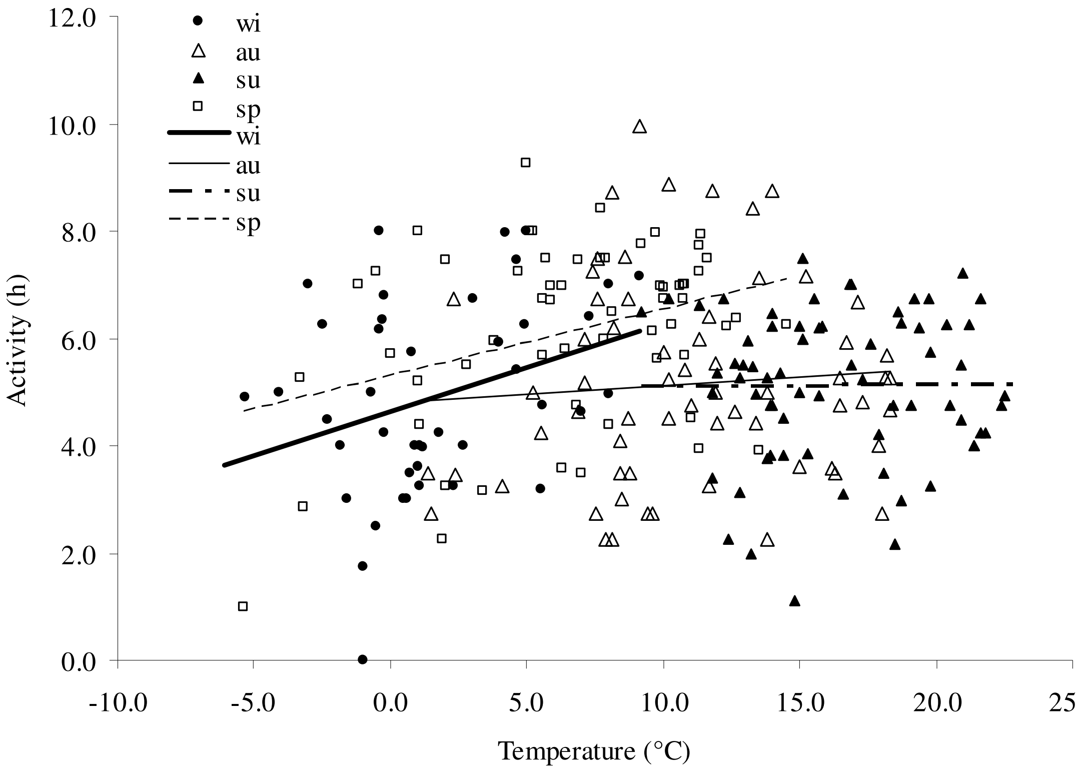

Fig. 4.2: Duration of nightly activity (NA) in relation to mean nightly temperature for 13 stone martens in four seasons. Pearson product-moment correlations: wi, sp ($p < 0.05$); su, au (n.s.).

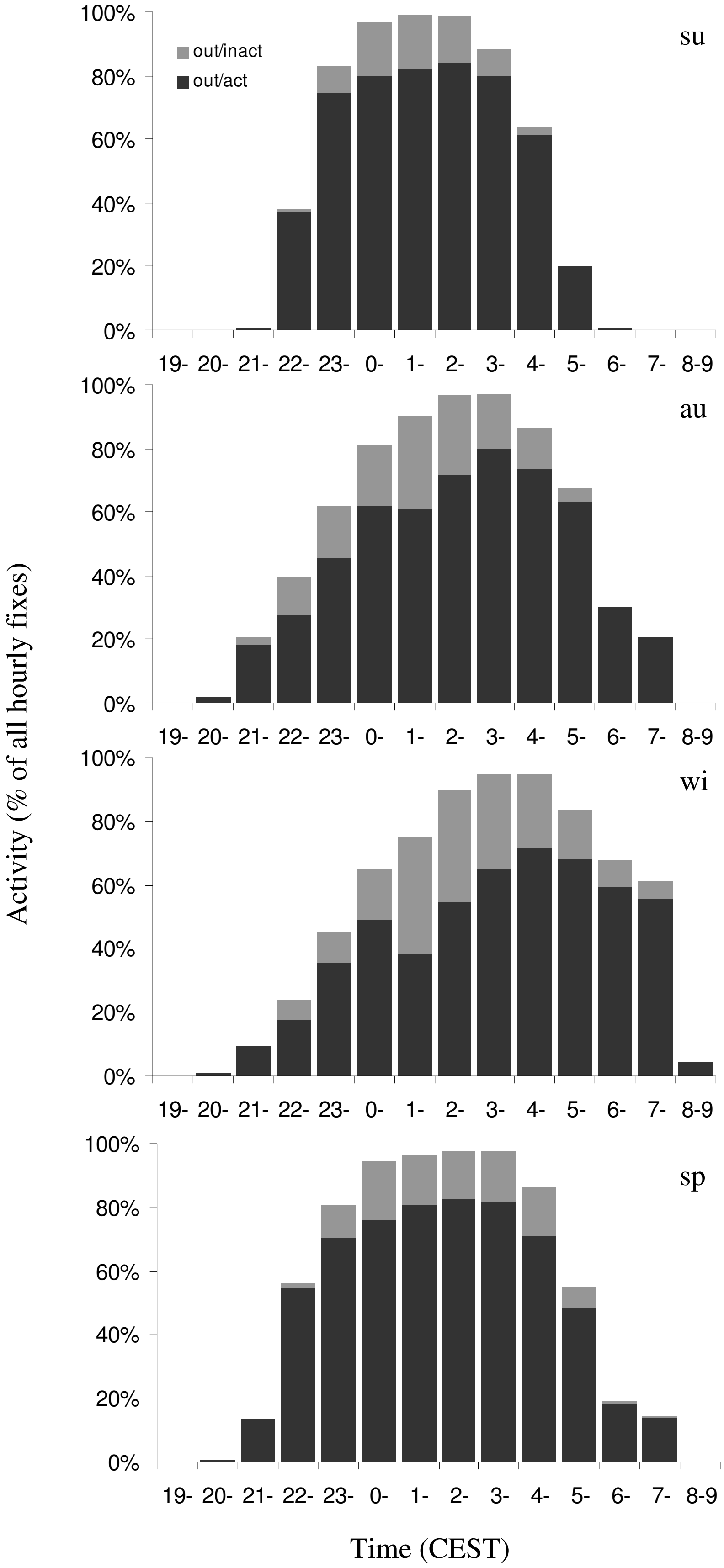

Fig. 4.3: Seasonal activity rhythms for 13 stone martens (male and females combined) in the towns of Bettembourg and Dudelange. out/inact: inactive during PAP; out/act: active during PAP.

activity rhythms in different seasons were also found to be statistically different (Table 4.6).

When considering male and female activity patterns separately (Fig. 4.4), there were striking similarities in overall appearance between the two sexes within any one season. This was especially true for both summer and spring (spring: most data came from only one male, M2) where no statistical differences were found (Table 4.6). However, male and female activity differed significantly from each other in autumn and winter (Table 4.6). Pairwise comparisons of hours revealed that this resulted mostly from differences in the early and late hours of the night. Thus, in autumn, male activity was higher than female activity from 2200 h to 0000 h and from 0500 h to 0700 h (Z-tests: $p < 0.05$), with hours from 0100 h to 0400 showing no differences. In winter, female activity was found to be higher early in the night (2200-2300 h; $p < 0.05$), while male activity was higher at the end of the night (0500-0800 h; $p < 0.05$). Again, the central parts of the night were similar for both sexes. Here it was particularly striking how rapidly male activity dropped after 0700 h.

4.3.2. Movement patterns

Nightly movement distance (NMD)

The longest recorded NMDs were observed on two spring nights for F10 and F11 with 10.0 and 10.1 km, respectively, and on a summer night for M2 with 10.1 km. Female martens moved on average between 1.08 and 8.33 km per night depending on the season (Table 4.7). Overall, both factors, season and marten, were found to have a significant effect on female NMD (season: $F = 7.23$; d.f. = 3,12; $p < 0.01$; marten: $F = 4.80$; d.f. = 8,12; $p < 0.01$). NMD was found to be significantly higher in spring than in autumn and winter (Table 4.5), while the other seasons did not differ from each other. The most pronounced seasonal effects were observed in F10 and F11, who drastically increased their mean NMD from winter to spring (Table 4.7, Fig. 4.5). Interestingly, their spring NMDs were higher than any seasonal mean NMD recorded for individual males (Table 4.7), although only one male was tracked in spring. However, males had on average higher seasonal NMDs than females, a trend that was most pronounced in summer. Males moved on average larger distances in spring and summer than in autumn and winter (Table 4.7).

Table 4.6: Chi-square tests to compare nocturnal patterns of hourly activity rates (proportion of outside/active fixes) between different seasons (sexes combined) and between sexes within seasons.

	Time	χ^2	**d.f.**	**p value**
Interseasonal				
su-au	2100-0700	103.195	10	<0.001
su-wi	2100-0700	200.773	10	<0.001
su-sp	2100-0700	52.356	10	<0.001
au-wi	2100-0700	42.082	10	<0.001
au-sp	2100-0700	22.516	10	<0.001
wi-sp	2100-0700	104.125	10	<0.001
Intersexual				
su	2200-0500	8.513	7	0.290
au	2100-0700	23.423	10	<0.001
wi	2100-0800	22.540	11	<0.05
sp	2100-0700	7.426	10	0.685

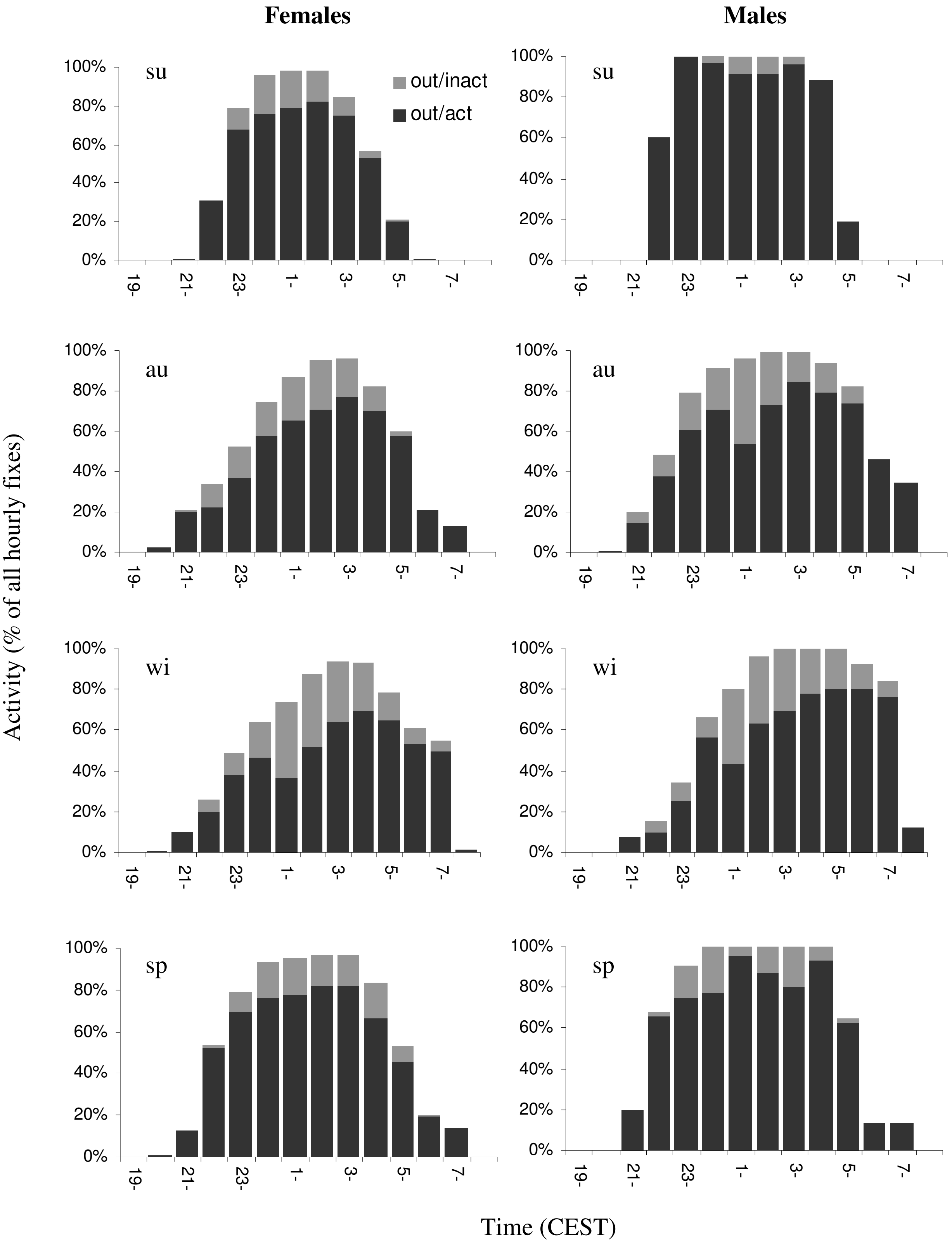

Fig. 4.4: Seasonal activity rhythms for male and female stone martens in the towns of Bettembourg and Dudelange. out/inact: inactive during PAP; out/act: active during PAP.

Table 4.7: Mean nightly movement distance (NMD; km) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1 (13,8,6,-)[a]	3.19	1.84	1.89	
F2 (14,8,6,8)	2.27	1.24	0.72	2.55
F4 (9,8,6,12)	2.48	2.08	1.93	2.19
F6 (-,-,-,6)				3.33
F7 (4,7,6,-)	1.70	1.33	1.08	
F8 (5,-,-,-)	1.57			
F9 (-,7,7,8)		2.10	2.57	3.84
F10 (-,7,7,9)		3.61	3.09	8.33
F11 (-,-,7,9)			3.39	7.89
M1 (-,12,6,-)		3.81	3.48	
M2 (8,7,-,9)	7.78	3.14		6.54
M4 (8,7,7,-)	7.19	3.55	5.49	
mean ± SD				
females	2.24 ± 0.65	2.03 ± 0.85	2.10 ± 0.99	4.69 ± 2.72
males	7.48 ± 0.42	3.50 ± 0.34	4.49 ± 1.42	6.54

[a] number of nights considered for the su, au, wi and sp seasons, respectively

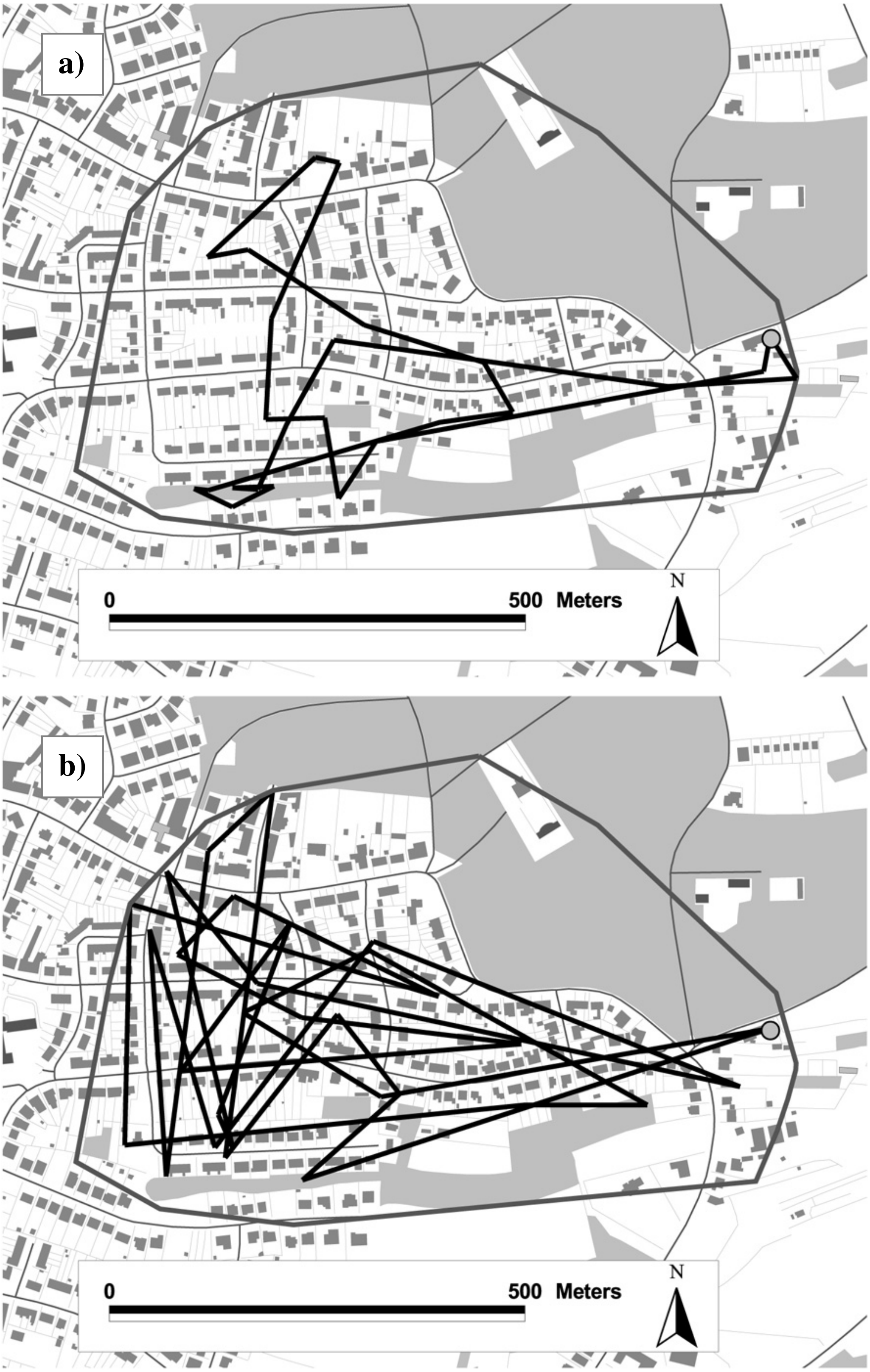

Fig. 4.5: Examples of typical movement paths for female F11 in the town of Dudelange in (a) winter (3.1 km) and (b) spring (8.8 km). Grey polygon: MCP95 home range; grey dot: den site where nights started and ended.

Speed

The speeds at which female martens moved varied significantly depending on season (season: F = 6.19; d.f. = 3,12; $p < 0.01$; marten: F = 3.33; d.f. = 8,12; $p < 0.05$). They moved faster in spring than in autumn and winter (Table 4.5). This was particularly pronounced in F10 and F11 who, in spring, effectively doubled the speeds at which they travelled while they were active (Table 4.8). Males also generally moved at greater speeds in spring and summer than in autumn and winter. In summer the two males moved on average 2.4 times faster than the females (Table 4.8).

Nightly range (NR)

The areas that female martens covered each night during their activities were significantly influenced by season, although a significant proportion of the observed variation was also due to inter-individual differences (season: F = 4.91; d.f. = 3,12; $p < 0.05$; marten: F = 19.19; d.f. = 8,12; $p < 0.001$). Spring NR was significantly larger than winter NR (Table 4.5), while other seasons did not differ significantly from each other. Across all seasons, males covered on average two to three times larger areas per night than females did (Table 4.9). The males M2 and M3 greatly reduced their NR from summer to autumn.

The animals covered each night on average between 14.9 and 72.3% of their MCP95 seasonal home ranges (Table 4.9). In females, NR/SR was significantly affected by season and marten (season: F = 10.14; d.f. = 3,12; $p < 0.01$; marten: F = 6.35; d.f. = 8,12; $p < 0.01$). Females used larger proportions of their seasonal range in summer than in autumn and winter, and in spring they used larger proportions than in winter (Table 4.5). Males showed a similar trend and in any given season both sexes used on average very similar proportions of their seasonal home ranges (Table 4.10).

4.4. Discussion

4.4.1. Activity patterns

This study has clearly demonstrated the stone marten’s distinctly nocturnal lifestyle. All other studies that have radio tracked this species have come to the same general conclusion, irrespective of the environment that the animals lived in (e.g., Broekhuizen 1983; Herrmann 2004; Lachat Feller 1993b; Posillico *et al.* 1995; Skirnisson 1986).

Table 4.8: Movement speed (km·h^{-1}) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1 (12,7,5,-)[a]	0.73	0.48	0.46	
F2 (14,8,4,5)	0.56	0.37	0.26	0.46
F4 (9,7,6,11)	0.52	0.41	0.48	0.57
F6 (-,-,-,6)				0.59
F7 (4,5,5,-)	0.32	0.26	0.29	
F8 (5,-,-,-)	0.29			
F9 (-,7,7,8)		0.34	0.46	0.53
F10 (-,5,7,9)		0.48	0.47	1.18
F11 (-,-,5,9)			0.59	1.09
M1 (-,11,6,-)		0.68	0.66	
M2 (8,6,-,8)	1.16	0.50		0.98
M4 (8,7,6,-)	1.18	0.55	0.87	
mean ± SD				
females	0.48 ± 0.18	0.39 ± 0.09	0.43 ± 0.12	0.74 ± 0.31
males	1.17 ± 0.01	0.58 ± 0.09	0.77 ± 0.15	0.98

[a] number of nights considered for the su, au, wi and sp seasons, respectively

Table 4.9: Mean nightly ranges (NR; ha) for 12 stone martens expressed as 100 % MCPs.

Marten	**su**	**au**	**wi**	**sp**
F1 (13,8,6,-)[a]	25.7	18.4	15.4	
F2 (14,8,6,8)	11.0	7.6	3.1	10.1
F4 (9,8,6,12)	15.5	11.7	10.4	11.6
F6 (-,-,-,6)				11.2
F7 (5,7,6,-)	3.2	2.6	2.2	
F8 (5,-,-,-)	3.7			
F9 (-,7,7,8)		13.3	16.0	21.2
F10 (-,7,7,9)		25.3	22.7	38.2
F11 (-,-,7,9)			24.6	24.5
M1 (-,12,6,-)		42.6	38.67	
M2 (8,7,-,9)	36.0	27.0		42.3
M4 (8,7,7,-)	53.3	39.7	53.9	
mean ± SD				
females	11.8 ± 9.3	13.2 ± 8.0	13.5 ± 8.8	19.5 ± 10.9
males	44.6 ± 12.2	36.4 ± 8.3	46.3 ± 10.8	42.3

[a] number of nights considered for the su, au, wi and sp seasons, respectively

Table 4.10: Mean nightly range as percentage of the MCP95 (see Chapter 3) seasonal home range (NR/SR) for 12 stone martens.

Marten	su	au	wi	sp
F1	48.0	34.4	28.7	
F2	52.7	36.4	14.9	48.5
F4	63.6	48.2	42.7	47.9
F6				75.9
F7	72.3	57.1	49.0	
F8	35.3			
F9		42.0	50.5	67.0
F10		47.3	42.5	71.4
F11			67.1	66.6
M1		50.0	45.3	
M2	56.4	42.3		66.2
M4	55.8	41.6	56.5	
mean ± SD				
females	54.4 ± 14.3	44.2 ± 8.2	42.2 ± 16.6	62.9 ± 11.9
males	56.1 ± 0.4	44.6 ± 4.7	50.9 ± 7.2	66.2

Nevertheless, the degree to which stone martens restrict their activities to nighttime hours seems to be more pronounced in this study than what has been reported elsewhere. In a Dutch rural area, emergence and return times were very closely coupled to sunset and sunrise, respectively, throughout the year (Broekhuizen 1983: see Fig. 4.6). The same pattern was observed by Skirnisson (1986) in a forest-dwelling female marten. In both of these studies the martens emerged earlier and returned later as the nights became longer. Furthermore, during summer they often emerged before sunset and retreated into their dens after sunrise (Broekhuizen 1983; Skirnisson 1986). The fact that the urban stone martens never emerged before sunset in summer and delayed the onset of their activity in autumn and winter until after 2100 h (2000 h CET - winter time) suggests that these animals strongly avoided human activities. In fact, road and pedestrian traffic had considerably slowed by 2100 h. Similarly, the observed return threshold at around 0800 h (0700 h winter time), as well as the sharp drop from very high male activity levels to very low levels between 0700 h and 0800 h in winter, coincided with the start of the morning rush hour (from 0700 h to 0800 h winter time). Skirnisson (1986) tracked a village-dwelling female that always returned to the den before 0600 h when farming activities started at the farm where she was denning and Herrmann (2004) reported a female that delayed the onset of her movements until after farming activities had ceased after 2000 h. In principle, the late emergence times of martens in my study could be a result of martens not needing to be active so long in urban areas owing to higher food abundance. However, this explanation is unlikely since, as I point out below, it is only the timing of activity onset and cessation that differs between rural and urban environments, not so much the total duration of the activity period.

