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SPATIAL BEHAVIOUR OF THE YELLOW-NECKED MOUSE (*Apodemus flavicollis*, MELCHIOR 1834) AT CONTRASTING POPULATION DENSITY AND RESOURCE AVAILABILITY

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Alla mia Matilde

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RIASSUNTO

Questa ricerca si inserisce in un più vasto progetto finanziato dal Centro di Ecologia Alpina della Provincia Autonoma di Trento e dall'Unione Europea con il Progetto integrato EDEN (*Emerging Diseases in a changing European environment*), che ha la finalità di analizzare i fattori favorenti l'emergenza di alcune zoonosi di interesse umano, in relazione ai cambiamenti climatici globali. In particolare, vengono studiati sia patogeni a trasmissione diretta come il Cowpoxvirus e l'Hantavirus, sia a trasmissione indiretta, ovvero veicolati da vettori, quali la zecca dei boschi (*Ixodes ricinus*); esempi ne sono la malattia di Lyme e la TBE (*Tick-Borne Encephalitis*, encefalite virale da zecca). Particolare attenzione viene rivolta a questa ultima patologia proprio perché è in deciso aumento nel Nord Italia, con una media annuale di 7 casi umani in Trentino-AltoAdige e oltre 10 casi per il Veneto. I dati per questa tesi sono stati raccolti in un'area endemica per la TBE in Trentino.

La zecca dei boschi completa il proprio ciclo vitale parassitando diverse specie ospite, tra cui i piccoli roditori rappresentano gli ospiti primari dei primi stadi di sviluppo (larva e ninfa). Questi mammiferi fungono pertanto da serbatoi dei patogeni che causano le suddette malattie; in particolare il topo selvatico dal collo giallo (*Apodemus flavicollis*), che è la specie più diffusa nelle faggete trentine, essendo l'ospite primario degli stadi immaturi di sviluppo della zecca dei boschi, assume un ruolo cruciale nell'ecologia di queste zoonosi. Ampliare le conoscenze sul comportamento spaziale di questa specie risulta di fondamentale importanza da un punto di vista epidemiologico, infatti, non solo perchè definisce l'esposizione degli individui a parassiti e patogeni, ma influenza strettamente anche i contatti tra individui e quindi la dinamica spazio-temporale di alcune patologie. Ai fini di questo progetto di ricerca si è ritenuto opportuno esaminare il comportamento spaziale di questa specie sia per la sua valenza da un punto di vista epidemiologico sia perché è un roditore che è stato poco studiato, soprattutto in Italia, e quindi poco conosciuto. Scarse e poco approfondite sono infatti le ricerche condotte nell'area alpina su *A. flavicollis*; fino ad oggi, in Italia, non sono ancora stati compiuti studi specifici su questo piccolo mammifero e sono praticamente inesistenti gli studi di telemetria.

Lo scopo di questa ricerca è monitorare nel tempo la struttura della popolazione in termini di composizione in classi di età (i.e. adulti e giovani) e rapporto sessi, stimare la densità di popolazione e la disponibilità di risorse trofiche per metterle poi in relazione all'uso dello spazio da parte di entrambi i sessi. In particolare tale progetto si prefigge di verificare le seguenti predizioni:

a) Le femmine sono territoriali: le femmine dei mammiferi basano il loro successo riproduttivo sull'acquisizione delle risorse, in modo tale che la distribuzione e l'abbondanza delle risorse