The activity rhythms of urban martens showed a general pattern of high activity throughout the night in summer and spring with generally lower levels in autumn and winter. This general pattern mirrors the one observed in rural and village-dwelling martens (Lachat Feller 1993b; Skirnisson 1986). Temperature seems to be an important factor regulating the martens’ activity, especially during the colder seasons. Curtailing of activity with decreasing temperatures has also been observed elsewhere in stone martens (Herrmann 2004; Lachat Feller 1993b; Skirnisson 1986) and pine martens (Zalewski 2000). Interestingly, urban martens responded very similarly to each 1 °C-

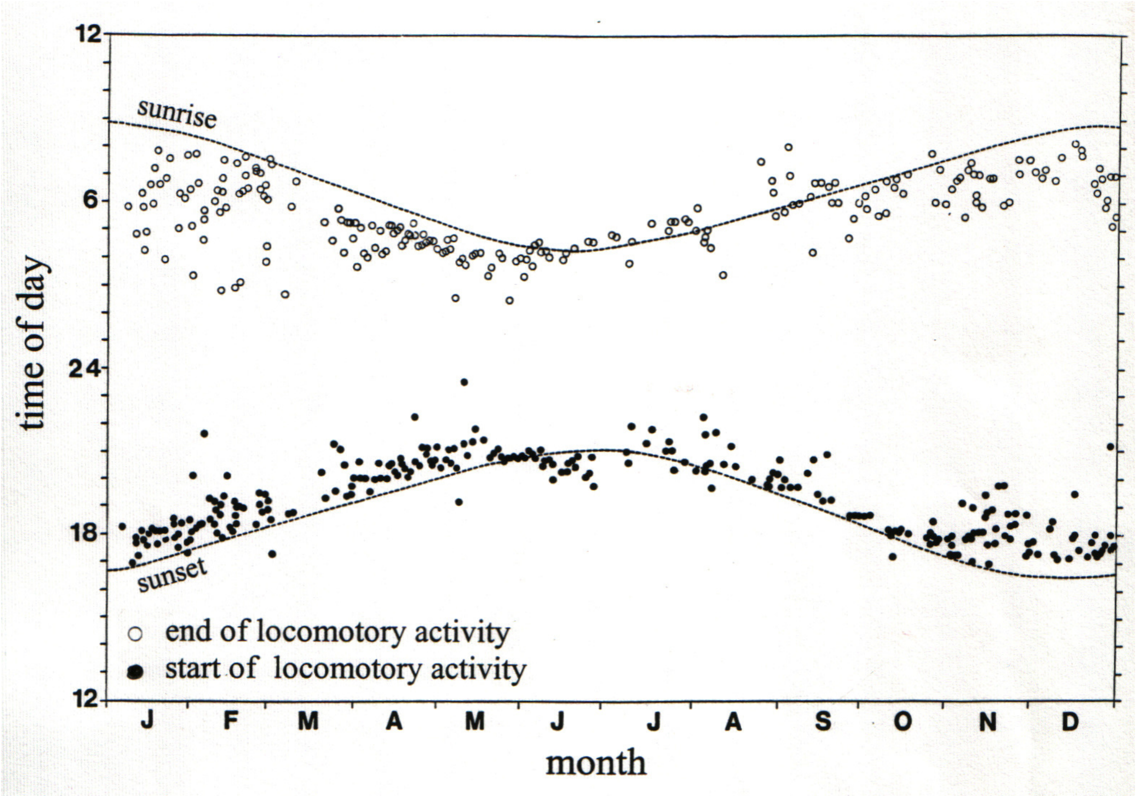

Fig. 4.6: From Broekhuizen (1983) – "Fig. 3 – p.617: Times of day of start (black dots) and end (open circles) of nocturnal movements of radio-tracked beech [stone] martens. The lower broken curve gives the time of sunset, the upper broken curve gives the time of sunrise."

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decrease in temperature as did forest and village martens (Herrmann 2004; Skirnisson 1986).

The general decrease in activity in autumn and winter was associated here with a shift of peak outside-the-den activity towards later parts of the night. This, however, has not been seen in rural martens (Genovesi 1993; Herrmann 2004; Skirnisson 1986). Herrmann (2004) observed a similar pattern for village martens on weekends in winter and summer. This suggests that during short nights the martens used the entire dark period for their activities, but within longer nights they preferentially used the later hours of the night with the least human disturbance. Thus activity rhythms, as well as emergence and return times, of urban stone martens suggest that behavioural adaptation to human activities occurs primarily by temporal avoidance rather than tolerance.

In Switzerland, activity duration (male and female combined; 5.1 - 6.9 h) was similar to that of females in the present study, while in Germany activity (6.2 - 8.2 h) was generally slightly higher than in urban martens, apart from spring (5.6 h) where urban martens were active longer. However, owing to a different methodology, they included both inside the den as well as outside activity in their estimates. One can hence assume that, in these studies, the activity, which I defined as NA (i.e., activity occurring between emergence and return), was actually similar or even lower than in the urban environment considered here. In the Netherlands, rural martens were, however, found to be active outside the den for on average around 8 h per night irrespective of season and sex (Broekhuizen 1983), which was similar to urban males and 1 - 2 h longer than urban females. However, it was not directly clear whether activity levels referred to by Broekhuizen (1983) were PAP or NA.

4.4.2. Mobility

Few studies have collected detailed movement data on stone martens, and when these are available they are often based on very few animals. However, Genovesi *et al.* (1997) reported NMDs for 16 forest and rural martens. Females moved on average 1.45 km and males 5.32 km in all seasons combined. They found no significant seasonal changes. Interestingly these martens had much larger territories (males: 421 ± 231 ha, females: 217 ± 134 ha) than in the present study (see Chapter 3), yet urban females moved much longer distances, especially in spring. Male distances were similar in both environments. Similarly, urban martens of both sexes moved longer distances than rural martens with comparable territory sizes did in Switzerland (Lachat Feller 1993b). On the other hand, Skirnisson's (1986) forest female moved further (5.9 km for 200 ha) in autumn and winter and similar distances in spring and summer to any of the urban martens. A village female moved further (3.3 km for 63-111 ha) in autumn/winter than most urban females, while a forest male moved similar distances in spring and summer (6.9 - 9.5 km for 292 ha) but further in winter (6.6 km) than urban males. Although some of these data are conflicting, the available evidence suggests overall that the urban martens may have moved generally larger distances in relation to their home range size, especially in spring and summer, than forest and rural martens elsewhere.

The observed seasonal variation in nightly activity and in the various movement parameters always revealed the same general pattern insofar as spring and summer were the most active periods. In males the evidence suggested that their peak mobility occurred in summer, although spring data were only available for M2. This is in line with other studies that have found male mustelids to be most active and mobile during the mating season (Jędrzejewski *et al.* 2000; Zalewski *et al.* 2004). The crucial period for females seemed to be spring, when they moved the longest distances at the highest speeds, covering the largest areas and the largest proportions of their seasonal home ranges. There was a very clear change in behaviour from winter to spring, while other season transitions were less pronounced. Thus, the seasonal peak in female mobility did not occur during the mating season in summer as has been described for pine martens (Zalewski *et al.* 2004), but during spring when they usually give birth and rear their young . Incidentally the female (F10) with the highest spring mobility values was also the only one that actually reared young during the study period (see Chapter 3, Table 3.10). Nonetheless, these high movement values may not be solely related to the rearing and provisioning of young, since F11 showed similar movement patterns in terms of NMD, speed and NR/SR. Both females, however, showed very strong territorial behaviour in that they systematically patrolled parked cars and were frequently seen marking them with urine (see Chapter 6). The fact that females covered by far the largest proportions of their home ranges in both spring and summer also testifies to high territoriality during this period.

4.4.3. Conclusion

The martens in both towns showed some clear evidence of behavioural adaptation to human activity in urban environments. Although they lived in very close association with humans they remained wary of them and shifted their activity such as to reduce potential contact rates with humans. This can be seen in their more pronounced nocturnal lifestyle, their late emergence from dens in winter when nights were longest, and their return to their dens before traffic picked up in the mornings. Furthermore, they shifted their peak activity to the later parts of the night when human activity was at its lowest.

Although urban habitat is generally seen as a more resource rich environment (Adams *et al.* 2006), and territories here are generally smaller, I did not observe martens to show greatly reduced activity and mobility rates as was predicted. On the contrary, there was some evidence that they may have been on average at least as active and mobile as their forest or rural counterparts. Spring especially seemed to be a time when females were highly mobile. This may have been due to the relatively high population density in this environment (see Chapter 3), which would lead females to be particularly territorial. Furthermore, the observations that martens scent mark cars (see Chapter 6) suggest that they may often come into contact with strange marten scent via cars that are moved between territories. Seiler *et al.* (1994) showed a male stone marten to increase his activity around experimentally introduced faecal scent marks. Thus, strange scent on cars may lead to the perception of a much higher intruder pressure in urban than in non-urban systems, ultimately stimulating the observed high incidence of territorial behaviour (see Chapter 6 for further discussion).

Chapter 5: Den Selection and Patterns of Use

5.1. Introduction

Stone martens are strictly nocturnal (see Chapter 4) and usually spend the entire day hidden away inside a den. While they den to a certain extent in vegetation and other natural features (Genovesi and Boitani 1997; Herrmann 2004; Skirnisson 1986), they also frequently rely on anthropogenic structures, especially in rural areas and small villages (e.g., Herrmann 2004; Lachat Feller 1993a; Skirnisson 1986). This sets them apart from most other marten species, which rarely den in buildings (but see Birks *et al.* 2005). Apart from low disturbance and protection against predators, good insulation seems to be a particularly important factor in making a structure suitable for denning. In rural areas, stone martens often find such conditions in straw and hay stacks in barns (Herrmann 2004; Lachat Feller 1993a; Michelat 2001). In urban areas where barns are usually absent, stone martens have a reputation for using attics and roof spaces of buildings that are at the same time inhabited by humans. Conflicts can then arise due to persistent noise (especially when young are reared), odours or staining resulting from their faeces and urine, or damage done to the roof insulation (personal observation; Ludwig 1999). Similar problems have been described for other urban mammals such as grey squirrels, raccoons and brushtail possums (see also Chapter 7; Adams *et al.* 2004; O'Donnell and DeNicola 2006; Pietsch 1994). Although this aspect of the stone marten's denning behaviour is widely known at an anecdotal level, few studies have attempted to quantify the extent to which martens rely on such buildings for denning purposes in urban areas (e.g., Müskens and Broekhuizen 2005).

The aims of this study were to quantify the relative importance of inhabited buildings and other non-inhabited structures to the stone marten's denning ecology in urban areas. I predicted a higher reliance on inhabited buildings and a lower reliance on natural den sites than in more rural areas. I also studied patterns of den use to investigate the extent to which this may influence the potential for marten-human conflict.

5.2. Methods

The general telemetry procedures for locating martens in their dens (section 2.5.3.), as well as details of sample sizes (Table 2.3) and den classification (Table 2.4), were outlined in Chapter 2.

5.2.1. Den selection

For this analysis, all diurnal fixes were pooled and analysed according to season, sex and den type, irrespective of the marten they originated from. I included data from all individuals, including F3, F6 and F8 that were located considerably less often than the other martens (Table 2.3).

5.2.2. Den use patterns

Several studies that have investigated den use patterns have employed a den reuse index based on the ratio between the number of different den sites identified and the total number of locations (e.g., Baghli and Verhagen 2005; Hadidian *et al.* 1991; Zalewski 1997a). This index is greatly dependent on how often the animal was located in its den and seems to be of limited value when applied to animals that only use a very limited set of den sites. Hence I did not use this index but instead used two separate measures to characterise the pattern of den use by the martens.

i) A monthly den-shift index (DSI) derived from O'Donnell and DeNicola (2006):

$$DSI = S / PS,$$

where S is the number of detected day-to-day den shifts and PS the maximum number of possible day-to-day shifts if the marten had shifted dens each time it was located on consecutive days. The index varies from 1 to 0, such that a marten that never returned to the previous day's den has a DSI of 1 and one that never shifted between dens has a DSI of 0. DSI was calculated for each month separately and a seasonal DSI was calculated as the mean of the monthly DSIs making up each season. DSI is not dependent on the number of different dens that were used during a given period. No DSI was calculated for those marten-month combinations where less than 10 diurnal fixes were available, so F3 was completely excluded from this analysis.

ii) Biweekly den use (BDU; dens per 15 locations). This analysis quantified the number of different den sites in which a marten was located during the first 15 daytime fixes in each month. Subsequent fixes were discarded from the analysis. I only used 15 fixes to make it comparable with Skirnisson's (1986) data and to avoid having to resort to extrapolating the number of den sites from varying numbers of fixes as this would artificially inflate the number of dens. I made an exception for M1 and M2 for which only 14 diurnal fixes were available for August, and extrapolated their number of dens to 15 fixes. All other months where not enough data were available were discarded. F3 was completely excluded from the analysis. A seasonal BDU was calculated as the mean of the monthly BDUs making up each season. BDU did not take into account how often each individual den was used.

Although a marten that has a large BDU will also have an increased DSI, there does not have to be a correlation between these two measures. In fact, a marten that has a BDU of 2 (i.e., 2 dens per 15 days) could alternate between these 2 dens each day and have a DSI of 1 or could use the same den 7 days in a row, then shift to a second den and stay there for 8 days in a row, resulting in a DSI of 0.07.

5.2.3. Statistical analysis

Statistical analyses for den selection were only employed for comparisons of gross den categories (i.e., inhabited buildings, uninhabited buildings, buildings of unknown inhabitation status, other structures, natural and unidentified). I used chi-square tests to check for differences in den selection between different seasons and different sexes. DSI and BDU were tested for normality and homogeneity of variances. Depending on whether these assumptions were met or not, I tested for seasonal differences using a one-way ANOVA or a Kruskal-Wallis test, respectively. The significance level was always set at 0.05.

5.3. Results

5.3.1. Den selection

The vast majority of all identified den sites (95.7%; N = 141) and of denning events (99.5%; N = 2324) were located within the urban perimeter of both towns. Fifteen dens were located outside the animals' MCP95 home ranges (e.g., F2, M2, M4; Figs. 5.1 and 5.2).

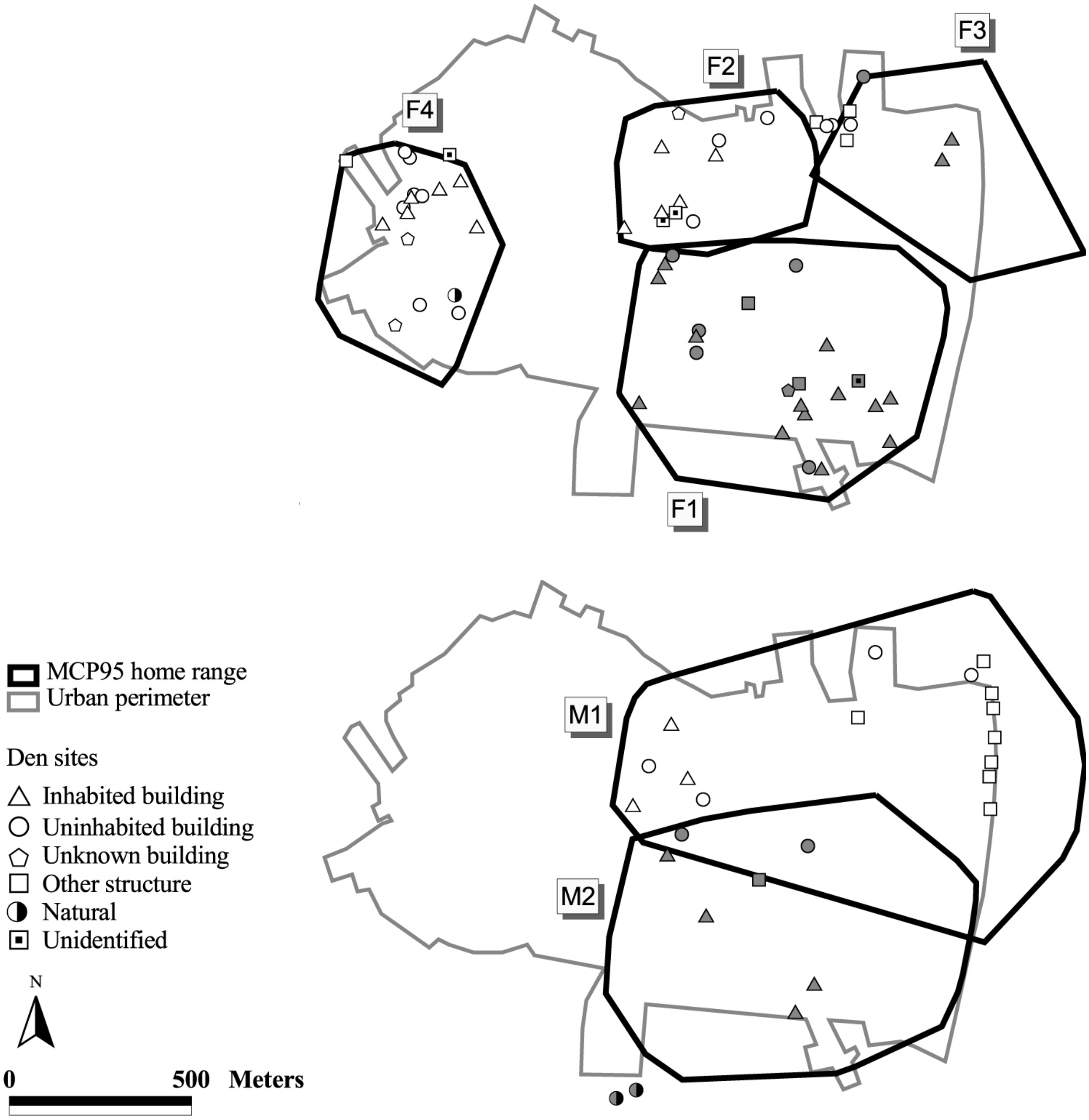

Fig. 5.1: Location and type of den sites of female (top) and male (bottom) stone martens in the town of Bettembourg.

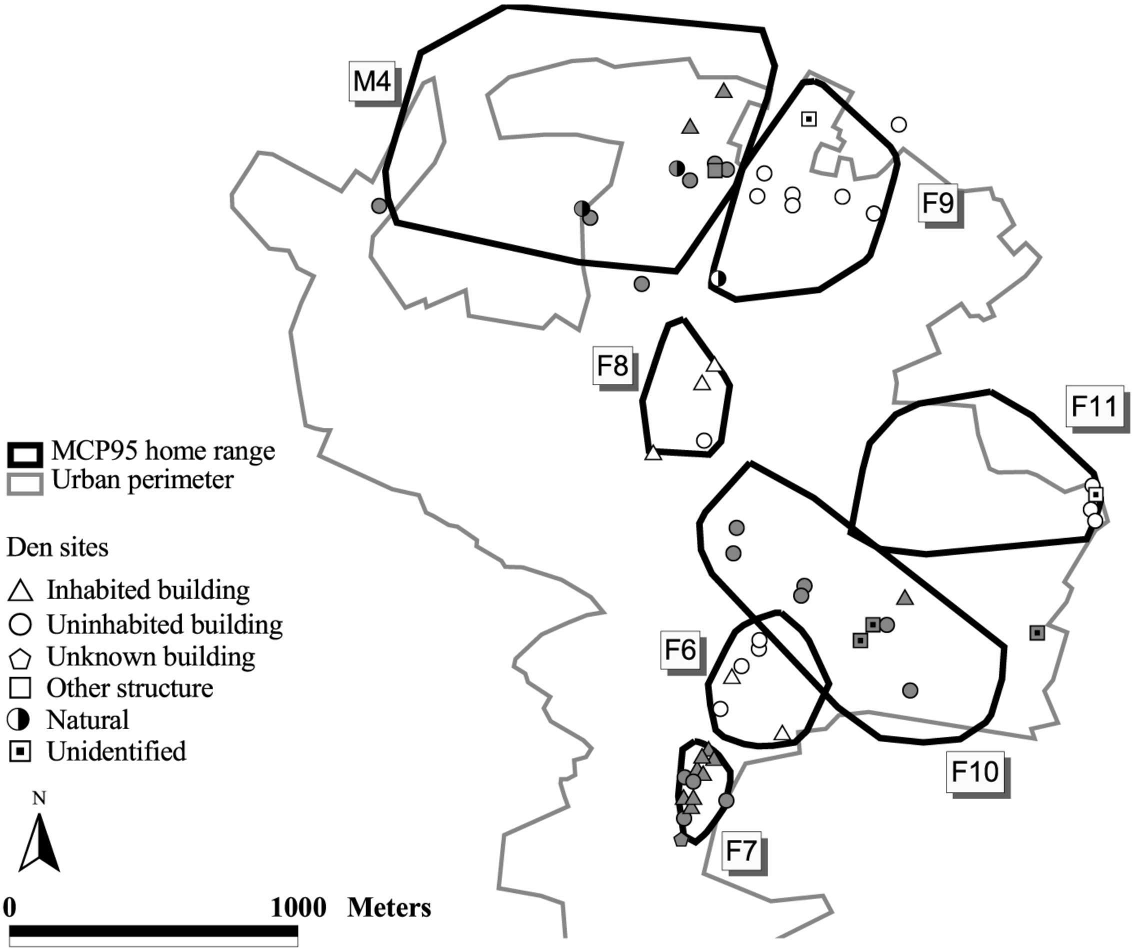

Fig. 5.2: Location and type of den sites of male and female stone martens in the town of Dudelange.

However, all of these were used only rarely. The martens denned on 98.5% of their days in anthropogenic structures and on only 0.6% of days in natural dens. Although a wide variety of den types were recorded, buildings were by far the most frequently used den sites with 97.1% use, while other anthropogenic structures were used on only 1.5% of days (Table 5.1).

Den selection was found to differ significantly between different seasons (Chi-square test: $\chi^2 = 182.176$; d.f. = 15; $p < 0.001$; Fig. 5.3). Due to the very limited use of den sites other than buildings I restricted further analyses of seasonal differences to the use of inhabited and uninhabited buildings. Martens used inhabited buildings significantly more often in winter than in any other season and they used them more often in autumn than in summer. Inhabited buildings were used in similar proportions in spring as in summer or autumn (Table 5.2; Fig. 5.3). Uninhabited buildings, on the other hand, were used significantly less frequently in winter than in other seasons and in autumn than in summer. Uninhabited buildings were used in similar proportions in spring as in autumn or in summer (Table 5.2; Fig. 5.3).

Male and female den selection differed significantly from each other ($\chi^2 = 99.581$; d.f. = 5; $p < 0.001$; Fig. 5.4). Males used inhabited buildings less often (Z-test: $Z = -6.56$; $p < 0.001$) and uninhabited buildings more often than females did ($Z = 7.09$; $p < 0.001$). Males also used other anthropogenic structures ($Z = 3.17$; $p < 0.01$) and natural den sites ($Z = 2.07$; $p < 0.05$) more often than females did.

The single most commonly used type of den was under the roof of inhabited family homes or apartment blocks followed by empty or ruined houses and garages (Table 5.1). Farm buildings (e.g., barns) were used on only about 5% of all days. On only one occasion did a marten (F1) spend the day inside the engine compartment of a car (which was not in use anymore). Furthermore, the martens never denned in trees or in underground burrows. However, some of the den sites classed as unidentified (0.9%) may have been natural den sites that, due to their location behind houses, were inaccessible for closer inspection at the time.

Table 5.1: Den selection (% fixes in different types of den site) by 13 stone martens in the towns of Bettembourg and Dudelange.

Den type	**su**	**au**	**wi**	**sp**	**tot**
family home, apartment block	26.5	35.0	49.6	30.8	36.0
business, public building	4.6	4.2	9.2	5.7	5.9
empty/ruined house	24.1	23.5	13.5	27.2	22.0
warehouse	3.3	3.5	7.7	0.0	2.1
garage	22.1	10.3	8.0	20.9	16.4
shed (wood and stone)	9.3	9.4	2.7	5.5	6.6
farm building (active and inactive)	2.2	7.9	5.8	4.7	5.4
other/unknown uninhabited building	0.0	0.3	0.3	0.0	0.2
building of unknown inhabitation status	1.1	1.5	2.2	4.9	2.5
total building	**93.2**	**95.6**	**99.0**	**99.7**	**97.1**
culvert	0.0	0.3	0.0	0.0	0.1
car	0.2	0.0	0.0	0.0	0.0[a]
noise protection wall along motorway	0.9	1.5	0.5	0.2	0.8
pile of steel girders	0.2	0.0	0.0	0.0	0.0[a]
firewood pile	0.9	0.0	0.0	0.0	0.2
other/unknown	1.3	0.2	0.2	0.0	0.3
total other anthropogenic structures	**3.5**	**2.0**	**0.7**	**0.2**	**1.4**
bramble	0.9	0.0	0.0	0.2	0.2
hedge row	0.0	0.0	0.0	0.0	0.0
tree	0.0	0.0	0.0	0.0	0.0
dense brush	1.3	0.3	0.0	0.0	0.3
underground animal burrow	0.0	0.0	0.0	0.0	0.0
total natural	**2.2**	**0.3**	**0.0**	**0.2**	**0.5**
unidentified den	1.3	2.0	0.3	0.0	0.9

[a] = 0.04

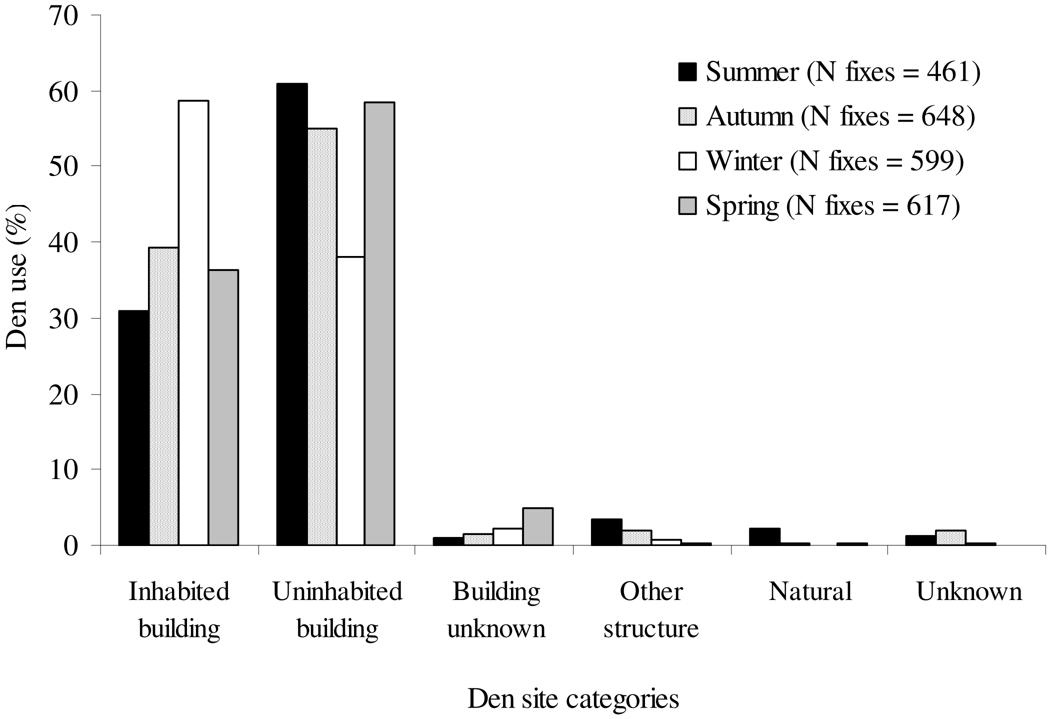

Fig. 5.3: Seasonal den selection of stone martens (sexes combined; N = 13) in urban environments.

Table 5.2: Z-tests to compare proportions of den use between different seasons.

Den type	**Seasons**	**Z statistic**	**p value**
Inhabited buildings	su-au	-2.84	< 0.01
	su-wi	-9.41	< 0.001
	su-sp	-1.88	0.060
	au-wi	-7.04	< 0.001
	au-sp	1.00	0.317
	wi-sp	7.98	< 0.001
Uninhabited buildings	su-au	2.01	< 0.05
	su-wi	7.59	< 0.001
	su-sp	0.86	0.387
	au-wi	6.06	< 0.001
	au-sp	-1.22	0.221
	wi-sp	-7.23	< 0.001

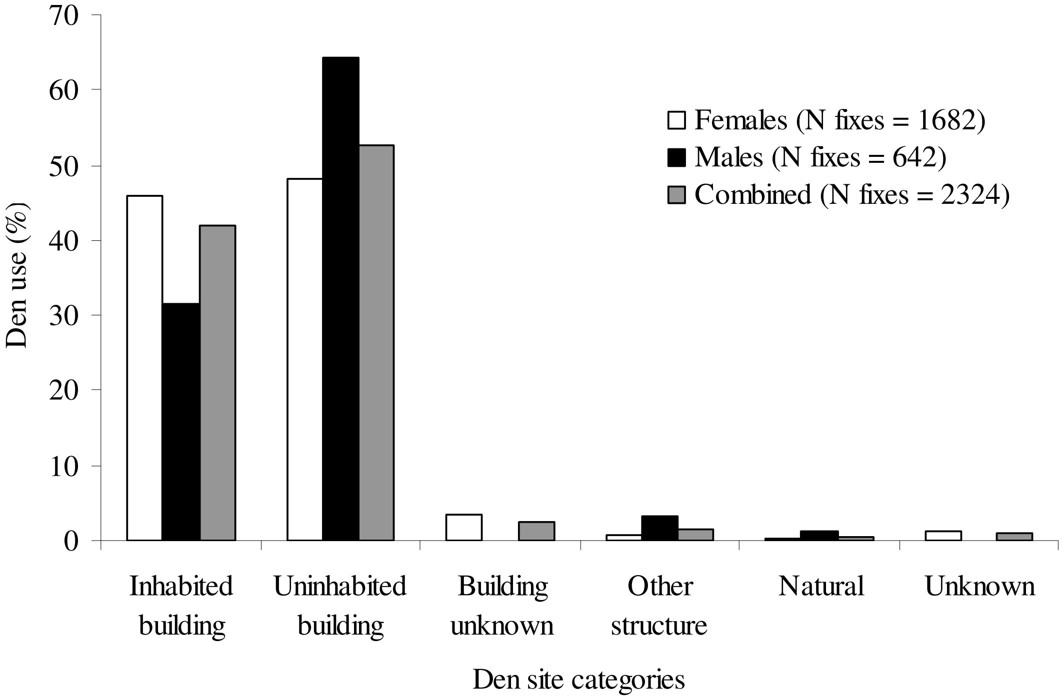

Fig. 5.4: Den selection (seasons combined) of male (N = 3) and female (N = 10) stone martens in urban environments.

5.3.2. Den use patterns

An average of 12.8 den sites were identified for each of those martens that were located more than 100 times (N = 10; Table 5.3). The number of identified den sites directly related to the number of diurnal fixes obtained for each animal (linear regression: $R^2 = 0.85$; $p < 0.001$; Fig. 5.5). Based on this regression equation, martens would be predicted to use around 20 den sites during a 12-month (365 days) period. However, for each marten only a limited number of den sites (mean: 2.7) accounted for over two thirds (or 66%) of all recorded den use with the most frequently used den accounting for between 20.5 and 89.9% of each individual's diurnal fixes (Table 5.3). All of the most commonly used dens were located in buildings, four of which were classified as inhabited (family homes and business). Interestingly, among these favoured sites, the inhabited ones were all used less frequently than the uninhabited ones (Table 5.3).

Mean monthly BDU was relatively constant, with martens using on average between 3 and 5 den sites for every 15 diurnal locations (Fig. 5.6; sexes combined). The highest recorded monthly BDU was 8 dens for F1 in April while the lowest was 1 den for the females F7, F10 and F11 in one or more months in spring. Mean seasonal BDU values overlapped considerably between males and females (Table 5.4) so the two sexes were pooled and analysed together. The number of den sites that the martens used per 15 locations did not differ significantly between different seasons (one-way ANOVA: F = 0.76; d.f. = 3, 32; p = 0.525).

Individual DSIs were highly variable, ranging from 0 (F10 and F11 - March) to 1 (M4 - August). Mean monthly DSI, however, was relatively constant and high throughout the year, fluctuating slightly between 0.55 and 0.70. DSI only dropped below 0.50 in March, which was mostly due to a low female DSI (Fig. 5.7). Three females never (F10; F11) or only rarely (F7; DSI = 0.13) shifted dens during this month. There was considerable overlap in seasonal DSI between males and females (Table 5.5), so data from the two sexes were pooled and analysed together. Although mean seasonal DSI was lower in spring than in the other three seasons (which were very similar; Table 5.5) no significant seasonal differences in DSI were found (Kruskal-Wallis test: H = 1.23; d.f. = 3; p = 0.747).

Table 5.3: Den use characteristics for martens that were located more than 100 times in their diurnal den sites.

Marten	Fixes	Total dens	Inhabited dens	Single use[a]	Top 66 %[b]	Top den (%)[c]	Top den (type)[d]
F1	312	22	13	5	4	20.5	inhabited house
F2	308	17	5	7	3	33.1	garage
F4	292	18	6	3	5	20.9	inhabited house
F7	192	13	8	2	3	28.6	inhabited house
F9	208	9	0	2	3	39.9	barn
F10	210	10	1	4	1	66.7	ruined building
F11	109	4	0	2	1	89.9	garage
M1	289	15	3	5	2	44.3	garage
M2	165	9	4	3	2	58.2	empty house
M4	188	11	2	4	3	26.6	business
Mean ± SD	227 ± 69	12.8 ± 5.3	4.2 ± 4.0	3.7 ± 1.6	2.7 ± 1.3	42.9 ± 22.5	

[a] number of dens that were used only once
[b] number of most commonly used dens making up at least 66 % (two thirds) of all recorded uses
[c] % use of the most commonly used den
[d] description of the most commonly used den

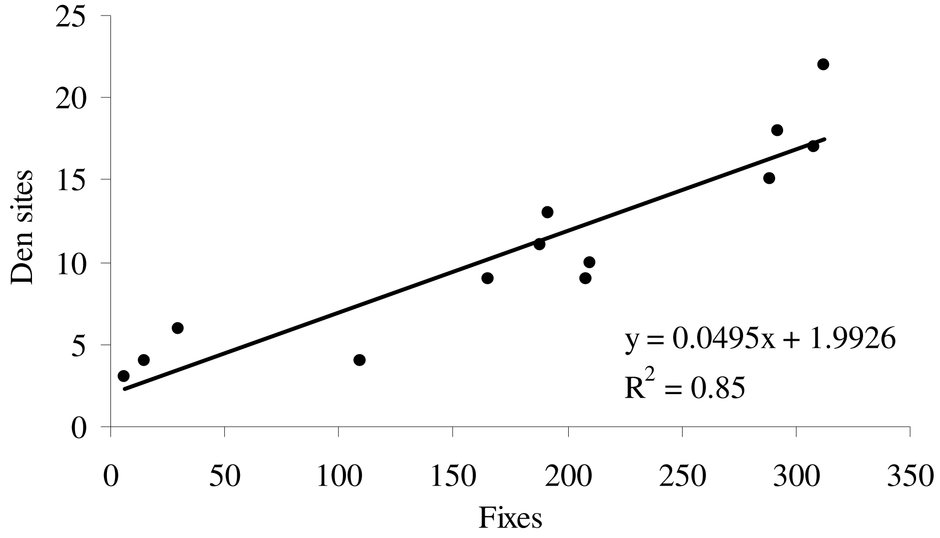

Fig. 5.5: Relationship between the number of diurnal fixes (x) and the number of den sites (y) identified for each marten (N = 13).

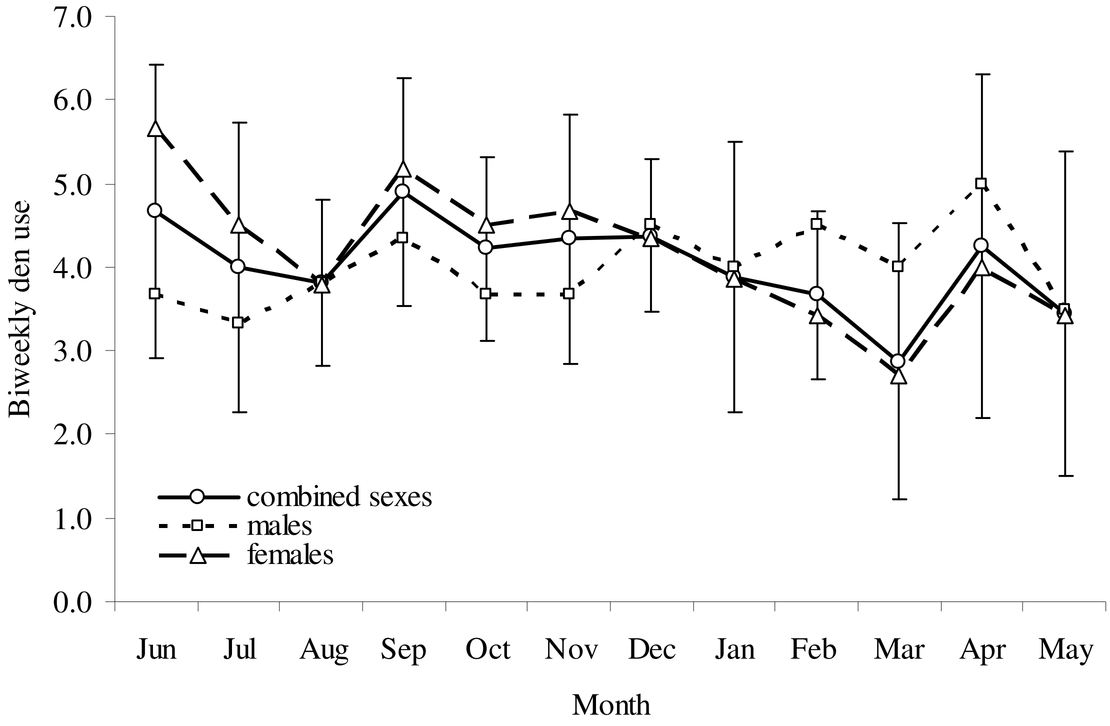

Fig. 5.6: Mean biweekly den use (BDU; dens per 15 locations) for stone martens in the towns of Bettembourg and Dudelange. Error bars show standard deviations for BDU of both sexes combined.

Table 5.4: Mean seasonal biweekly den use (BDU; dens per 15 daytime locations) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1	5.3	6.0	4.7	5.7
F2	3.3	5.7	3.3	4.7
F4	6.0	4.7	6.0	4.3
F6				6.0
F7	3.0	4.0	3.3	1.0
F8	4.0			
F9		4.7	3.3	3.0
F10		3.7	3.3	1.0
F11			2.5	1.3
M1	2.7	3.7	4.3	3.7
M2	3.4	3.0		5.0
M4	4.7	5.0	4.3	
mean ± SD				
females	4.3 ± 1.3	4.8 ± 0.9	3.8 ± 1.2	3.4 ± 2.1
males	3.6 ± 1.0	3.9 ± 1.0	4.3 ± 0.0	4.3 ± 1.0
combined	4.0 ± 1.2	4.5 ± 1.0	3.9 ± 1.0	3.6 ± 1.9

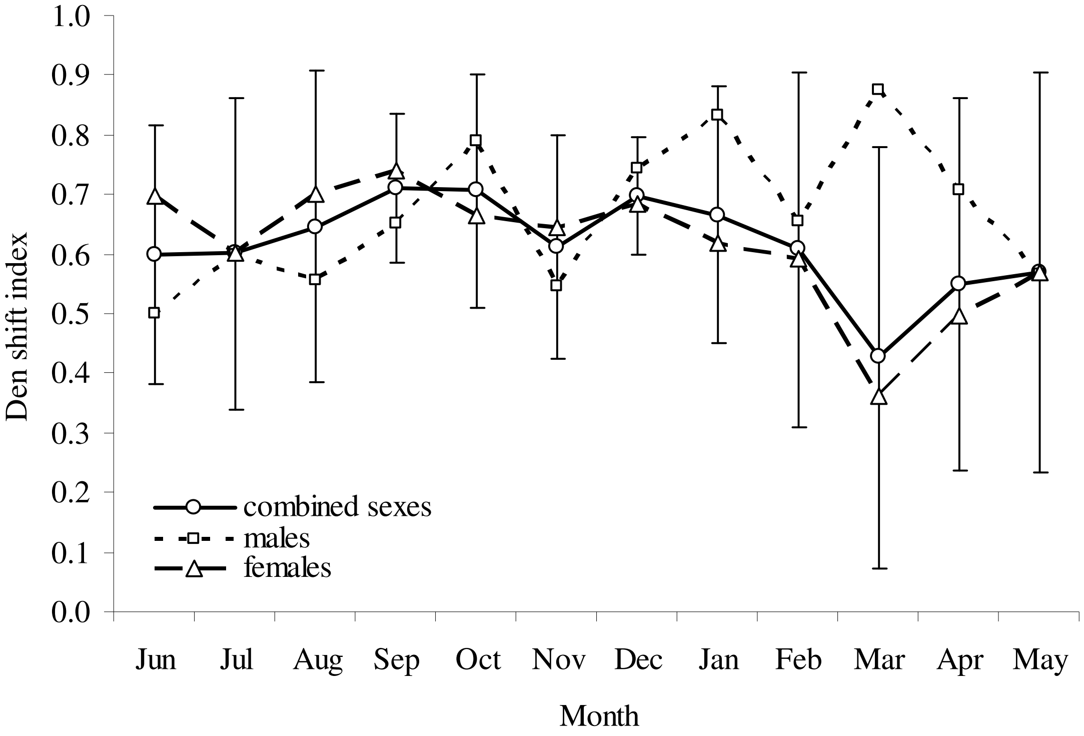

Fig. 5.7: Mean monthly den shift index (DSI) for stone martens in the towns of Bettembourg and Dudelange. Error bars show standard deviations for DSI of both sexes combined

Table 5.5: Mean seasonal den shift index (DSI) for 12 stone martens.

Marten	**su**	**au**	**wi**	**sp**
F1	0.76	0.83	0.76	0.71
F2	0.43	0.73	0.65	0.73
F4	0.88	0.65	0.62	0.66
F6				0.76
F7	0.57	0.43	0.38	0.13
F8	0.76			
F9			0.85	0.71
F10		0.72	0.79	0.00
F11			0.25	0.06
M1	0.45	0.60	0.67	0.68
M2	0.41	0.58		0.70
M4	0.79	0.81	0.81	
mean ± SD				
females	0.68 ± 0.18	0.67 ± 0.15	0.61 ± 0.22	0.47 ± 0.34
males	0.55 ± 0.21	0.66 ± 0.13	0.74 ± 0.10	0.69 ± 0.01
combined	0.63 ± 0.19	0.67 ± 0.13	0.64 ± 0.20	0.51 ± 0.31

Mean monthly BDU and mean monthly DSI were found to be positively correlated (Pearson product-moment correlation: $r = 0.668$; $N = 12$; $p < 0.05$). However, this was mostly due to the month of March where three females only used one den. When March was ignored and only those months were considered where the vast majority of martens had a BDU of at least 2, BDU and DSI were no longer correlated ($r = 0.367$; $N = 11$; $p = 0.267$).

5.3.3. Den sharing

Although five of F2's 17 identified den sites were also used at one point or another by M1 only two of these sites were used by both animals simultaneously. One of these sites accounted for 95.3% of all recorded simultaneous uses ($N = 43$) (a spacious disused garage) and the other for 4.7%. January and March were the only months where M1 and F2 were never located together in the same den. There was a rapid increase in simultaneous den use from May to July (no data were available for August), when both martens spent up to 64% of all days together in the same den (Fig. 5.8). During the rest of the year, simultaneous den use fluctuated between 5 and 12%. Overall M1 and F2 shared a den on 25.9% of days ($N = 166$).

Seven of F1's 22 identified den sites were also used at one point or another by M2. In four of those sites both martens were located together ($N = 19$) in the following proportions: 57.9%, 26.3%, 10.5% and 5.3%. M2 and F1 showed a much more balanced pattern of den sharing throughout the year (Fig. 5.8). Between April and November simultaneous den use was recorded on between 0 and 21% of all days. No data were available from December to March. Overall M2 and F1 shared a den on 12.4% of days ($N = 153$).

While martens with overlapping ranges commonly used den sites that were also frequented by a marten of the opposite sex (i.e., M1 and F2, M2 and F1, M1 and F3), martens with adjacent territories never shared (simultaneously or sequentially) a den with a neighbour.

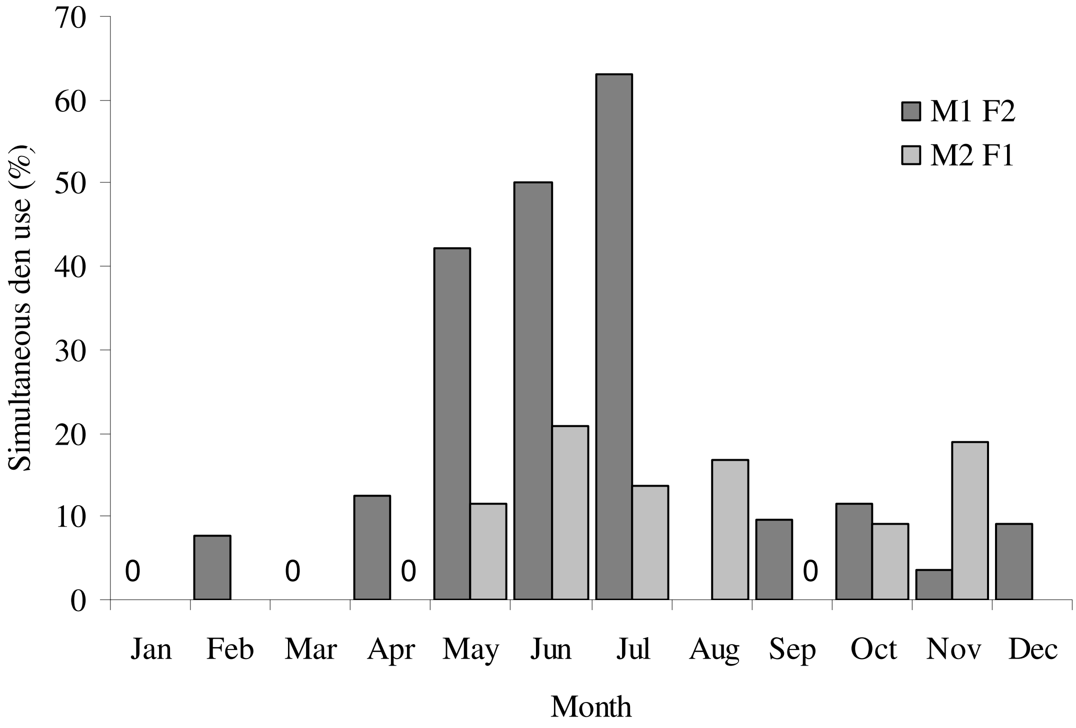

Fig 5.8: Monthly pattern of simultaneous den use within male-female pairs (M1-F2 and M2-F1) of stone martens with overlapping home ranges. Simultaneous den use is expressed as the percentage of the days on which both martens were located and found to be in the same den site. 0 means 0%; where nothing is indicated no data were available.

5.4. Discussion

5.4.1. Den selection

Unlike urban raccoons, which regularly move outside urban areas for daytime denning (Michler *et al.* 2004), urban stone martens almost exclusively used dens within the urban perimeter of their respective towns. Their den selection was characterised by an extremely high reliance on buildings (97.1%) and an extremely low use of natural den sites. The high use of buildings in itself is not unique to urban habitats. In rural environments, Genovesi and Boitani (1997) found martens to use buildings on 64.3% of all days and Lachat Feller (1993a) on 92.1% of days. However, these buildings were usually not inhabited by humans and the vast majority of denning took place in barns or other structures that contained straw or hay. In a rural village in Germany, 36 of 40 dens that were used by martens in winter and spring and 23 of 37 that were used in summer and autumn were associated with straw stores (Herrmann 2004). In Switzerland, 75.5% of all denning occurred in straw and hay (Lachat Feller 1993a) and in France the presence of martens in rural buildings was strongly correlated with the availability of these substrates (Michelat 2001). Skirnisson (1986) reported similar results for village-inhabiting martens.

The present study documents by far the highest use of inhabited buildings (41.9%) by martens recorded to date. In rural villages, Herrmann (2004) only located two of 40 dens in inhabited buildings (a family home and a school), although he did not state how often these sites were used. Lachat Feller (1993a) reported that only 0.4% of all denning events occured in inhabited houses. Skirnisson (1986) tracked a male that, after having shifted his territory from a forested and rural area into an adjacent village, denned on 92% of days in an inhabited house (over a two-month period), while another village female never used inhabited buildings for denning. Müskens and Broekhuizen (2005) tracked four martens in habitat that probably most closely resembled that of the present study, but their animals only spent 3.7% of days in buildings that were simultaneously used by humans. Urban raccoons in Germany also only used inhabited buildings on 19.6% of days, while buildings as a whole were used on 42.8% of days (Michler *et al.* 2004). In the US urban raccoons used buildings on 15% of days, 90% of which were inhabited (Hadidian *et al.* 1991). Brushtail possums, however, showed more similar den use to that of urban martens, denning in buildings (mostly inhabited) on at least 87.1% of days (Statham and Statham 1997).

Thus, stone martens in urban areas seem to rely increasingly on inhabited buildings when their preferred choice from rural areas (barns) is scarce or absent. This is in line with F9's den selection. She was the only marten with a choice of several farm buildings in her territory and spent about 50% of her days in barns without ever being located in inhabited buildings. Furthermore, the seasonal shift from uninhabited buildings to inhabited buildings in winter strongly suggests that martens exploited the superior thermal properties (owing to insulation material and artificial heating) of this type of den site during the coldest months of the year. This was also reflected in the fact that the den sites that provided the least thermal benefits (i.e., other anthropogenic structures and natural dens) were used almost exclusively in summer. In the city of Nijmegen, martens were also shown to select for den sites with high insulative properties in cold temperatures and vice versa (van Bostelen and Verhoog 1992). Similar seasonal shifts to better-insulated den sites were also documented by Skirnisson (1986) and Lachat Feller (1993a) in rural martens. Waechter (1975) experimentally demonstrated that captive martens, when given a choice, preferentially used artificially heated den boxes in winter, even though the same boxes without the heating were not preferred in the previous autumn.

The reason why females tended to use more inhabited and fewer uninhabited den sites than males is not immediately obvious. However, Lachat Feller (1993a) also observed females to use more anthropogenic (better insulated and protected) and fewer natural (less insulated and protected) den sites than males. Similarly, pine marten females select for better sheltered den sites than males (Zalewski 1997b). These gender differences may be related to a female preference for these sites for litter-rearing purposes. However, data concerning this are largely missing. The only female to rear young successfully (F10) while being tracked in my study did this in an uninhabited ruined building, where cats were regularly seen moving in and out. F1 reared a litter in an inhabited apartment house (after her collar had already stopped functioning). It is, however, known from numerous complaints that martens frequently rear young in inhabited buildings (personal observation).

5.4.2. Den use patterns

In comparison to pine martens that frequently den in trees and thus may use very large numbers of dens (> 150 per year, Zalewski 1997a), the stone marten's pattern of den use seems to be rather conservative and is characterised by a relatively small number of dens that are regularly revisited. This general pattern does not seem to be very dependent on the habitat that the animals are living in. Most studies have identified on average no more than 20 den sites for each marten (e.g., Herrmann 2004; Lachat Feller 1993a; Müskens and Broekhuizen 2005). Also, a few den sites usually account for the bulk of the denning events while the majority of dens are used only occasionally (Herrmann 2004; Müskens and Broekhuizen 2005).

Ebersbach *et al.* (1995) compared the distribution of stone marten and pine marten dens across their respective home ranges and concluded that stone marten home ranges were poorly described by the distribution of den sites within them. This seems to be confirmed by the current study. Although dens were rather evenly distributed across the home range for some martens (e.g., F1, F4, F10), they were clustered in others with some areas not getting any denning use (e.g., F9, F11, M4, M1). However, since few dens usually accounted for the bulk of all recorded den uses, denning as such was always clustered irrespective of the spatial distribution of den sites within the home range.

The average number of dens that martens visited per 15 days was relatively low in the current study. The fact that there was no positive correlation between BDU and DSI (when March was excluded) illustrates that martens did not necessarily shift less when they used fewer dens. In fact it was generally rare for martens to spend several days in a row in the same den. There are few data to compare den use patterns and when they exist they are based on very few animals, making comparisons difficult. Libois and Waechter (1991) used Skirnisson's (1986) data to calculate shift indices. A rural female showed a period of frequent shifting (0.89) followed by a period of higher stability (0.45). In another female a shift index of 0.51 was observed from September to February followed by a shift index of 0 until the end of May, while she was rearing young. Once the young left the den her shift index increased to 0.79. The two martens showed clear seasonality, which did not correspond to the general trend in the current study. However, F10, who successfully reared young, showed the same pattern when her shift index dropped from 0.95 in February to 0 in the following three months. F1, F4, and F7 also momentarily stopped shifting between dens in March but resumed ‘normal’ denning behaviour again within a couple of weeks. It was assumed that these females may have given birth but failed to rear their litters (see Chapter 3; Table 3.10).

The generally high DSI observed here could be an adaptation to or a result of using a high proportion of human-inhabited den sites. Prolonged stays in an inhabited building will often prompt the owners to try and disturb the animals. Thus, frequent changing of dens in urban habitats may be the result of sporadic disturbance. Alternatively, shifting could be a strategy allowing martens to avoid human interference. This is further supported by the fact that the four martens that had their favourite den in inhabited buildings used these dens to a lesser extent than those martens that had their favourite den in uninhabited buildings.

BDU seemed to be lower and more stable across the year in urban than in rural martens. Skirnisson (1986) found that rural martens used up to 12 or 13 den sites per biweekly period in summer, but often only one in winter and spring. Two explanations can be put forward for this difference. Firstly, the fact of not having young to care for would have liberated most females from having to stay with their litter in a single den. Secondly, the high availability of well-insulated den sites in urban environments presents the martens with a choice of several suitable den sites during the cold period, while martens living in a mostly forested environment may be limited in the availability of such dens in winter.

5.4.3. Den sharing

M1 and F2 showed a clear peak in den sharing leading up to and during the mating period in summer. Similarly, Skirnisson (1986) followed a single pair of martens whose den sharing peaked in the same period. He also detected a second peak in early February and hypothesised this to be related in some way to the implantation of the blastocyst during the same period, but no such secondary peak was found in the present study. Frequently sharing a den during the reproductive period may be a form of mate-guarding ensuring the male successful copulation when the female is receptive. Although this pattern may be expected in martens, M2 and M1 showed no clear peaks in den sharing during the year. However, the den site that accounted for most of their common use was a large complex of buildings where it was impossible to determine the exact location of the martens. This may have obscured the occurrence of den sharing. Overall, adult male-female den sharing was intermediate between that observed by Genovesi and Boitani (1997) (43%) and by Müskens *et al.* (1989) (12%).

The fact that martens with overlapping home ranges commonly shared dens while neighbouring martens never did is in accordance with the intrasexual territoriality that was observed based on the spatial organisation of this population (Chapter 3). Müskens *et al.* (1989) made essentially the same observations regarding the sharing of dens in overlapping and neighbouring territories, although they did observe an adult male repeatedly sharing a den with a subadult male.

5.4.4. Conclusion

Although inhabited buildings were used more in this study than in any other, martens nevertheless spent the majority of days inside uninhabited buildings, possibly allowing them to avoid human disturbance as much as possible. However, the high use of inhabited buildings, especially in winter, also demonstrated that stone martens have learned to take full advantage of the well-protected and insulated den sites that urbanised areas have to offer. This behaviour likely increases the potential for marten-human conflict in comparison to rural villages where the animals find and use a number of alternative dens, especially in barns. As traditional farming practices disappear, and with them the structures that martens often use as den sites, a shift towards more inhabited houses may be expected in what are now rural villages where, according to other studies, these problems seem to be less frequent.

The martens in this study were also found to maintain a relatively constant den use pattern (i.e., high den shifting and low biweekly den use) across all seasons. This is probably due to a combination of factors. The low reproductive rate in urban areas (Chapter 3; Lammertsma *et al.* 1994) frees females from being constrained to a single den in spring, and a range of better-insulated den sites may give martens a larger choice of potential den sites in winter compared to rural or forested areas. In addition, human disturbance may be kept to a minimum by frequently changing between different dens.

Chapter 6: Stone Martens and Cars

6.1. Introduction

Stone martens are well known for climbing into car engine compartments, where they can cause damage by tearing up noise insulating mats under car bonnets or by chewing rubber and plastic parts such as ignition leads, coolant hoses, or electrical wiring (Kugelschafter *et al.* 1984/85; Langwieder and Höpfl 2000). This behaviour pattern has been referred to as the 'car-marten-phenomenon' (Kugelschafter 1989). It was first observed in Switzerland in the late 1970's (Kugelschafter *et al.* 1984/85) and has since spread through Germany, Austria (Kugelschafter *et al.* 1997; Langwieder and Höpfl 2000) , the Netherlands (e.g., Müskens and Broekhuizen 2005), Luxembourg (this study) and other regions in central Europe. In 1998 martens caused damage worth an estimated 20 million € (~£ 14 million) on about 160000 cars in Germany alone, with about 3.8 of 1000 registered cars being affected (Langwieder and Höpfl 2000).

This so-called 'car-marten phenomenon' has earned the stone marten a negative reputation (personal observation) and has sparked the development of a host of different marten repellents such as sprays or ultrasound devices (see Kugelschafter *et al.* 1997). While car manufacturers and insurance companies have focused on determining which types of cars or parts are attacked by martens (Kugelschafter *et al.* 1984/85; Langwieder and Höpfl 2000), wildlife biologists have focused on explaining the observed behaviour (for a review see Ludwig 1996). The latter studies have mostly involved captive animals (Kugelschafter *et al.* 1984/85; Kugelschafter 1989; Kugelschafter *et al.* 1989) and have been supplemented by studies on the temporal and spatial distribution of damage occurrences in small towns (Kugelschafter *et al.* 1993; Ludwig 1996; Müskens and Broekhuizen 2005). So far only one study has used telemetry to look at how free-ranging martens make use of cars during their nightly activities (Müskens and Broekhuizen 2005).

Based on these studies, Ludwig (1996) retained three main hypotheses for explaining the car-marten-phenomenon:

i) Species-specific exploratory behaviour: Stone martens tend to explore unknown objects through biting them.
ii) Play behaviour: Young martens scratch and bite objects during play.
iii) Aggressive biting: This is primarily attributed to territorial males who are setting up their territories in spring. When entering engine compartments, martens leave behind their scent passively through scent glands on their feet (see Skirnisson 1986, p.81) or by actively scent marking. At territorial borders the same cars may be visited alternately by territorial neighbours, who react to the other male's scent by aggressive biting into objects carrying the scent. Cars could also move strange scent between different territories (Ludwig 1996).

These hypotheses deal with the actual reasons for the biting and scratching itself but do not necessarily deal with the reasons why the animals associate with cars in the first place. Based on observations of food remains, foot prints and hair inside engine compartments, Kugelschafter (1989) concluded that engine compartments have become an important element in the stone marten's environment. Popular belief is that martens enter engine compartments to seek out the heat of recently used engines. Observations on a captive marten that always denned inside a car even though it had a choice of several other structures, including its normal den box, suggest that cars may be attractive for denning or resting purposes (Kugelschafter *et al.* 1984/85).

The objective of this chapter was to determine why martens incorporate cars into their nightly activities. I described and quantified the patterns of road and car use of individually radio-tagged martens in order to test three hypotheses:

i) Thermal benefit: The main reason for associating with cars is due to a thermal benefit they gain from warm engines. This predicts that martens mostly associate with cars during the coldest season and rest there for longer periods.
ii) Safe environment: Martens primarily use cars as a safe environment for hiding, resting or food consumption purposes. No clear seasonality in road or car use would be predicted.

iii) Territoriality: Car visiting behaviour is mostly due to territorial behaviour. This predicts that martens should most strongly associate with cars during the seasons when they are most territorial (i.e., spring / early summer; Chapter 4; Herrmann 2004).

In addition I studied the spatio-temporal distribution of car damage in the two study towns in order to relate observed behaviour directly to observed car damage.

6.2. Methods

6.2.1. Road and car use

The general telemetry procedures that were employed to collect data were outlined in Chapter 2. Whenever I received a stationary signal from the direction of a car I would initially wait to make sure that the animal was inactive. I then carefully walked past the car or row of cars with the telemetry receiver to ensure that the animal was really inside the car. Thereafter the car was not approached again so as to avoid disturbing the animal. The animal was said to be 'resting' when it remained inside a car engine compartment for at least two consecutive fixes (i.e., at least 15 min).

Three different measures were employed to quantify road use:

i) Road fixes: ArcView 3.3 was used to draw a 10 m buffer on either side of the centre line of each road that was contained within the urban perimeter of the two study towns. Active outside-the-den fixes falling within this 10 m buffer or adjacent car parks were considered to be road fixes. However, fixes that fulfilled these criteria but were located inside buildings were discarded. The extent of road use was defined as the number of road fixes per radio tracking night (RoadFix).

ii) Visible fixes: The majority of the time when martens were visible at fix time they were located in or close to a road (usually somewhere between the rows of houses on either side of a road). Thus the number of visible fixes per radio tracking night (VisFix) was employed as a second way of measuring road use.

iii) Observations: All direct observations of stone martens that were made while radio tracking were recorded, irrespective of whether they occurred at fix time or between fixes. The number of observations per night (VisObs) was thus employed as a third measure of road use. Additionally, I wrote down notes on the observed behaviour that were then used to provide a general description of marten behaviour in roads.

Because the duration of the martens' activities varied between seasons (see Chapter 4) it was possible that seasonal variation in RoadFix, VisFix and VisObs would simply reflect overall activity changes. In order to account for such seasonal activity changes I calculated for each night i) the percentage of all active fixes that were also road fixes (%RoadFix), ii) the percentage of all active fixes that were also visible fixes (%VisFix) and iii) the number of visual observations per active hour (VisObs/NA; see Chapter 4 for a definition of NA).

6.2.2. Spatio-temporal distribution of car damage

Information on the distribution of marten-damaged cars in the study area was gathered through a postal survey. The survey was conducted first in Bettembourg in March 2006 (for damage having occurred in 2005). It was then repeated in Bettembourg and widened to Dudelange in February 2007 (for damage having occurred in 2006). The survey cards were the size of normal postcards and were distributed through the regular mail to all households in Bettembourg (~3100) and in Dudelange (~8000). The card asked for the following information:

1) Your car was damaged by a stone marten in 2005(06): yes ____ no____
2) Approximate date when damage occurred: a) ____ / ____ / 2005(06)
b) ____ / ____ / 2005(06)
c) ____ / ____ / 2005(06)
3) Name and address : ____
4) Phone number: ____

In order to maximise returns the survey was announced in the local media (newspaper, radio, TV), all text on the cards was in two languages (French and German) and cards could be mailed back without a stamp. Although the survey was designed to also get information about no damage, I assumed that most people whose cars were not damaged were unlikely to return the cards, while most people whose cars were damaged would return them. I also assumed that damage done in both study towns to visitor cars (which would have been missed by the survey) would be balanced out by resident cars that were actually damaged outside the study towns.

All cars that were parked in roads or driveways between 0100 and 0300 h were counted in Bettembourg (2006: 28/03 - 30/03; 2007: 07/03) and Dudelange (2007: 28/03 - 25/04). I chose this time of the day because after 0100 h most visitors would be expected to have left the town and most residents to have returned home for the night. The nights on which cars were counted were all outside school holidays, when many residents go on holiday.

6.2.3. Car dealership survey

I initially intended to gather data on the seasonal and spatial distribution of car damage throughout the country by getting car-dealerships to systematically record marten-related damage. After an initial postal survey of 129 car dealerships, 29 dealerships initially agreed to record the required data. However, while some seemed to regularly record damage, others only did so for a while or indicated that they had encountered no damage at all, essentially making the data unreliable for further analyses. Hence I have only used the received reports (N = 176) to determine the age of damaged vehicles.

6.2.4. Statistical analysis

Data from F3 were not used in the analyses for the present chapter owing to inadequate number of fixes for this animal. Depending on sample size I used either a G-test or a chi-square test to analyse for seasonal effects on the frequency distribution of car resting events and car damage reports (Fowler *et al.* 1998). Kruskal-Wallis tests were employed to test for seasonal variation in the females' road use as the data did not fit the assumption of homogeneity of variance, while Mann-Whitney U tests were used for post hoc pairwise comparisons. The significance level was always set at 0.05.

6.3. Results

6.3.1. Resting in cars

Resting events in cars that lasted for at least 15 min (i.e., at least two consecutive fixes) were rare. In 268 nights of radio tracking, involving 12 martens, only 19 such events were recorded (Table 6.1). Three martens (F2, F6, F7) never spent two or more consecutive fixes in a same vehicle, while the remaining martens were found to rest in cars on average (± SD) only once every 12.3 ± 6.8 nights (median visit duration: 1 h, range: 0.25 - 3.5 h). On six of those car-resting occasions and on five shorter car visits a note was left on the car asking the owners to report damage. From none of them was a damage report received.

There was no seasonal effect on the temporal frequency of car resting events, which did not differ significantly from the seasonal frequency of radio tracking nights (G-test: $G = 1.234$; d.f. = 3; $p > 0.05$). Nor did the length (i.e., number of consecutive fixes) of these stays in cars differ significantly between the different seasons (Kruskal-Wallis: $H = 1.14$; d.f. = 3; $p = 0.768$): the median duration of car resting events was 4 fixes in summer, 4 in autumn, 3 in winter and 2 in spring. The mean nightly temperatures for nights where martens rested in cars ranged from 2 to 19 °C, with 58% of the nights being above 10 °C (Table 6.1).

6.3.2. Road use

Visibility

The number of visible fixes per night (VisFix) differed significantly between different seasons in females (Table 6.2; Kruskal-Wallis test: $H = 17.43$; d.f. = 3; $p < 0.01$). Similarly, %VisFix differed significantly between seasons (Table 6.2; $H = 16.61$; d.f. = 3; $p < 0.01$). In both measures, spring and summer were significantly higher than both autumn and winter (Mann-Whitney tests: $p < 0.05$), while spring and summer, and autumn and winter did not differ from one another ($p > 0.05$). The same trend was observed in males and there seemed to be a trend for male values to be on average higher than female values (Table 6.2).

The same trend that was seen for VisFix was also true for all recorded observations (VisObs) of focal martens (Table 6.3). Thus the number of observations per night and the number of observations per active hour differed significantly between seasons (VisObs: $H = 17.98$; d.f. = 3; $p < 0.001$; VisObs/NA: $H = 16.11$; d.f. = 3; $p < 0.01$). In summer and spring, observations were significantly more common than in autumn and winter ($p < 0.01$; except VisObs/NA su-au: $p > 0.05$), while summer and spring, and autumn and winter were not significantly different from one another ($p > 0.05$). The

Table 6.1: Occurrences of stone martens spending at least two consecutive fixes (i.e., at least 15 minutes) inside the engine compartment of a vehicle parked along the road.

Season	Marten	Date	Fixes [a]	Time	Temp [c] (°C)
su	F1	02/08/2005	3[b]	0245-0315	14
su	F1	17/08/2005	7	2330-0100	15
su	F1	28/07/2005	4	2430-0115	19
su	F4	06/08/2005	6	2315-2430	12
su	F8	03/08/2006	3	2330-2400	14
su	F9	24/08/2006	4	0245-0330	13
au	M1	10/09/2005	2	2400-2415	16
au	M2	18/09/2006	7	2130-2300	15
au	M2	06/11/2006	4	0500-0545	2
wi	F9	03/12/2006	14	0100-0415	8
wi	F9	10/12/2006	3	0545-0615	3
wi	F10	19/02/2007	2	0300-0315	2[d]
wi	M4	14/02/2007	4	0115-0200	3[d]
wi	M4	14/02/2007	2	0515-0530	3[d]
sp	F4	26/04/2006	2	0145-0200	11
sp	F9	22/04/2007	2	0315-0330	11
sp	F11	18/03/2007	2	0330-0345	2
sp	F11	10/04/2007	5	2430-0130	8
sp	M2	15/04/2006	8	2245-2430	10

[a] number of consecutive fixes
[b] exact number unknown, but minimum 2 and maximum 4
[c] average nighttime temperature (2000 h – 0800 h)
[d] minimum temperature, since average was not available

Table 6.2: Road use expressed as mean number of fixes (VisFix) and mean percentage of active fixes (%VisFix) where a marten was visible on or close to a road each night.

Marten	**VisFix**				**%VisFix**			
	su	**au**	**wi**	**sp**	**su**	**au**	**wi**	**sp**
F1	1.6	1.3	0.5		10.4	8.5	4.5	
F2	1.5	0.3	0.3	1.8	9.1	2.1	2.4	8.5
F4	1.9	0.9	0.7	1.3	10.8	5.0	4.7	8.1
F6				4.0				19.3
F7	1.8	1.0	0.7		9.2	6.0	5.3	
F8	2.0				10.6			
F9		0.4	0.9	3.6		1.6	3.7	13.3
F10		0.7	0.9	6.4		2.6	3.7	23.9
F11			1.0	10.0			4.7	34.8
M1		1.9	1.7			9.1	8.3	
M2	7.9	1.6		6.6	31.0	6.7		26.2
M4	3.6	1.1	0.7		16.0	4.7	2.7	
mean ± SD								
females	1.8 ± 0.2	0.8 ± 0.4	0.7 ± 0.2	4.5 ± 3.3	10.0 ± 0.8	4.3 ± 2.7	4.1 ± 1.0	18.0 ± 10.3
males	5.8 ± 3.0	1.5 ± 0.4	1.2 ± 0.7	6.6	23.5 ± 10.6	6.8 ± 2.2	5.5 ± 4.0	26.2

Table 6.3: Road use expressed as mean nightly number of focal marten observations (VisObs) and mean nightly number of observations per hour that martens spent being active each night (VisObs/NA).

Marten	**VisObs**				**VisObs/NA**			
	su	**au**	**wi**	**sp**	**su**	**au**	**wi**	**sp**
F1	5.7	3.6	2.5		1.5	1.0	0.8	
F2	3.9	2.1	1.2	5.5	0.9	0.6	0.4	0.9
F4	5.2	3.4	2.7	4.0	1.1	0.8	0.6	1.1
F6				8.8				1.6
F7	5.0	3.0	2.0		0.8	0.7	0.5	
F8	4.4				0.8			
F9		1.3	3.1	8.5		0.3	0.5	1.2
F10		2.9	3.4	20.2		0.5	0.5	2.8
F11			3.1	19.8			0.6	2.8
M1		3.8	3.8			0.7	0.8	
M2	17.3	4.3		15.6	2.6	0.7		2.4
M4	12.3	1.6	3.0		2.0	0.2	0.4	
mean ± SD								
females	4.8 ± 0.7	2.7 ± 0.9	2.6 ± 0.8	11.1 ± 7.1	1.0 ± 0.3	0.6 ± 0.3	0.6 ± 0.1	1.7 ± 0.9
males	14.8 ± 3.5	3.2 ± 1.5	3.4 ± 0.6	15.6	2.3 ± 0.4	0.6 ± 0.3	0.6 ± 0.3	2.4

same trend was observed in males, which again seemed to be more visible than females, especially in spring and summer (Table 6.3).

Road fixes

The number of road fixes (RoadFix) for females changed significantly between different seasons (Table 6.4; H = 15.16; d.f. = 3; $p < 0.01$). The same was true for %RoadFix (Table 6.4; H = 17.01; d.f. = 3; $p < 0.01$). As with previous measures, road fixes were significantly more frequent in spring and summer than in autumn and winter ($p < 0.05$). Again, the same trend was seen in males although they were on average located more often in roads than females (Table 6.4).

All road use variables showed marked individual variation. In spring, especially, F10 and F11 spent much more time in roads than did the other females, exhibiting a frequency of road use very similar to that of the males (Tables 6.2, 6.3, 6.4).

Behaviour in roads

Often martens would quickly cross the road to enter another set of gardens without spending much time in the road or showing much interest in the cars that were parked there. This was especially true in autumn and winter. However, a definite change in behaviour occurred in spring. Typical observations of martens in roads in spring would consist of the animal running from car to car, often crossing the road back and forth between rows of cars on either side of the road. F6 was regularly seen moving systematically between cars on car parks that were located within her home range. Beneath a car, an animal often lifted up its nose repeatedly, clearly sniffing the underside of the car. Martens were also observed to directly scent mark parts of cars (mostly the rear axle) with their urine (Fig. 6.1). This scent marking behaviour could be confirmed for martens F9, F10 and F11, as well as for F9’s and F10’s respective untagged mates (all in Dudelange) and for an unknown marten in Bettembourg. While the other tagged individuals performed similar behaviour (especially M2 and M4), the actual placing of urine scent marks on cars could not be definitely confirmed as I only became aware of this practice during the later part of the project.

This investigatory and scent marking behaviour was frequently accompanied by the animal briefly climbing onto the front or rear axle, the tail still being visible. When

Table 6.4: Road use expressed as mean nightly number of road fixes (RoadFix) and mean nightly percentage of all active fixes that were within 10 m of the centre of the road (%RoadFix).

Marten	**RoadFix**				**%RoadFix**			
	su	**au**	**wi**	**sp**	**su**	**au**	**wi**	**sp**
F1	2.9	1.1	0.5		18.5	7.6	5.3	
F2	1.4	0.4	0.4	2.0	8.3	3.3	2.4	9.6
F4	1.7	0.8	0.5	1.8	9.8	4.5	3.3	12.9
F6				5.3				24.8
F7	3.2	1.4	1.2		15.8	7.9	8.8	
F8	2.4				13.0			
F9		0.6	1.9	5.3		2.7	8.7	19.3
F10		0.9	1.9	7.7		3.1	7.3	28.4
F11			0.9	10.3			4.1	36.2
M1		2.1	2.0			9.7	10.5	
M2	8.4	2.7		7.4	32.9	13.3		29.7
M4	3.8	1.4	0.9		16.0	6.0	3.3	
mean ± SD								
females	2.3 ± 0.8	0.9 ± 0.4	1.0 ± 0.6	5.4 ± 3.3	13.1 ± 4.2	4.8 ± 2.3	5.7 ± 2.6	21.9 ± 9.9
males	6.1 ± 3.3	2.1 ± 0.6	1.4 ± 0.8	7.4	24.4 ± 11.9	9.7 ± 3.6	6.9 ± 5.1	29.7

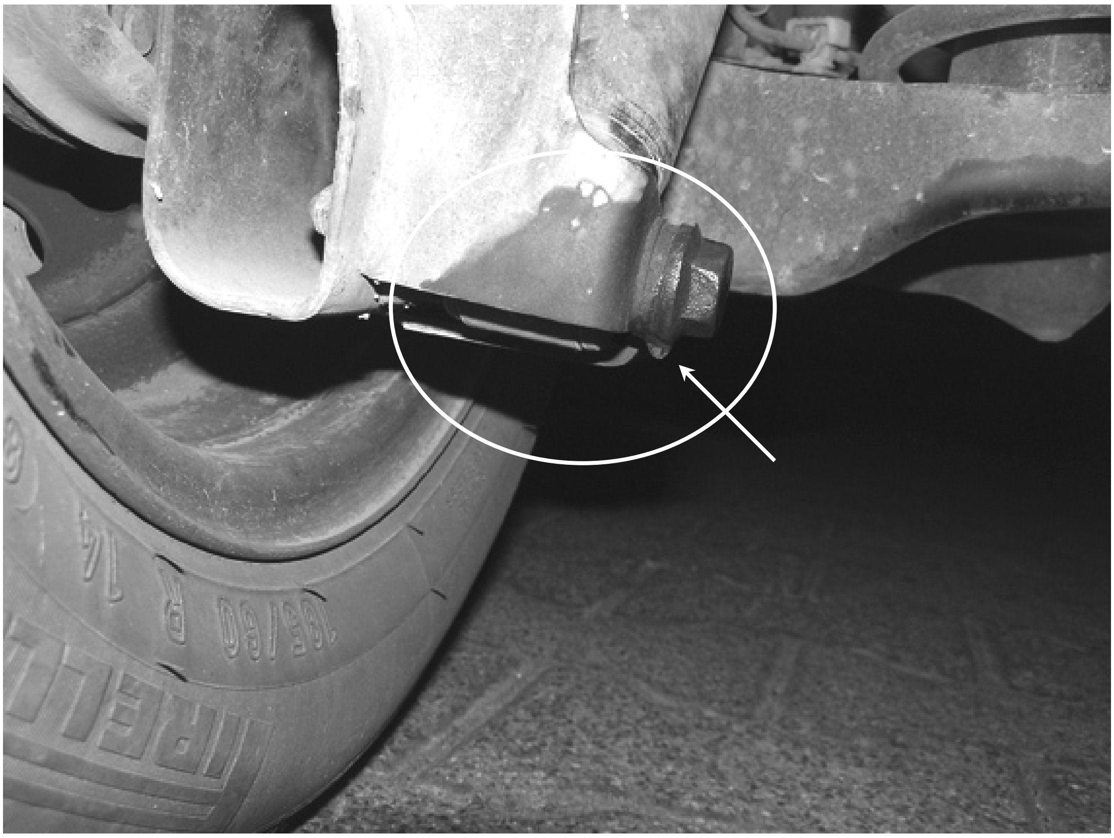

Fig. 6.1: Fresh urine scent mark (arrow) on the rear axle/suspension of the car that was used for radio tracking. The encircled area was regularly marked by various radio-collared and non-collared male and female stone martens.

climbing down from the axle the marten would often remain still for a few seconds, its rear end pushed high against the axle and the tail lifted above the axle. Some martens seemed to perform a ‘handstand’ whereby they briefly moved one or both hind legs onto the axle with the front legs remaining on the ground. These were presumably scent marking behaviours. On many occasions a marten would completely disappear into an engine compartment. These visits usually only lasted seconds rather than minutes and were much more common than the longer ‘car rest’ periods described above. It remained unconfirmed whether the martens also scent marked inside engine compartments. Martens were, however, frequently observed placing urine or faecal scent marks on the road under cars or close to car tyres. This systematic car-patrolling behaviour was exhibited by most martens (much less so in the juvenile F8) but was most commonly observed in M2 (spring, summer), M4 (summer), and F6, F9, F10 and F11 (all in spring). In August the behaviour became less frequent and was only seen occasionally until the following spring. The video sequence in Appendix 1 illustrates a range of these behaviours.

6.3.3. Spatio-temporal distribution of car damage

As expected, return of survey cards reporting no damage was low (Bettembourg 2005/2006: 120/134; Dudelange 2006: 295). In Bettembourg, damage was reported from 19 cars in 2005 and 24 in 2006. With 1896 cars counted in 2006 and 1924 cars in 2007, this equates to damage being reported from about 1.0 and 1.2% of cars that were parked outside at night. In Dudelange, 87 damage incidents were reported for 4680 counted cars, equating to about 1.9% of road-parked cars. Even if three times as many cars were actually damaged as were reported to have been damaged, only about 3 to 6% of all cars that were parked outside at night would have been damaged by martens in any one year.

Individual female MCP95 home ranges encompassed on average (± SD) 3.8 ± 3.9 (N = 4; 2005) and 5.7 ± 3.9 (N = 10; 2006) damage reports, ranging from a minimum of 0 to a maximum of 11 damaged cars. Male MCP95 home ranges contained on average 9.5 ± 0.7 (N = 2; 2005) and 7.0 ± 4.4 (N = 3; 2006) damage reports (Fig. 6.2). Although in some cases damaged cars were located close to actual home range borders (e.g., F6, F10) there was no clear pattern of damage primarily occurring at borders. Indeed, in some cases damage only occurred in the interior of a territory (e.g., F11; Fig. 6.2).

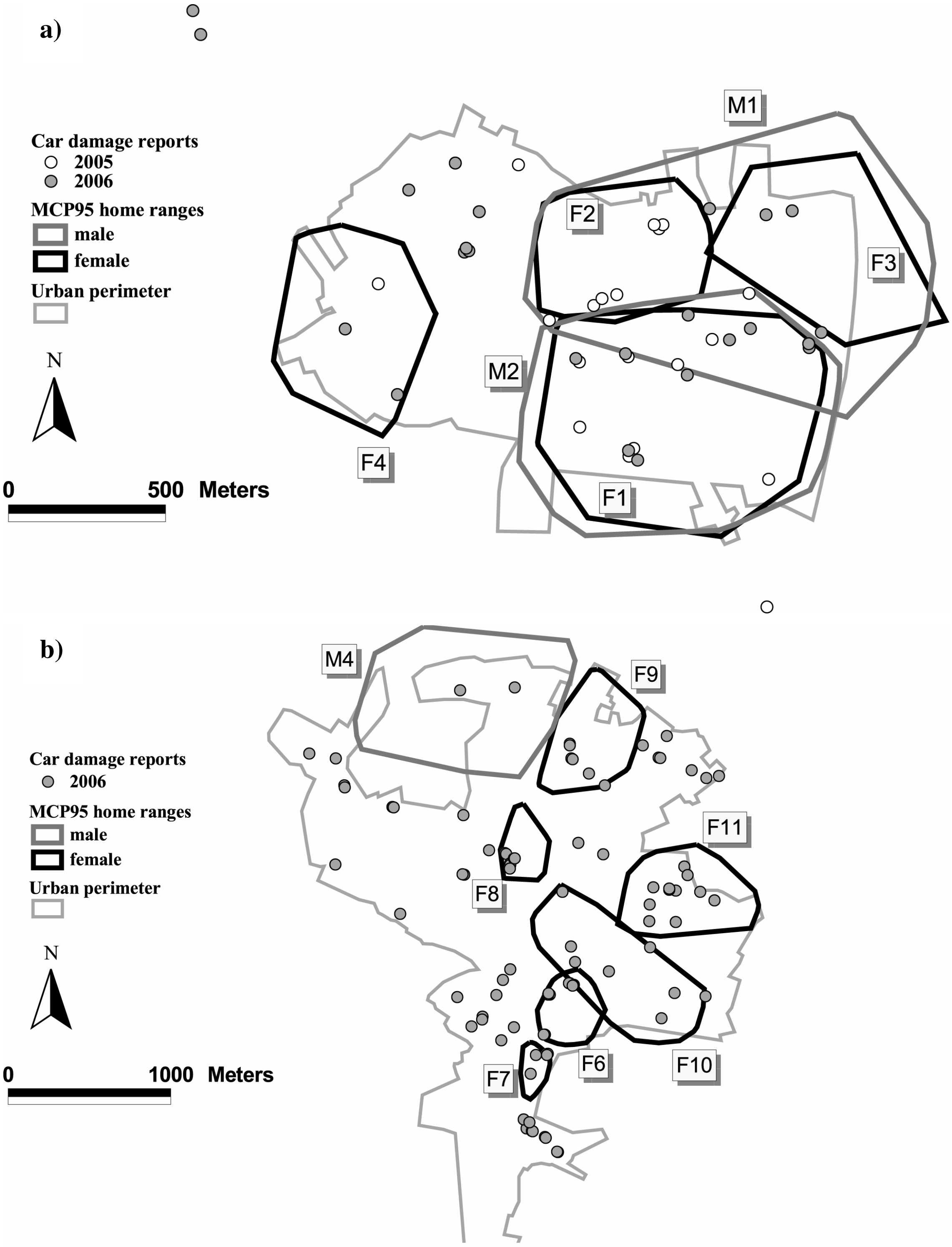

Fig. 6.2: Spatial distribution of marten-related car damage reports in (a) Bettembourg and (b) Dudelange.

Based on population estimates of eight adult martens in Bettembourg and 23 to 29 in Dudelange (see Chapter 3), each individual marten would have been responsible for 2.4 (2005) or 3.0 (2006) damage reports in Bettembourg per year and between 3.0 and 3.8 reports in Dudelange (2006).

A total of 130 damage incidents were reported from both towns. For 117 of these the month or season in which the damage was noticed was indicated. Car damage was not distributed equally across the four seasons, being most frequent in spring (41) followed by autumn (31), summer (25) and winter (20) ($\chi^2 = 8.37$; d.f. = 3; $p < 0.05$).

6.3.4. Age of damaged cars

Damage reports (N = 176) that were received from several car dealerships from across the country indicated that almost 30% of marten-damaged cars had been damaged in the same year as they were bought. Overall, 79% of cars that were serviced with marten-related damage were less than three years old (Fig. 6.3).

6.4. Discussion

6.4.1. Marten-car associations

Cars for resting and thermal benefit

Despite occasional reports of dead martens being found in car engine compartments, presumably having been killed while sleeping in a car, I showed in Chapter 5 that cars are not used as daytime den sites. On only one occasion (out of 2324 daytime fixes) a marten was found to den inside a car. Müskens and Broekhuizen (2005) also only recorded this behaviour once in 353 days. Thus, even though Kugelschafter *et al.* (1984/85) found that a captive marten chose the engine compartment of a car over any other available den site, this certainly does not reflect the normal behaviour of free ranging martens.

Nighttime resting in cars on the other hand was shown to occur, without, however, being very frequent. The fact that there was no seasonality in this behaviour, that it seemed to occur just as often on warmer nights than on colder nights, and that the animals did not stay in cars longer in winter than in other seasons, suggests that the behaviour was not related to thermal benefits that could be gained from recently-used

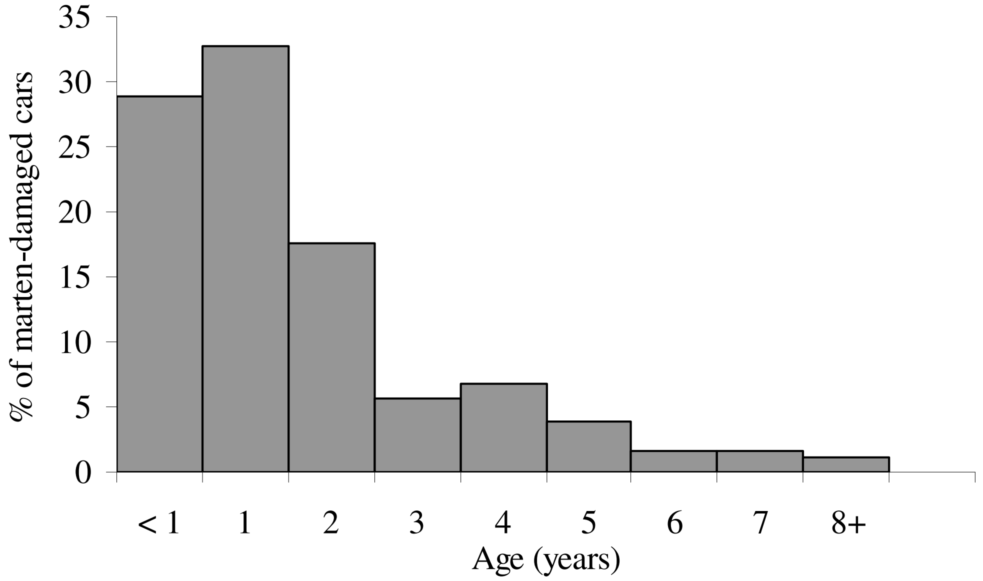

Fig. 6.3: Number of years since the year of manufacture of cars (N = 176) that were reported by 11 car dealerships to have been serviced for stone marten-related damage. The sample contains the following car makes: 14 Audi, 1 Citroen, 5 Fiat, 3 Ford, 42 Hyundai, 2 Kia, 11 Mercedes, 26 Nissan, 4 Opel, 4 Peugeot, 15 Seat, 14 Skoda, 36 VW. Data on the overall age structure of cars that were serviced (for marten-related and any other problems) by these dealerships were not available.

cars. This was in line with multiple observations of radio-collared martens passing under the warm car that was used for radio tracking, without climbing in, despite sub-zero temperatures. This relatively rare use of cars for prolonged resting periods also confirmed results from the Netherlands and thus was not unique to the present study (Müskens and Broekhuizen 2005). Thus neither the exploitation of warm engines nor the general use of cars as nighttime rest sites seem to be a main driving factor for inciting martens to associate with cars.

Safe environment

Kugelschafter (1989) and Ludwig (1999) noted that stone martens have learned to incorporate cars into their nightly activities, suggesting that they use cars as safe environments for resting, consuming or storing food items, or hiding from disturbances. In the present study, martens were indeed occasionally observed to escape into cars after having being disturbed by humans or chased by cats. They have also been found resting in cars; and there have been occasional reports of people finding an egg, a bread roll or a road-killed hedgehog (*Erinaceus europaeus*) under the bonnet of their car (personal observation). However, these observations cannot account for the seasonal increase in the use of roads that was clearly observed in the radio-collared martens. If martens were to make a habit of carrying food items to cars in order to consume them there, they would be expected to be located on roads with similar frequency all year round. More likely, hiding in cars occurs because the animals are active in the roads in the first place and cars happen to be the best hiding places in roads.

Territoriality

While male and female martens spent most of their time in gardens in autumn and winter, they shifted a significant proportion of their activity onto roads in spring and summer. The actual increase in road activity was likely to be even higher than was shown by the measured variables since spring and summer observations would usually last much longer than brief winter observations. This clear seasonal change in road use corresponded well with the seasonal changes in activity and movement levels that have generally been attributed to heightened territoriality in spring and summer before and during the reproductive period (Chapter 4; Herrmann 2004). This direct link between increased activity and heightened territoriality has often been assumed and could be confirmed here through frequent observations of scent marking behaviour. Interestingly, martens were observed directly marking cars with their urine. While martens had previously been suspected to passively or actively leave their scent on cars during their visits to engine compartments (e.g., Ludwig 1996), the systematic urine marking of cars has not previously been described. Urine marking is indeed the predominant form of scent marking in stone martens, with faecal marking being less common (Grünwald 1990; Ludwig 1995). Interestingly, females marked features on cars that were at least 15 cm above ground and in doing so had to adopt a position fundamentally different from the crouched position that had previously been described for females. Instead it resembled more the males' upright standing position (Grünwald 1990; Ludwig 1995).

In natural environments stone martens would usually leave their scent marks on permanent features (as would all other scent marking mammals), with the only other martens to encounter them being the marten's mate, immediate neighbours or the occasional dispersing or wandering strange marten. In urban areas, however, where they scent mark cars, their scent is likely to be moved between neighbouring and also non-neighbouring territories. This could increase encounter rates with strange scent and thereby artificially simulate increased intruder pressure. According to the 'dear enemy' phenomenon territorial animals usually react more strongly towards territorial signals from strangers than from familiar neighbours, as strangers are perceived to pose a higher threat (Temeles 1994). This effect has mostly been studied in songbirds, but mammals have also more recently been shown to exhibit the 'dear enemy' phenomenon (e.g., Palphramand and White 2007; Rosell and Bjørkøyli 2002).

Palphramand and White (2007) showed that Eurasian badgers responded more strongly to faeces from strangers than to faeces from neighbours, with the overall responses being significantly higher during the breeding season than during the rest of the year. This fits well with the observed seasonal changes in road use and, ultimately, in associations between stone martens and cars. Martens were observed to over-mark the very scent marks that had, on previous nights, been placed by other martens on the car that was used for radio tracking (see Fig. 6.1). Although there is debate about the function of over-marking, Ferkin and Pierce's (2007) competition hypothesis seems to fit best for solitary and asocial mammals. According to this hypothesis, a territorial animal may gain a competitive advantage from ensuring that its scent marks remain the uppermost marks within its territory. From this it follows that residents should monitor their territories to ensure that their scent remains on top of that of other same sex conspecifics (Ferkin and Pierce 2007).

Seiler *et al.* (1994) showed that strange scent (faeces) increased investigatory behaviour of a free ranging male marten around the areas where it had previously detected the scent. Similarly, urban red foxes responded to experimentally introduced scent marks by increasing their presence and scent marking activity in the general area of these simulated intrusions (Baker *et al.* 2000). This would explain why, in spring and summer, martens spent more time in roads around cars where, based on previous experience, they could expect to frequently encounter ‘intruder’ scent. This apparently leads urban martens to invest more time and energy into patrolling their territories, ultimately accounting for the relatively intense movement and activity levels that were observed here (see Chapter 4). Previous studies that suspected a link between territorial behaviour and the car-marten phenomenon have assumed that territorial males were the driving force behind it (Kugelschafter *et al.* 1993; Ludwig 1996). However, I have shown here that at least some females also engage in car patrolling and marking behaviour.

6.4.2. Car damage

Temporal distribution

The car-marten phenomenon had previously been linked to territoriality because the vast majority of damage incidents have been reported to occur between March and July (Kugelschafter *et al.* 1984/85; Kugelschafter *et al.* 1993; Langwieder and Höpfl 2000). This is also in line with the present study, which found the highest rate of damage in spring. This peak in reported damage also coincides with the observed increase in road use in general and car patrolling and marking behaviour in particular.

Große-Johannböcke (1995) observed four captive male stone martens engaging in ‘aggressive biting’ of branches and wooden support structures of their enclosures. This behaviour was only observed from February onwards and was thought to correspond to the car damage occurring during the same period (Große-Johannböcke 1995; Ludwig 1996). However, it was not clear whether this behaviour could be triggered by strange scent alone. Anecdotal evidence from the present study cannot confirm this. The car used for radio tracking was repeatedly visited and marked by several martens, male and female, throughout the study towns. Also, when not in use for radio tracking it was parked at night in a different town where the presence of martens had also been confirmed. Thus, even though this car clearly carried the scent of strange martens it apparently did not trigger aggressive biting as it was never damaged during the two-year study period. Also, visual observations of martens marking or over-marking outside the engine compartment did not show any behaviour resembling aggressive biting.

Other explanations for damage could be the martens' species-specific exploratory behaviour (Kugelschafter *et al.* 1989; Ludwig 1996) or even an affinity for volatiles released from warm rubber or plastic components of engine parts (Kugelschafter *et al.* 1984/85; Kugelschafter *et al.* 1989). Any of these explanations could be accommodated by the territorial hypothesis in that it would be sufficient for territoriality to establish increased contact rates between martens and cars in spring and summer with subsequent damage being an indirect consequence of this. In fact the observation that mostly new cars seemed to get damaged could indicate that other factors than territoriality may be involved. However, it would be necessary to have data on the age distribution of cars serviced by these dealerships as well as cars parked on the streets in order to show that martens specifically target new cars. In older cars (like the one used for telemetry), dust, dirt and oily substances may deter martens from biting into the parts that get frequently damaged in new and clean cars. Interestingly, however, in the town of Borgharen in the Netherlands, of 21 cars that were damaged, all were between three and ten years old (Müskens and Broekhuizen 2005). This was attributed to the fact that most new cars are parked inside garages.

Spatial distribution and frequency of damage

As in Müskens and Broekhuizen's (2005) study, marten-related car damage was reported from all mapped male and female territories. However, since male and female territories overlapped (Chapter 3) damage could not be attributed to individual martens or sexes. However, as described earlier, both sexes may be expected to be involved in the car-marten-phenomenon. In Luxembourg, damage was reported from territories where young were reared (e.g., F1 in 2005, F8 in 2006) and from territories where definitely no young were reared (e.g., F2 in 2005/6, F4 in 2006). This lends further support to Kugelschafter *et al.*'s (1993) observations that car damage cannot be primarily linked to the play behaviour of juveniles, which they derived from the observation that young martens have not left the maternal den at the time of year when damage reports start increasing.

I also found no indication that damage clustered around territorial borders where cars could get alternately visited and marked by neighbouring martens (Ludwig 1996). This reflected the distribution of damage in Borgharen (Müskens and Broekhuizen 2005) and was in line with the ‘dear enemy’ phenomenon (Temeles 1994). If cars scented with strange marten odour have a higher probability of being visited than cars marked with scent from neighbours, damage would be expected to occur throughout the territories.

In the Netherlands, damage was reported from around 3% of cars parked outside (N = 565; Müskens and Broekhuizen 2005), which is slightly more than in the present study. However, as their survey was less likely to have missed damage, the overall damage occurrence in the Luxembourg and Dutch study areas may have been similar. Older studies have reported higher proportions of cars being damaged (Kugelschafter *et al.* 1993; Ludwig 1996). This could be mostly due to the fact that the design of engine compartments has changed within the last 10 to 20 years, with many cables or hoses nowadays being less easily accessible to martens. Nevertheless, damage frequency may vary between different regions (Langwieder and Höpfl 2000). This has been attributed to a learning process that spreads car use behaviour from mother to juveniles and ultimately throughout a marten population (Kugelschafter 1989; Ludwig 1996). This may also explain why in some urban areas in Eastern Europe the behaviour seems to be already established (e.g., Krakow, Poland: M. Eskreys-Wójcik, personal communication) whereas in others it has just recently started to manifest itself (e.g., Budapest, Hungary; M. Tóth, personal communication).

6.4.3. Conclusion

Several conclusions regarding the car-marten-phenomenon can be drawn from this study. Although martens do use cars occasionally for nighttime resting, this does not seem to be related to the thermal benefits that recently used engines could potentially provide. Also, the use of cars as safe cover for food consumption or hiding purposes cannot explain road use. While martens certainly do use cars for these purposes they do so only rarely and it seems unlikely that they would deliberately shift their movements into roads in order to take advantage of cars for these purposes.

The seasonality in road use combined with the observed car patrolling and scent marking behaviour, however, suggests that this phenomenon is strongly associated with territorial behaviour. Thus, martens have learned that scent from strange martens is usually carried by cars. Consequently, in spring and summer, when defence of a territory matters most to them, they frequently visit and scent mark cars. This is a self-reinforcing system in that the more cars are being scent marked, the higher the probability of encountering strange scent becomes, and the more time the martens should invest in patrolling and marking cars. Hence, territoriality presents a mechanism for increasing contact rates between martens and cars in the period of the year when most car damage occurs. Whether the actual damage is directly related to territoriality through aggressive biting in response to strange scent, or indirectly through exploratory biting or biting induced by synthetic volatiles, remains unclear (Kugelschafter *et al.* 1984/85; Ludwig 1996).

Chapter 7: Fate of Translocated Wild-caught and Captive-reared Stone Martens

7.1. Introduction

Dealing with problem wildlife in urban areas can be a challenging task. Measures taken to alleviate human-wildlife conflict often need to take into account population ecological considerations, animal welfare issues and public attitudes (Conover 2002; Kirkpatrick and Turner 1997). Possible solutions range from simple education of the affected public over exclusion (O'Donnell and DeNicola 2006), fertility control (Porter and Underwood 2001), translocation (Craven *et al.* 1998) and lethal control of the species concerned (Henderson *et al.* 2000).

While affected people often want to get rid of the offending animal, they usually regard lethal control as cruel and thus prefer to give the animal a ‘second chance’ by translocating it to a different location (Conover 2002). Mammals such as grey squirrels (*Sciurus carolinensis*), brushtail possums and raccoons that commonly use human structures for denning in urban areas are often subjected to live-trapping and subsequent relocation elsewhere (e.g., Adams *et al.* 2004; Pietsch 1994; Rosatte and MacInnes 1989). In some instances the removal of adults or the opening of den sites due to persisting noise will reveal the presence of pre-weaned young (Matthews *et al.* 2004; O'Donnell and DeNicola 2006). In such cases wildlife rehabilitation centres often take charge of orphaned juveniles, captive-rear them, and release them into the wild at an appropriate age (Matthews *et al.* 2004; Robertson and Harris 1995b).

Conover (2002) identified several important questions relating to translocations. These addressed issues such as homing behaviour, survival and welfare of animals translocated to novel habitats, the risk of simply transferring the problem to a different area, and whether translocation actually solved the problem it was supposed to. Craven *et al.* (1998) also stressed the fact that translocations carried out by untrained private individuals usually do not give adequate consideration to habitat and other factors.

While small-scale management relocations of adult wild and juvenile captive-reared mammals are common practice, little is usually known about the fate of these animals.

In Luxembourg the stone marten causes conflicts by denning in buildings (Chapter 5) and damaging car engine components (Chapter 6). While the stone marten used to be a hunted species up to 31st July 2007, with an open season between 15th October and 28th February, hunting has since been closed year-round. It is, however, still classified as a nuisance species and can thus be legally live-trapped and eliminated all year round by private persons when causing problems on private property (Code de l'Environnement, 2002, Vol. 1, p.3). However, this piece of legislation may be subject to change in 2008 or 2009 in the context of a general revision of hunting laws (F. Wolff, personal communication).

People affected by martens and seeking advice about how to deal with them often express the wish for someone to trap the animal for them or lend them a trap so they can deal with it themselves. However, they usually do not want the animal to be harmed and thus consider translocation to a forested area a better solution (personal observation). Although no official records of such relocations exist they are undoubtedly taking place. In other countries (e.g., the Netherlands and Germany), it is also not unusual for martens to be trapped and released elsewhere by private persons even though these practices are illegal without having acquired a special license to do so (G. Müskens and B. Ludwig, personal communications).

Juvenile pre-weaned martens are occasionally found in attics or intentionally removed from roof voids. These get handed in each year at the only wildlife rehabilitation centre in Luxembourg. Similar facilities, as well as private hand-rearing attempts, exist in other countries (G. Müskens and B. Ludwig, personal communications). Those martens that do survive get released at a later stage. However, virtually nothing is known about the post-translocation behaviour and survival of wild-caught and captive-reared stone martens across the animal's geographic range (but see Herrmann 2004; Rasmussen *et al.* 1986; Skirnisson 1986).

During the course of my study I was informed about the planned translocation of an urban stone marten that was considered to be a nuisance, and about the planned release, into the wild, of several orphaned martens that had been reared in captivity. Although my project was not primarily concerned with translocation, the fact that translocation is used to deal with marten-human conflict in urban areas made it relevant to the broad aims of the study. I therefore took the opportunity to radio collar the animals in question and monitor their behaviour after release. The aims of this study were to provide a general description of the survival, movements and den selection of wild-caught and captive-reared stone martens after their translocation to a novel habitat. A published paper based on the present chapter can be found in Appendix 2.

7.2. Methods

7.2.1 Study area

The wildlife rehabilitation centre where the martens were kept prior to their release was located in Dudelange. The study took place in and around Bettembourg and Dudelange, which were described in Chapter 2. The region around these two towns was made up of a patchwork of small rural villages, agricultural and forested areas.

The translocated martens were released in the villages of Abweiler and Peppange. Abweiler was located 1.8 km from the urban perimeter of Bettembourg. The village had 80 inhabitants (Commune de Bettembourg 2007) and several farms with used and unused barns. Private houses, farms and their respective gardens covered an area of 8 ha including an orchard of 1 ha. North of Abweiler was a large continuous beech (*Fagus sylvatica*) forest with a few interspersed spruce (*Picea abies*) plantations covering about 700 ha.

Peppange was located 0.8 km from the urban perimeter of Bettembourg, east of the motorway. The village had 650 inhabitants (Commune de Roeser 2007), covered an area of approximately 28 ha, and had several active and inactive farm buildings, and about 1.2 ha of orchards. Both villages were selected for the releases due to their proximity to the general study area, their low traffic, and their rural character potentially providing the martens with den sites in barns and a rich food supply.

7.2.2. Study animals and captivity

One wild-caught marten and five orphaned juveniles, hand-reared at the wildlife rehabilitation centre, were included in the study (Table 7.1).

Wild-caught marten

This male (designated M3) was live-trapped in a storage facility in the town of Pétange where martens were purportedly causing damage/disturbance, and was handed in at the wildlife rehabilitation centre on 12/05/06. The marten was found to be in good condition. Based on its developed testes and good dentition the animal was classified as a relatively young adult male in breeding condition. Prior to its release it was kept for three nights in an outdoor enclosure of 8 m^2 with a wooden den box. The marten was kept on a diet of cat food, which it readily consumed.

On the day of release it was sedated by introducing an isoflurane-oxygen mix (4% isoflurane) via a hose into its den box. Once the marten was motionless it was fitted with a mask receiving the isoflurane mix at a flow rate of 1 $L \cdot min^{-1}$. I then measured it and fitted it with a radio collar as described in Chapter 2.

Captive-reared martens

The exact origin and dates of arrival at the centre of the five juveniles (three females: CRF0, CRF1, CRF2; two males: CRM1, CRM2) who were subsequently included in the study was not known. This resulted from the fact that the martens were kept in groups made up of mixed origins. Hence, I limit myself here to outlining the general protocol used for rearing orphaned juveniles at the centre. The numbers of juveniles handed in were 4, 20, 15, and 6 for the years 2004 to 2007 respectively. They were mostly received in late March and early April, weighing between 120 and 150 g.

The martens were initially kept on a liquid diet of Fortol (Intervet International B.V.). Once they were able to eat solid food, their diet was first switched to a Fortol/cat food mix, then to cat food supplemented with dead poultry chicks. Two weeks before being released they were also fed live laboratory mice and rats. At the age of two to three months, the martens were transferred to 8 m^2 outdoor enclosures containing two wooden den boxes. Hollow tree trunks and branches were provided as hiding and climbing possibilities. They were kept in groups of three to five individuals. Once they

Table 7.1: Summary data of translocated wild-caught and captive-reared (CR) stone martens.

ID	Sex	Age	Weight (g)	Released	Town[a]	Status
M3	M	Adult	1518	15/05/06	A	dead 22/05/06
CRF0	F	Juvenile	1380 1350 [b]	26/09/05	B	road killed 5/11/05
CRM1	M	Juvenile	1735	19/09/06	P	signal lost 29/09/06
CRM2	M	Juvenile	1794 1635 [b]	19/09/06	A	dead 3/02/07
CRF1	F	Juvenile	1616	19/09/06	P	collar shed 27/01/07
CRF2	F	Juvenile	1425 1450 [b]	19/09/06	A	recaptured, collar removed

[a] Release town: (A) Abweiler; (B) Bettembourg; (P) Peppange
[b] Weight at death or recapture

were in the outdoor enclosures, physical contact between staff and martens was strictly avoided.

On the day of their release the martens were sedated as described above. In 2005 CRF0 was fitted with a backpack radio tag with an external antenna (Biotrack Ltd, UK; model TW-3; frequency band: 150 MHz; pulse rate: 50 pulses·min^{-1}) that was glued onto the fur between the shoulder blades. This type of tag had been successfully used in Ireland on American mink and Eurasian otters, remaining on the animals for around 14 days (L. Ó Néill, personal communication). CRF0 was additionally marked with a subcutaneous PIT tag. As the juvenile martens were at or close to adult weight prior to their release on 19/09/06 we decided to fit four of them with radio collars as described in Chapter 2.

7.2.3. Release and telemetry

Urban, village and rural habitats are likely to be completely saturated with marten territories in Luxembourg. Habitats that are devoid of martens in the long term are likely to be unsuitable for them. Consequently I did not attempt to specifically identify release sites that were not already occupied by martens.

Wild-caught marten

I released M3 after sunset at 2200 h at the edge of a large forest close to Abweiler (5.7 km from rehabilitation centre; 15 km east of the initial site of capture). For the first four nights, including the release night, I tracked the animal continuously following the general telemetry procedures outlined in Chapter 2. However, due to M3’s erratic movements I was not able to take fixes at regular intervals but instead took them opportunistically whenever the animal’s whereabouts were known or when it was within visual range. I only abandoned the marten in the morning when it had finally retreated into a den and stayed there for at least 30 min. I also took one diurnal fix per day on the animal to confirm that it had remained in the den where it had been last located in the morning.

Captive-reared martens

On 26/09/05 CRF0 was released in Bettembourg into a 2 ha large set of gardens surrounded by houses and containing multiple hiding places and fruit trees. The release site was within the territories of F2 and M1 and close to the recently vacated territory of F3 (see Chapter 3; Fig. 3.1). Unfortunately, the marten lost its tag the same night and could not be followed subsequently.

The four juveniles that were relocated on 19/09/06 were released in two male-female pairs. The Peppange release site (for CRM1 and CRF1) consisted of an area with gardens, old sheds, and several large brushwood piles, 4.3 km from the rehabilitation centre. In Abweiler I released the martens (CRM2 and CRF2) close to an old barn with straw piles inside. This site was located 5.6 km from where they were reared. In order not to interfere with the regular tracking of wild martens in Bettembourg and Dudelange (Chapter 3-6), I limited myself to locating the captive-reared martens during the day in their den sites. I initially attempted to locate them on a daily basis. When there was evidence that they had finally settled in an area I only located them at a rate of two to three locations per week.

7.2.4. Data analysis

I entered the telemetry data into ArcView 3.3 as described in Chapter 2. The minimum nightly distance travelled by M3 was calculated as the sum of straight-line distances between the opportunistic fixes using the Animal Movement Analysis extension (Hooge and Eichenlaub 2000). Nightly distances covered by captive-reared martens were expressed as the straight-line distances between den sites used on consecutive days. Den sites were defined according to the level 3 den classification presented in Chapter 2 (Table 2.4), with the difference that the category ‘inhabited building’ also included the direct surroundings of the house (i.e., garden).

Due to the small number of martens that got relocated I did not carry out statistical analyses but instead limited myself to a descriptive approach.

7.3. Results

7.3.1. Wild-caught marten

Night 1 (15/05/06) – M3 was released at 2200 h at the edge of a large forest (Fig. 7.1). Initially he ventured into the forest where he moved around for about one hour before radio contact was lost. Two hours after his release when contact was re-established, M3

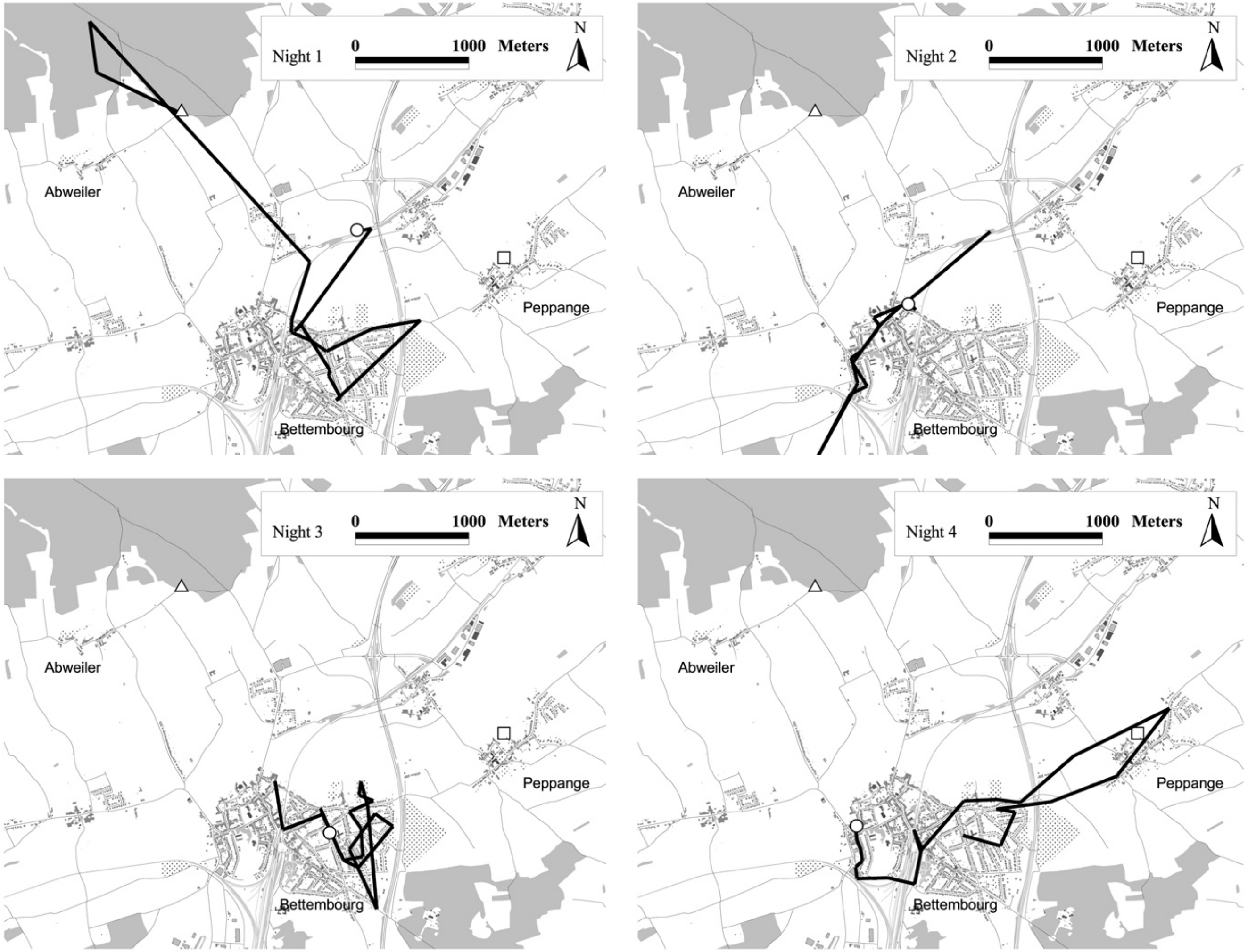

Fig. 7.1: Nightly movement patterns of a wild-caught stone marten (M3) translocated to a forest close to Abweiler. (triangle) release site; (circle) den site where night ended; (square) death.

was found right outside Bettembourg, which he entered at 0100 h. During the rest of the night M3 wandered about the home ranges of the males M1 and M2 (Figs. 3.1 and 7.1). He mostly walked along roads, spent little time in gardens and was frequently seen sniffing the pavement and walls. At 0320 h M3 was heard screaming and observed being chased down a road by M1. After having hidden/rested for 1 h he left the town and denned in dense vegetation. Visual observations of M3 gave the impression that his body was tense and stiff, and his walk less fluent than that of resident martens. He also seemed to pay less attention to passing cars or people. This impression persisted throughout the following nights.

Night 2 (16/05/06) – M3 left its den at 2200 h and moved straight back to Bettembourg, this time entering the western part (Fig. 7.1). He stopped at a complex of old, partly demolished buildings for about 1 h before moving on. At 2420 h he was seen being chased by an unknown marten northeast of F4's range (Fig. 3.1). After that he spent most of the night in F4's range. On two occasions martens (F4 and a larger untagged marten, presumably a male) were seen sniffing the road where M3 had passed moments earlier. Thus they seemed to be aware of his presence. M3 left the urban perimeter of Bettembourg only once heading southward, but after half an hour returned to the town. Before sunrise, M3 headed back to the demolished buildings he had rested in earlier that night. Before retreating for the day he was observed eating the remnants of a sandwich and scavenging from a bowl containing cat food.

Night 3 (17/05/06) – M3 left his den shortly after 2200 h. He spent most of the night in the territories of M1 and M2 (Fig. 7.1). Once he only narrowly escaped being hit by a car thanks to the driver braking sharply. Just before sunrise he moved about extensively in gardens and seemed to have trouble finding a suitable den site. At 0500 h he was still moving around in a set of gardens with M2 being located close to him. Presumably being chased away by M2, he finally settled inside the engine compartment of a car at 0600 h. M3 escaped from the car when the owner arrived at 0700 h. The marten then climbed into a car on the opposite side of the road, but changed cars twice more within the next 30 min after disturbances. At 0730 h he had finally settled inside a fourth car, where he stayed until at least 1530 h. After being disturbed again by the owner of that car he changed to a fifth and last car that day.

Night 4 (18/05/06) - He left the car at 2210 hours, spent some time in M2’s range before leaving Bettembourg and entering Peppange at 2315 hours (Fig. 7.1). He wandered around the whole village for 1 h, then headed back to Bettembourg where he spent the rest of the night in the territories of M1 and F4. Again he seemed to have trouble finding a den site but finally settled in or behind a building that was also regularly used by F4 for denning.

During the nights 1 to 4, M3 had moved minimum nightly distances of 9.2, 4.8, 5.8 and 7.1 km (based on opportunistic fixes), respectively. Thereafter M3 was not tracked at night anymore. The following day (20/05/06) he could not be located anywhere in the whole area. On the 21/05/06 he was located in a culvert under a small trail in the fields next to Peppange. A day later (seven days after release) M3 was found lying dead on the trail 5 m from the previous day’s den and 3.1 km from his release site (Fig. 7.1). M3’s den selection is summarised in Table 7.2.

As no obvious cause of death could be established, a post-mortem was performed by a wildlife veterinarian (L. Reiners) at the rehabilitation centre in Dudelange. While the exact cause of death could not be determined, several factors could be excluded. M3 had no concussion or other haematomas (i.e., not hit by a car), did not die of starvation (no muscle regression, some food in stomach), obvious disease, an excess of parasites, or rodenticide poisoning. He had no bite marks from martens or other animals, and was not shot. Death from poison other than rat poison or excessive stress and trauma related to its translocation could not be excluded. Overall the animal appeared to have been in good condition (L. Reiners, personal communication).

7.3.2. Captive-reared martens

CRF0

CRF0 was found road-killed on the 05/11/05 and was identified by her PIT tag. She died just 440 m from where she was released 40 days earlier, within the narrow overlap zone between F2’s territory and F3’s former territory (Fig. 3.1). She was in very good condition at the time of her death and had maintained her weight since the release (Table 7.1).

Table 7.2: Den selection (% use; Level 3) for one relocated wild-caught stone marten (M3) and four captive-reared martens after their release.

Den Type	**M3** (5)[a]	**CRM1** (7)	**CRF1** (59)	**CRM2** (59)	**CRF2** (59)
Inhabited Building			10.2	5.1	72.9
Uninhabited Building	40.0		11.9	28.8	
Other Anthropogenic	40.0	42.9	6.8	3.4	3.4
Natural	20.0	57.1	71.2	61.0	23.7
Unknown				1.7	

[a] sample size (in days)

While tracking the male M1 (Chapters 3-6), whose range had overlapped with that of F3, an untagged marten was observed within F3's former range during the night of the 02/10/05. During the same period a prebaited trap in F3's former range was visited several times by a marten without resulting in a capture. After CRF0's death there were no further sightings of an untagged marten in F3's former territory and all visits to the trap also stopped. Thus it seems likely that CRF0 had occupied the vacant territory adjacent to her release site.

CRM1

CRM1 denned the first two days in a culvert under a small road not far from his release site. After that he spent three days in a forest/field environment south of Peppange, then a couple of days in the surroundings of the village of Hellange (Fig. 7.2). On the ninth day after his release he was denning in dense vegetation in a dried up pond, 20 m from a motorway. Thereafter his signal was lost even though extensive searches were carried out throughout the region. During the nine-day period before his disappearance, seven diurnal fixes were taken on this male, none of which were in direct proximity of buildings. After having left the culvert where he initially stayed, he exclusively denned in dense brush.

CRF1

After being released CRF1 denned at the release site for four days, although she was located a few times in the nearby forest/field environment at night (Fig. 7.2). On the fifth day she had moved to the village of Hellange where CRM1 was also active at the time. On 27/09/06 both martens were denning together in a bramble thicket 1.9 km from the release site. She stayed in this village for six days, denning in close proximity to two inhabited houses on five occasions. On 01/10/06 CRF1 had crossed the border to France and was found on the outskirts of a small village (Zoufftgen) 4.6 km from the previous day's den site (Fig. 7.3.a). During that movement she had crossed at least one busy motorway and a large forest. At 0530 h on the 05/10/06 she was sighted as close as 1.5 km from the rehabilitation centre but then returned and denned close to Zoufftgen. She stayed in or around this village for 26 days before heading to the neighbouring village (Roussy-le-Village, 2.9 km). Here she finally settled in a patch of about 0.5 ha of hawthorn (*Crataegus monogyna*) thickets, denning in a large pile of brushwood 7.6 km from her release site (Fig. 7.3.a). This patch was completely isolated, being surrounded

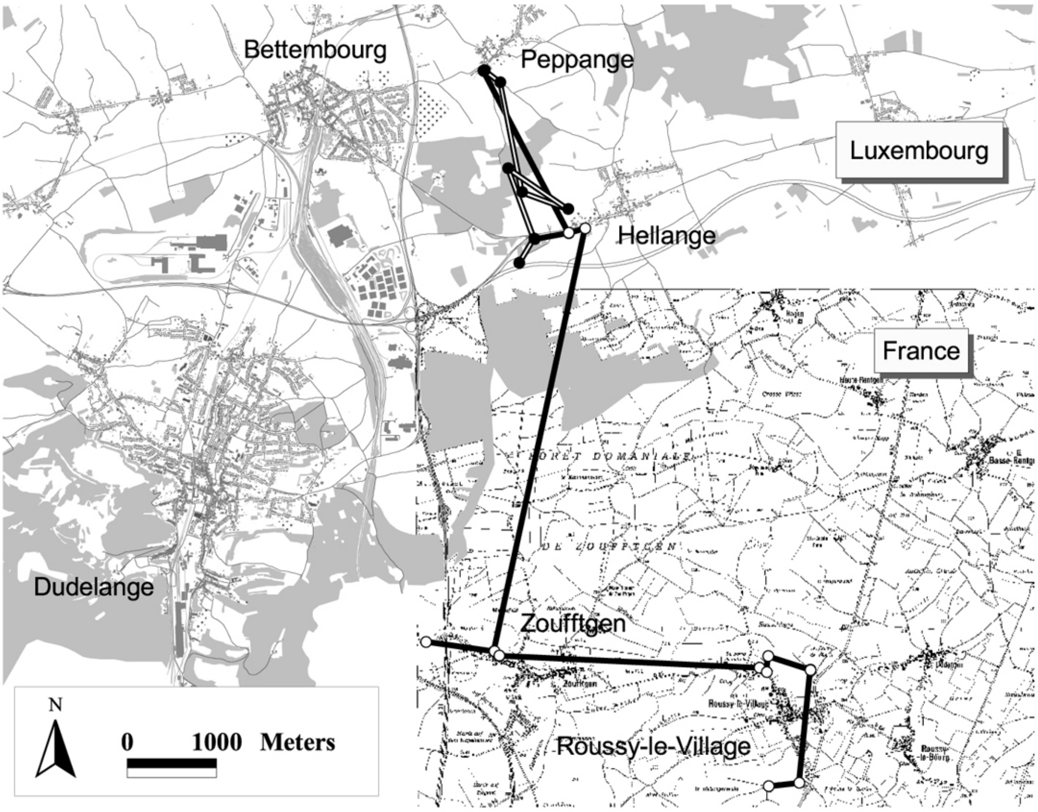

Fig. 7.2: Travel patterns (lines) and den sites (circles) for two captive-reared stone martens relocated to the village of Peppange: (grey line) CRM1; (black line) CRF1.

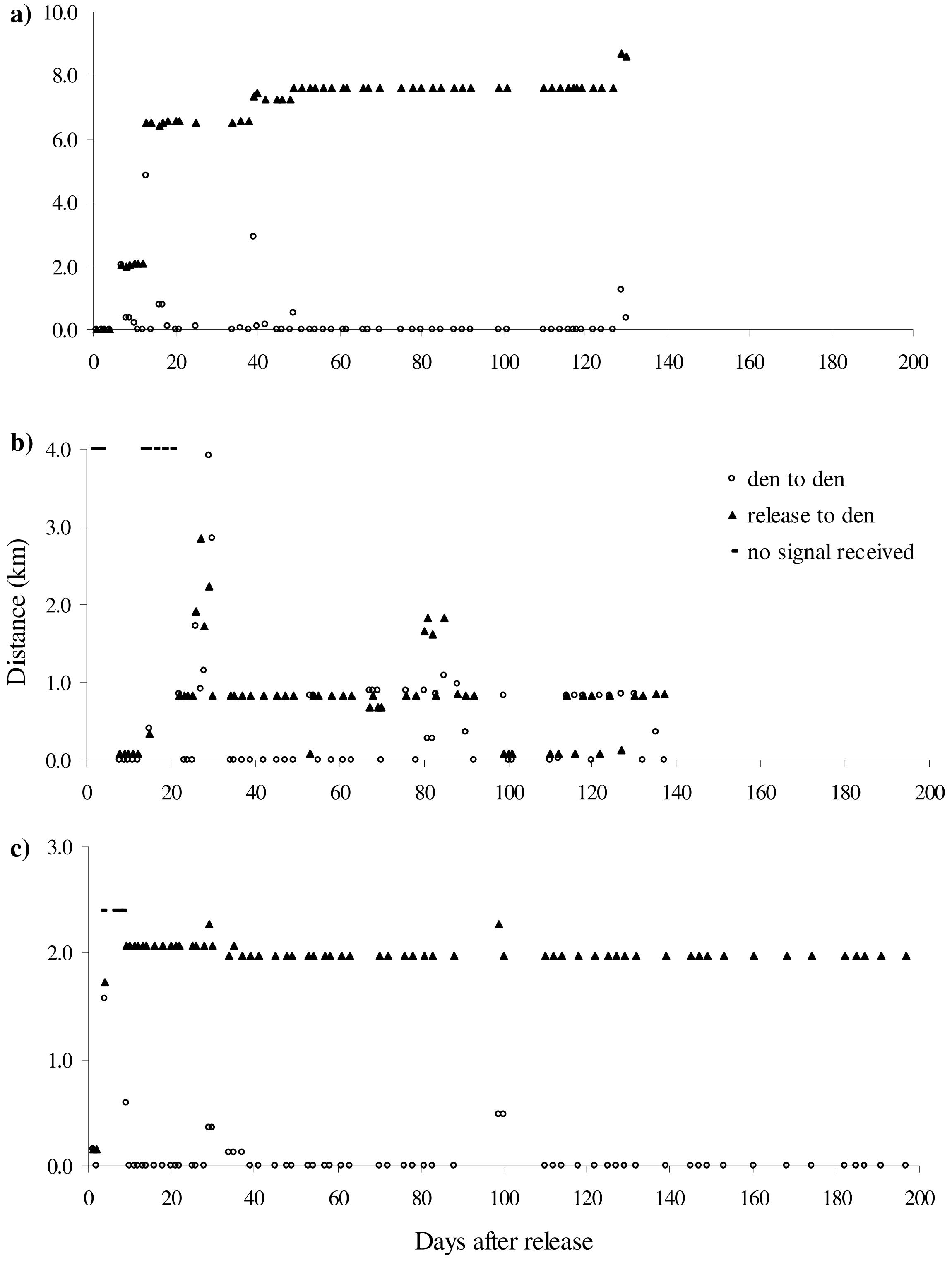

Fig. 7.3: Distance of den sites from release sites and distance of den sites from the previously known den site plotted against time in days for three captive-reared stone martens: (a) CRF1; (b) CRM2; (c) CRF2.

by bare pastures and fields. Every diurnal fix taken between 07/11/06 and 24/01/07 pointed her to this site. She also never seemed to leave this patch at night. On 26/01/07 she had crossed the entire village and spent the day in direct proximity to an inhabited house 1.2 km from the previous den. The next day she had shed her collar. The braided nylon had been completely frayed and the rubber coating showed significant scratch marks.

CRM2

Straight after his release, CRM2 could not be found for six days until he was located in a barn just a few meters from his release site. He stayed there for six days before contact was lost again for a week. Due to a badly tuned telemetry receiver the signal was only received from close range. Thus it was not known if the animal had moved large distances or had stayed within the general release area while it was not accounted for. After the necessary receiver adjustment had been made contact was not lost again.

On the 11/10/06 he was located in a hollow oak tree (*Quercus robur*) that was his most commonly used den thereafter. Between 14/10/06 and 19/10/06 he undertook an excursion that started and ended at this oak (Fig. 7.4). He first ventured 1.7 km, then another 0.9 km to the east, before heading back westward 1.1 km, then another 3.9 km (Figs. 7.3.b and 7.4). Here (2.2 km from the release site) he denned in dense brush only 15 - 20 m from CRF2, which he had presumably had no contact with since their release one month earlier. After this excursion CRM2 stayed in the general area of his release site (Fig. 7.4). He used a variety of different den sites in dense brush, hollow trees, bird nests and barns, spread over an area of about100 ha. He also occasionally spent the day in Abweiler close to his release site (Fig. 7.3.b). On 03/02/07, CRM2 was found dead, curled up in a cardboard box, in a small garden. His neck was injured by the collar he was wearing. He had lost about 160 g since his release (Table 7.1).

CRF2

CRF2 denned in a culvert close to her release site for two days. Contact was then lost for six days before she was relocated in a forest/field environment west of Abweiler (Fig.7.4). Here she first denned in dense brush before finding a cavity in a willow (*Salix* sp.) tree that served as den site for about 10 days. On the 23/10/06 she was for the first time located inside or in direct proximity to one of two neighbouring houses at the

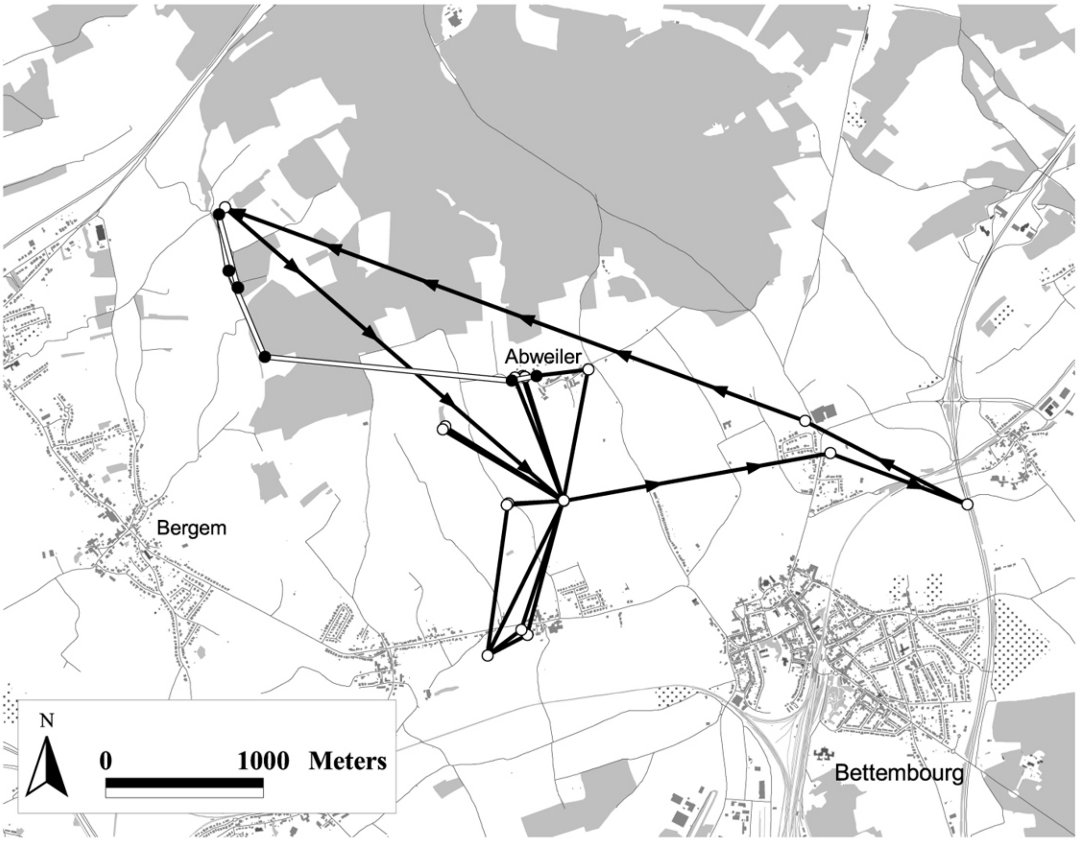

Fig. 7.4: Travel patterns (lines; arrows show five-day excursion route) and den sites (circles) for two captive-reared stone martens relocated to the village of Abweiler: (black line) CRM2; (white line) CRF2.

forest field interface, 2.0 km from her release site (Fig. 7.3.c). The house was in a bad state, but was regularly inhabited. Over the next 165 days she was located 45 times. On 43 occasions she denned in or around this house, once she was found in a willow tree, and once in dense brush 0.5 km from the house (Fig. 7.3.c). Whenever she was located at night, she was inside her den or within direct proximity (< 100 m) of it in a narrow strip of garden and woodland.

After CRM2 was found dead an attempt was made to recapture CRF2 to examine her neck and remove the collar. In mid February a trap was set and prebaited with eggs 50 m from her den. On the 29/03/07 an untagged stone marten (presumably a male based on its size) was caught and released without processing. On the 5/04/07 CRF2 was finally caught. As her neck was also injured she was brought back to the wildlife rehabilitation centre. Her neck was stitched up and she was kept for observation at the centre until the 24/04/07 when she was released close to her capture site. Even though she was severely injured she had not lost any weight since her release (Table 7.1). While staying at the wildlife rehabilitation centre it became apparent that she was shy and aggressive just like any free ranging marten.

Den sites

The captive-reared martens often denned in trees, bramble, and brushwood piles. Where den sites were classified as inhabited buildings the martens most likely found shelter in proximity to those houses (vegetation or anthropogenic structures other than buildings) rather than directly inside them (Table 7.2). Whether CRF2 denned inside the house where she had finally settled remained unclear. There was plenty of junk lying around the house that would also have provided many hiding places.

7.4. Discussion

Any conclusions drawn from these relocations need to be considered with care due to the small number of individuals involved. Nevertheless some general comparisons can be drawn with the outcomes of translocation experiments on other species.

7.4.1. Wild-caught marten

So far only one study has focused on the fate of translocated stone martens (Rasmussen *et al.* 1986). However, the authors did not radio track the animals but relied instead on capture-mark-recapture techniques. Of 53 translocated martens, 16 were recaptured within six months. One of those showed clear homing behaviour. It was recaptured in the same trap 10 days after first capture and after having been moved 30 km away (Rasmussen *et al.* 1986).

Skirnisson (1986) radio tracked a male that was trapped and subsequently kept for 136 days in captivity. After being released 8 km from its capture site, the animal moved a little over 4 km before its signal was lost the same night about 3.2 km from its release site. The fate of this marten remained unknown. Skirnisson (1986) also released an adult female (W6) 1.2 km from the site where she was trapped the same day. She moved 8 km and finally denned 2.2 km from her release site. Here she was killed the same day by a dog. These observations compare with M3's behaviour during the first night after translocation. None of the martens stayed at their release sites, but instead engaged in significant exploratory movements.

M3's brief stay in the forest and subsequent intensive exploration over four nights of the urban habitat of Bettembourg suggests a tendency to return to familiar habitat. This could either be seen as an attempt to find familiar features or scent within this habitat that would help it locating its former home range, or simply an avoidance of unfamiliar rural or forested habitats. This behaviour is comparable to that of translocated urban raccoons (Hagen *et al.* 1991; Rosatte and MacInnes 1989). Those released in unfamiliar (rural) habitat moved much longer distances than those relocated to another town. Furthermore, 60% of raccoons settled within 0.3 km of towns. These animals were located about 45% of the time inside residential areas during their nightly activities (Rosatte and MacInnes 1989). Urban brushtail possums translocated to forests also rapidly disappeared from the release sites and subsequently often used houses for denning (Pietsch 1994).

M3's and W6's rapid deaths also fit within the general picture of translocations. Reduced survival of relocated urban mammals has been reported for grey squirrels (41% dead after 1 month: Adams *et al.* 2004), raccoons (50% dead within first 3 months: Rosatte and MacInnes 1989), brushtail possums (88% dead within 1 week: Pietsch 1994) and white-tailed deer (83% dead within on average 185 days: Bryant and Ishmael 1991; 44% dead within first 3 months: Jones and Witham 1990). On the other hand a social group of six urban badgers relocated to a rural forested area via a soft release fared well thereafter (Brown and Cheeseman 1996). Causes of death are generally attributed to stress, territorial behaviour and aggression, unsuitable habitat, nonestablishment, disease transmission, and disorientation leading to competitive disadvantage and predation (Craven *et al.* 1998). Several of these factors applied to M3. Its translocation might have been less stressful had it taken place outside the stone marten's most territorial period (i.e., after spring; see Chapters 4 and 6).

7.4.2. Captive-reared martens

Research on captive and wild stone martens has shown that certain spatial preferences and behaviours are handed down from mother to offspring. Indeed young martens explore their environment by closely following their mother on her nightly activities as well as using the same den sites (Herrmann 2004; Weckert and Kugelschafter 1994). Juveniles reared in captivity without their parent, however, lack these experiences.

Nevertheless, at least four of the five captive-reared martens survived in the wild until six weeks after their release and three would have survived past 20 weeks if it had not been for CRM2's neck injury. Herrmann (2004) released a hand-reared juvenile male that survived for at least two months when its signal was lost. The survival of these martens seems to be higher than that reported for captive-reared and released fox cubs (Robertson and Harris 1995a) and hares (*Lepus europaeus*) (68.2% mortality within 10 days, Angelici *et al.* 2000). Food acquisition does not seem to be a major problem for these naïve martens. Some faeces recovered from CRM2's hollow oak den showed clear signs of berry seeds (unpublished data) and CRF2 may have been able to scavenge from the cat food that the owner of the house neighbouring her den always left outside for his pet cats. This may even have helped her to survive and maintain her weight despite her injured neck. Another factor that could have contributed to their survival was the very mild autumn and winter 2006/2007, with the months of September, October and January being the warmest on record (Administration de l'Aéroport 2007).

Whether the post-release movements described here correspond to natural dispersal behaviour is unknown. Few detailed accounts of dispersing juveniles exist. A juvenile female observed by Herrmann (2004) established a new home range about 6 km from her previous one after a 24 h dispersal followed by several smaller excursions in the following days. Two males followed by Skirnisson (1986) extensively moved outside the maternal home range for at least five to eight days before their signal was lost. A juvenile female that dispersed in the city of Nijmegen in the Netherlands (Broekhuizen *et al.* 1989) left her maternal home range in early November and moved around extensively before settling for a month in one area. Then she moved to another area where she stayed for around three months but started moving around again in March (Broekhuizen *et al.* 1989). These dispersal events were superficially similar to the movements observed for the martens released in 2006. Their dispersal was also characterised by an initial period of movements followed by one or two prolonged stays in restricted areas. However, for two of the captive-reared martens this use of a restricted area with little activity at night was more extreme than what has been observed elsewhere for wild martens. This could be due to a lack of previous experience of normal ranging behaviour. The extent to which injury may have influenced this is unknown.

Robertson and Harris (1995b) reported a similar behaviour pattern for captive-reared fox cubs. This was characterised by an initial erratic phase lasting on average 17.2 days followed by a restriction of activities to a small area, which was used intensively thereafter. They suggested that rather than searching for a vacant home range, dispersing foxes (wild- and captive-reared) search for a very small area to establish a temporary range and only attempt to establish a territory later (Robertson and Harris 1995b). This may also apply to stone martens.

There seemed to be a tendency for the martens to remain within the overall habitat that they were released into. The animal released in Bettembourg was still in the same habitat at its death and the village/rural-released animals neither settled directly in forest nor in larger urban settlements. Their den selection was also more similar to that described for rural martens (Herrmann 2004; Lachat Feller 1993a; Skirnisson 1986) than what was observed for urban ones (Chapter 5). Early experience of structures in their enclosure and the environment at their release site may have a lasting impact on later den and habitat selection as well as potential nuisance behaviour.

7.4.3. Conclusion

Numerous studies have shown that the live-trapping and translocation of nuisance wildlife to novel habitats mostly results in the death of the animals. This does not seem to be different for stone martens. Thus the intention of giving the animal a fair 'second chance' often results in little more than submitting it to extensive stress and perils. Furthermore, the animals seem to be likely to return to urban habitat and cause similar problems, while their vacated territories are probably reoccupied or taken over by a neighbour (Herrmann 2004). The experience gained from M3's case suggests that translocation may not be a good solution for dealing with problem martens. Exclusion from den sites in buildings should be emphasised (Ludwig 1999) and live-trapping only be used as a last resort.

In principle, rehabilitated orphaned martens seemed to be able to survive in the short-term after being released. While they may rapidly disperse from their release site, careful selection of a release environment nevertheless seems to be important. The fact that they did not have a mother to learn from may make them less prone to exhibiting nuisance behaviour (i.e., denning in inhabited houses; damaging cars). This should, however, not encourage people to remove juveniles from attics, but instead adults should be excluded from houses before the young are born in March. Further follow-up studies on the behaviour of translocated martens would be beneficial but the adverse effects of placing collars on juveniles need to be given serious consideration.

Chapter 8: General Discussion

Stone martens are common inhabitants of urban areas throughout central Europe, but their spatial ecology has received relatively little attention. The only knowledge that the general public usually has about these animals relates to the conflicts that arise from their denning and car use behaviour (personal observation). Therefore, the main aims of my study were (i) to provide a thorough description of the urban stone marten's behavioural ecology in order to identify potential differences between urban and non-urban martens; and (ii) to suggest conflict management recommendations based on this knowledge.

8.1. Overview of main findings

Chapter 3 showed that the stone martens I had trapped in urban areas essentially spend the entire year within this habitat. Their presence in towns seems to be independent of the availability of nearby forested or rural habitats, which are used very little by comparison with urban habitat. Chapter 3 also showed that urban stone martens maintained on average smaller territories than have been reported from forested, and to a certain degree, rural environments. However, in terms of their socio-spatial organisation, this reduction in territory size and the resulting moderate increase in population density seem to be the only real adaptations to urban habitat. Like their rural- or forest-dwelling counterparts, urban stone martens maintain a solitary lifestyle (i.e., they do not form groups or cooperate) based on intrasexual territoriality with little or no home range overlap between same-sex neighbours.

Chapter 4 showed that martens also adapted to urban environments through temporal avoidance of humans and their activities (e.g., traffic), increasing their degree of nocturnality by comparison with rural martens and shifting their activity to parts of the night when encounters with humans and moving cars are less likely. Somewhat surprisingly, they did not significantly reduce their activity levels or movement distances, even though they lived in relatively small territories and in a presumably resource rich environment. In Chapter 6, I hypothesised that this high level of activity was related to scent marking behaviour. Because martens frequently scent mark nonstationary objects (i.e., cars), the perceived intruder pressure in urban areas may be higher than in rural environments, leading to more pronounced territorial behaviour and, consequently, higher activity and mobility.

The findings from Chapter 5 demonstrate that urban stone martens rely to a very high degree on anthropogenic structures for denning purposes. To my knowledge, martens have not previously been shown to use buildings in general, and inhabited buildings in particular, as intensively as in the urbanised habitats described here. The fact that the animals increased their use of structures with better thermal properties (i.e., human-inhabited buildings) during the coldest season of the year illustrates that they have learned to optimally exploit the available denning resources in urban environments.

I demonstrated in Chapter 6 that martens occasionally use cars as nighttime rest sites all year round. However, they predominantly come into contact with cars during spring and summer. During this same period the animals directly scent mark cars but engage less in this behaviour during autumn and winter. The fact that these car-patrolling activities coincide with the period when most damage is reported strongly suggests that the car-marten-phenomenon is driven by the stone marten's territorial behaviour. Whether the biting and scratching of various parts under the bonnet is a direct aggressive response to strange scent or simply a by-product of higher contact rates between martens and cars remains to be determined.

Finally, Chapter 7 addresses the usefulness of translocation as a method of dealing with problem martens. A translocated radio-collared adult marten neither stayed in the forest where it was released nor survived for very long thereafter, suggesting that translocation is not the easy and marten-friendly management tool that it is often assumed to be.

8.2. Socio-spatial organisation and resource use

It is somewhat surprising that neither this study, nor any of the Dutch studies (e.g., Bissonette and Broekhuizen 1995; Müskens and Broekhuizen 2005), have found that stone martens significantly alter their socio-spatial organisation in response to urban habitat. Other urban mesocarnivores, such as red foxes, raccoons and Eurasian badgers, or large carnivores such as black bears, may show evidence of much reduced or even lack of territoriality (Cresswell and Harris 1988; Davison 2007), drastically decreased home ranges (Beckmann and Berger 2003a; Davison 2007), increased social group sizes (Baker *et al.* 2000; Gloor 2002), or aggregated spatial distributions (Beckmann and Berger 2003a; Hohmann *et al.* 2001; Prange *et al.* 2004), all of which result in (at least locally) much higher densities. Thus, the question then arises as to why urban stone martens remain strictly territorial, solitary and occur at only moderately elevated densities.

Resource (usually food) density and dispersion are generally invoked to explain reduced home range sizes, increased aggregation and group formation in urban environments. It is usually assumed that in female carnivores space use relates to food availability and in males to the distribution of females (Sandell 1989). Thus, food may have a direct effect on female spacing and indirectly influence male spacing. Although food in urban areas may be more abundant, some species such as skunks may not be able to exploit these resources as efficiently as others (e.g., raccoons: Gehrt 2004). This may also be the case for martens. They are rather small and inconspicuous and do thus not profit from being fed by householders as red foxes and Eurasian badgers commonly do (Baker *et al.* 2000; Davison 2007). Where pet cats are fed outside, the martens' small body size may to a certain extent restrict their access to this source of food due to interference competition with cats (this study, Chapter 1). They also lack the dexterity that allows raccoons easy access to a variety of anthropogenic foods (Prange and Gehrt 2004). Consequently, although martens certainly do not experience a shortage of food in urban areas, they nevertheless may not have access to the same amount of scavengeable anthropogenic food as do larger mesocarnivores. This seems to be in line with results from diet analyses from urban areas showing that stone martens make little use of scavenged food (for refs see section 1.4.2.). Hence, food availability in urban areas may simply not be sufficient to make territoriality unprofitable for martens (see Powell 1994).

Another type of resource that is important for stone martens are daytime and maternal den sites. Herrmann (2004) postulated that good quality den sites were a limiting resource in forested and rural areas but were abundant in urbanised habitats. He was also under the impression that denning in buildings had gradually become more common since the 1980s when he had collected his data. The results from Chapter 5 seem to support the view that good quality den sites do not constitute a limiting resource in urban areas.

Not only the abundance but also the dispersion of resources in space and time may influence the socio-spatial organisation of a population. According to the resource dispersion hypothesis (RDH: Macdonald 1983), environments where resources occur in patches with high but temporally unpredictable productivity would favour the formation of groups. A pair of individuals would need to maintain a minimum sized territory guaranteeing access to productive patches at any given time of the year. However, as patches often produce more food than needed by a pair of individuals, additional animals would be tolerated within the same area (Macdonald 1983). Thus, according to RDH, within-species differences in socio-spatial organisation are attributable to differences in the spatio-temporal distribution of food. Although RDH is usually only applied to food resources, other resources such as water or shelter sites may also be considered within this same framework (Blackwell 2007). Johnson *et al.* (2000) viewed urban areas as typical RDH-type habitats. Nevertheless, as of now there are no accounts of group forming in urban stone martens. This could potentially be explained by there being a lack of spatial correlation of yields between gardens within a territory, thus leading to a lack of clear patchiness or heterogeneity in the urban environment (see Blackwell 2007). This, however, seems unlikely considering that seasonal core area use showed differential use of certain areas within territories (Figs. 3.8 and 3.9). This strongly hints at the presence of distinct patches with varying access to food and shelter during different times of the year.

Another explanation for the lack of plasticity in the socio-spatial organisation of stone martens is that intrasexual territoriality may be a phylogenetically defined trait that is under little influence from environmental variables. This explanation was favoured by Herrmann (2004), who used it to explain why population densities in villages seemed to remain much lower than a resource (food and den site) based carrying capacity in such an environment would suggest. This also seems to apply to the current study. In fact, this ‘hard-wired’ intolerance of same-sex conspecifics is a definining characteristic of marten species in particular (Balharry 1993; Powell 1994) and mustelids in general (group formation in badgers and some otter species is generally seen as an exception among mustelids: Johnson *et al.* 2000, Powell 1979) . To date only few accounts of same-sex home range overlap between adult martens (*Martes* spp.) exist (e.g., *M. flavigula*: Grassman *et al.* 2005, *M. zibellina*: Miyoshi and Higashi 2005, *M. americana*: Powell 1994 and references therein). Since neither resource abundance nor dispersion seems to adequately explain the strict adherence of urban stone martens to intrasexual territoriality, the present study lends support to Balharry's (1993) and Herrmann's (2004) explanation of a phylogenetic inflexibility in socio-spatial organisation. An evolved aggression towards offspring of dispersing age may thus override any cost-benefit tradeoffs that are used to explain sociality in carnivores (Johnson *et al.* 2000). Future studies investigating relatedness between martens in towns such as Dudelange and Bettembourg should be able to provide a more in depth picture of social organisation and mating tactics of urban martens.

8.3. Urban adapters or exploiters?

The criteria for classifying urban animals as adapters or exploiters include factors such as their diet, peak densities, activity patterns, shelter use and whether they are native or invasive in the area (McKinney 2002, 2006). Although it may not always be possible or even desirable to attempt to class organisms into distinct categories it may help, nevertheless, to visualise general patterns.

Urban exploiters are often species that are not native to an area and have been introduced deliberately or accidentally by humans to urban environments outside their geographical range. Adapters on the other hand are usually natives that have invaded urban areas from surrounding natural areas. As of now there is only one report of a non-native stone marten population (Long 1995) and, unlike red foxes, martens have never been reported from urban areas outside their native geographical range. In terms of diet, adapters can be distinguished from exploiters in that the former make use of both natural resources (such as cultivated plants or free-ranging animals) and anthropogenic resources (such as garbage or deliberate feeding), while exploiters are often completely dependent on anthropogenic resources. Although a diet analysis was not performed as part of the present study, it is apparent from the studies on diet reviewed in Chapter 1 (section 1.4.2.) that urban martens clearly fulfil the urban adapter criteria with respect to diet.

According to McKinney (2006), another distinguishing feature between adapters and exploiters is the way they find and use shelter in urban areas. In this respect, the stone marten differs somewhat from other urban mesocarnivores in that it seems to be more dependent on human structures. Urban exploiters often live completely within, or both within and outside of, buildings (McKinney 2006). Although stone martens spend the bulk of their nighttime activity outside of buildings (Chapter 4), I showed in Chapter 5 that they almost exclusively rely on buildings for daytime denning. This is unlike urban badgers and foxes that usually continue to dig their own setts or dens (Davison 2007; Marks and Bloomfield 2006) or urban raccoons that often continue to rely on natural den sites such as trees (Hadidian *et al.* 1991).

Density is another important factor. Both adapters and exploiters reach higher densities in urban than in non-urban areas. However, adapters usually reach these elevated densities in areas of intermediate urban development while exploiters reach them in the urban core (McKinney 2006). Stone martens occurred at higher densities in my study than in other non-urban studies (Chapter 3). When compared to inner-city areas, the present study sites could be defined as being of intermediate development. Although stone martens are known to occur in intensely developed urban cores (e.g., Budapest: M. Tóth, personal communication) nothing is known about the densities that they achieve in such habitat. A currently ongoing diet and radio tracking study on martens in the suburbs and urban core of the city of Krakow may shed more light on how marten densities (and socio-spatial organisation) respond to development levels higher than the ones considered here (M. Eskreys-Wójcik, personal communication).

In summary, stone martens are best described as typical urban adapters. Although their pattern of socio-spatial organisation may be inflexible (see above), martens seem to be able to adapt other aspects of their behaviour, such as activity patterns, den selection and diet, to the challenges that they face in a human-dominated environment. This flexibility is probably an important contributor to the success of martens in urban areas. Delibes (1983) hypothesised that, in central Europe, the stone marten was excluded from forested habitat and pushed into urban areas by interspecific competition with the pine marten. More plausible, however, seems to be that the behavioural flexibility of stone martens exceeds that of pine martens, and this has helped them to start exploiting a previously unexploited niche. The higher density of urbanised areas in central Europe, as opposed to the Iberian Peninsula, would have promoted the move into this type of habitat and the rapid spread of the requisite behavioural adaptations through the stone marten population.

The stone marten's ability to restrict its movements to the night, especially while rearing young, sets it apart from the pine marten and has been hypothesised to be a reason why the former has been able to adapt to urban habitat (see Broekhuizen and Müskens 2000; Zalewski 2001). Furthermore, Skirnisson (1986), Herrmann (2004) and the present study (Chapter 4) have demonstrated that this degree of nocturnality can be further amplified in village and town environments, allowing the stone marten to better avoid human activities. It is currently unknown to what extent such behavioural adaptations predispose young martens that have grown up in towns and cities to preferentially disperse within or between other urban areas and settle in this same type of environment. Future research employing a combination of genetic analyses and telemetry to quantify the degree of mixing between urban and surrounding rural populations would be desirable.

8.4. Conflicts and management

8.4.1. Densities

When considering human-marten conflicts and how to deal with them, it is useful to first reflect on how current knowledge may inform us about potential future developments of urban marten populations. Human-wildlife conflicts often become aggravated as wildlife population densities increase, a development that may then be paralleled by a decrease in tolerance towards the animals (Conover 2002). The question thus arises as to what is the potential for further increases in marten densities in towns in Luxembourg and elsewhere in Europe. In Dudelange and Bettembourg the marten population was characterised by strict intrasexual territoriality. There was no suggestion of group formation and all habitat within the urban perimeter of the towns was saturated with marten territories (although some areas may have been temporarily unoccupied after the death of the occupant). Where no martens were tracked, their presence was confirmed with the help of direct sightings, as well as reports of den sites and car damage (see Fig. 6.2). In the Dutch town of Borgharen the situation was similar although on a somewhat smaller scale (Müskens and Broekhuizen 2005). Therefore, unless martens considerably reduce their territory sizes it seems unlikely that population densities in these towns would increase much.

Another important consideration in this context is the reproductive success of females in an urban environment. Although Herrmann (2004) hypothesised reproduction to be much higher in urban than in rural or forested areas, this has so far not been confirmed (Chapter 3; Lammertsma *et al.* 1994). Thus at higher population densities female martens do not seem to be able to reproduce or rear young successfully every year. To summarise, urban population densities of stone martens are likely to remain relatively low, owing to the constraints of intersexual territoriality and a low reproductive rate.

8.4.2. Denning-related conflicts

Urban or suburban stone martens quite often chose to den in inhabited buildings (Chapter 5), which can lead to conflicts ranging from noise disturbance to damaged roof insulation. The only long-term solution to this problem is to prevent the animals from entering the roof space or attic in the first place, by blocking up any entry holes (≥ 5 cm diameter) that may be found in the roof (see also Ludwig 1999). The danger, however, is that if this is done when a marten is already in residence, the marten may be trapped inside the den. One-way doors, as are occasionally used in North America to exclude squirrels from buildings (by letting the animal leave the den but preventing re-entry), have to date been neither designed nor used for martens.

Due to rapid habituation to potential deterrents such as strong odours (e.g., mothballs, toilet blocks), noise (e.g., loud radio) or regular visits to an attic that is used for denning, these measures may at best have a transient effect without solving the problem permanently (personal observation; Ludwig 1999). However, such short-term effects may be sufficient for deterring martens from using the den in the days preceding more permanent exclusion measures. Several observations gained from the current study may help in guiding such efforts.

Observation 1

Stone martens may visit up to 20 dens over the course of a year with the majority of denning occurring in uninhabited buildings.

Recommendation

The often relatively large number of available dens will leave the marten with alternatives in the event that one of them is made unavailable as a result of exclusion measures. Since many of these sites, especially those containing favoured dens, are uninhabited (see Chapter 5), the likelihood of directly transferring the conflict to another inhabited house is limited. Exclusion of martens from inhabited houses should therefore be favoured as a method dealing with denning-related problems.

Observation 2

Individual den sites are often used intermittently and den use may change on a seasonal basis. Hence, an individual den may be visited regularly during one season but never or rarely during subsequent seasons.

Recommendation

The absence of marten disturbance after a prolonged period of conflict does not mean that the animal has permanently abandoned the den. Rather than viewing this period as one where no more action is needed it should be viewed as an opportunity to make the roof permanently inaccessible to martens without the risk of trapping the animal inside the den.

Observation 3

While rural martens may leave their den soon after sunset, irrespective of season, this was found not to be the case in urban areas, where average time lags of up to six hours between sunset and emergence were observed in autumn and winter.

Recommendation

Rural house owners are sometimes advised to wait with blocking entry holes to a marten's den until after sunset to avoid trapping the animal inside the den. This may be valid in urban areas in summer and late spring but is inadvisable in autumn, winter and early spring. In fact all exclusion measures should be preceded by attempts to deter the animals from using the den site. Exclusion measures should generally be avoided between March and June when young martens may use the den. Daily rather than intermittent noise disturbance during this period is a good indication that a female is rearing her offspring in the den.

8.4.3. Car-related conflicts

I have shown in Chapter 6 that stone martens frequently associate with cars in spring and early summer. While these visits are usually brief, martens may also occasionally rest for longer periods in cars during their principal activity period. Nevertheless, based on damage reports from both of my study towns only a tiny fraction of car visits is likely to result in damage. Assuming that damage reports from this study and from Müskens and Broekhuizen's (2005) study are more or less valid representations of the proportion of cars that get damaged over the course of a year (between 3 and 6%), a car that is parked outside would be likely to be damaged only about once every 16 to 33 years on average. This serves to illustrate that the risk of damage to any one car that is regularly parked on the road is not very high.

Nevertheless it is worth exploring what options there are to prevent martens from damaging cars at all. Kugelschafter *et al.* (1997) tested a variety of mechanical, olfactory, auditory and electrical deterrents on captive stone martens. They found the animals to be rather indifferent towards any kind of strong-smelling or bitter-tasting substances (including commercially available anti-marten sprays). Cables or hoses that were sheathed with corrugated plastic tubing, however, were generally safe from marten attack. Another promising approach was the use of a (commercially available) system comparable to conventional electric fencing. Electrodes that are connected to the car battery are installed inside the engine compartment and give the marten an electric charge when it touches them, scaring it away. However, due to health and safety issues, such systems are illegal in some countries, including Luxembourg. The widely used and commercially available ultrasound devices that can be installed under the car bonnet show little effectiveness in deterring martens (personal observation; Ludwig 1999).

I have demonstrated in Chapter 6 that stone martens intentionally leave their scent marks on cars and that marten scent seems to be a driving force in promoting marten-car contact rates. Hence the removal of scent from cars should lower the attractiveness of a specific car to a passing marten and thus lower the probability of damage occurring. While, theoretically, this may make sense, it is probably hard to implement in reality. Scent may be left in places inaccessible to humans and a conventional car wash may not be effective enough to make scent marks undetectable to martens. After a passage through a carwash (including washing of the underside of the car) the scent mark seen in Fig 6.1 had indeed been removed (at least optically) from the car that was used for radio tracking. Nevertheless, the exact same spot was over-marked again during the next tracking session just three days later. This anecdotal evidence suggests that a conventional wash may indeed be unable to totally remove scent marks.

8.4.4. Managing urban marten numbers

Management of human-wildlife conflicts can potentially be achieved by removing the animals that are responsible for causing the damage (i.e., ‘the culprits’: Conover 2002). This can involve either lethal (i.e., hunting, kill-trapping or live-trapping with subsequent euthanasia) or non-lethal (live-trapping with subsequent translocation) control.

Hunting

Hunting can usually only take place outside of human settlements. However, there is now strong evidence from the present study (Chapter 3) and from a Dutch study (Müskens and Broekhuizen 2005) that martens (especially females) encountered in urbanised habitats are likely to be rarely encountered in surrounding rural areas. Consequently, any hunting aimed at reducing marten-human conflicts in nearby towns would miss the subset of the population containing the culprits and so would probably achieve little. Considering the strict territoriality displayed by urban martens, it seems unlikely that a year-round hunting ban, as has recently been implemented in Luxembourg, would cause a buildup of marten densities in urban areas due to dispersers from surrounding rural areas. Furthermore, since stone martens occur at low densities in rural and forested areas (see Chapter 3 for references) a year-round hunting ban is justified.

Removal trapping

A more direct way of targeting the martens that are actually responsible for causing conflict would be to directly remove them at the site of conflict. These measures are usually employed in a ‘corrective’ way, which means that they are used only after damage has already been recorded (Conover 2002). Kill-trapping, which was employed by Nicht (1969) to produce his urban marten density estimates, has nowadays been banned from many countries, leaving live-trapping as the only alternative. Regardless of how a trapped animal is disposed off (by euthanasia or translocation), the ultimate question is whether this would actually solve the initial problem.

Removal trapping is often viewed as the easiest option by affected house or car owners (personal observation), the rationale being that the nuisance animal will be quickly trapped and translocated to non-urban habitat (see Chapter 7) thereby solving the problem. In reality, however, live trapping of adult martens is a notoriously slow process, as Chapter 2 and previous studies have demonstrated (e.g., Herrmann 2004; Lachat Feller 1993b; Müskens and Broekhuizen 2005; Skirnisson 1986). Also, there are usually at least a male and a female in an area and trapping both often proves to be impossible, as has been experienced by virtually all authors of the above studies. Furthermore, even if a territory is vacated, the fact that most urbanised habitat is saturated with martens means that a vacated territory will sooner or later be reoccupied (Herrmann 2004; Skirnisson 1986). The new resident is probably able to locate den sites used by previous occupants due to the scent left behind inside the den and on house walls or trees that were used to access the den. Hence, after removal of a marten, the blocking of entrances to the den would still be necessary to prevent future problems.

The translocation of a marten after it has been trapped may also raise a number of concerns, which have been dealt with in Chapter 7 (see also Appendix 2). They mostly relate to animal welfare issues associated with the stressful process of trapping, transportation to and release in a habitat with which the marten may have no or little previous experience. Although more data on the behaviour and fate of translocated martens would be desirable, the existing evidence suggests that they may not be able to rapidly find a territory, may return to urbanised areas and may suffer from decreased survival. Another problem with removal trapping is its timing. Since trapping attempts carried out by inexperienced members of the public are difficult to control or may be allowed all year-round (e.g., in Luxembourg), there is a risk that females with dependent young are removed. In late May and early June juveniles that still rely on their mother may be caught outside the den and translocated (personal observation). Both scenarios will result in the certain death of the young martens.

8.5. Conclusion

Urban stone martens show a number of characteristics that are typical of urban adapters. As such, they would be expected to reach their highest densities at intermediate levels of urbanisation not unlike the conditions in which they have been studied here. The martens in my study did not colonise the relevant towns recently: rather, they have had time to adapt to the conditions and establish stable populations. Nevertheless, they show no signs of group formation or overlapping home ranges, which would be necessary for them to reach densities similar to those reported for other urban adapter species. It may thus be reasonable to assume that future populations will remain at the present densities.

In towns with stable populations, the severity of the various marten-human conflicts, namely denning in attics and damaging of cars, can also be expected to remain relatively constant. Managing these conflicts proves to be complicated. I have shown in this study that urban martens are not just a few individual animals that occasionally or temporarily exploit such habitat. Rather, they constitute a permanent subset of the entire marten population and display a number of behavioural adaptations to urban areas. Hence, although removal trapping of individual martens is often viewed as an easy option, it is in reality unlikely to provide a long-term solution. In cars, the sheathing of vulnerable cables and hoses with corrugated plastic tubing may be a relatively cost-effective and lasting method of avoiding further damage. Denning conflicts should always be addressed by trying to make buildings marten-proof. Due to a number of welfare concerns, removal trapping should only be applied as a last resort after other action has proved to be unsuccessful. Furthermore, a ban on removal trapping for purposes of conflict management during the litter-rearing season (15 February-15 July) should be considered in Luxembourg.

8.5.1. Future studies

There are still some questions concerning martens in urban areas that remain unanswered and that could usefully act as a focus for future study:

i) *Urban adaptation*: Imprinting to a specific habitat at a young age may predispose juveniles to remain within a given habitat or disperse to similar habitat. By focusing radio tracking on juveniles it may be possible to get a better idea of where young urban martens disperse to and finally settle. However, due to the welfare issues highlighted in Chapter 7, this might only be possible if expandable collars can be developed for use on young martens. However, non-invasive genetic typing techniques, as have been applied to other carnivores (e.g., Frantz 2004) may constitute an alternative means of gaining information about the social structure of martens within towns as well as the extent of genetic mixing between urban and adjacent non-urban martens.

ii) *Socio-spatial organisation in urban cores*: Stone martens are known to exist in urban cores containing little to no green space. However, nothing is known about marten home range size, home range overlap or densities in areas with a high level of urban development. If martens are able to switch to an increasingly anthropogenic diet they may be able to reach high densities in urban cores. Otherwise, they may occur at lower densities in urban cores than in my study sites, as would be expected of a typical urban adapter.

iii) *Car damage*: It seems clear that territorial behaviour and scent marking are, at least indirectly, involved in marten-related car damage. Whether strange scent triggers aggressive biting, as has been suggested by Ludwig (1996), remains unclear. Behavioural field bioassays have been used successfully to study responses of free ranging mammals to various types of conspecific scent (e.g., beavers: reviewed in Herr 2005). In principle, similar experiments could be employed to study martens' responses to objects treated with or without strange marten scent. However, in practice the difficulty of predicting where martens would be most likely to encounter the experimental installations would be an important limiting factor. Consequently, such 'scent-playback' experiments might only be realistic for captive martens.

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Appendices

Appendix 1:

List of behaviours seen in the accompanying video sequence, illustrating some of the car patrolling behaviours described in section 6.3.2. All sequences show the female marten F11 displaying typical behaviour for that time of the year (April). All sequences from 00:01:04 onwards were filmed within two hours of each other.

Time	Behaviour
00:00:29	sniffs underside of car
00:00:38	‘handstand’ - possible scent marking behaviour
00:00:41	sniffs underside of car
00:00:59	scent marks rear axle; compare to Fig. 6.1
00:01:13	scent marking / urinating / defeacating under car
00:01:41	sniffs underside of car, then climbs onto front axle
00:01:46	climbs down from front axle and briefly (3 sec) remains still with tail over axle - possibly scent marking
00:02:34	scent marks road
00:02:54	climbs briefly into car

Video download:

http://www.mnhn.lu/recherche/proj_anthro_fouine.asp

Appendix 2:

Herr, J., Schley, L. and Roper, T.J. (in press) Fate of translocated wild-caught and captive-reared stone martens (*Martes foina*). *European Journal of Wildlife Research*. DOI 10.1007/s10344-007-0158-3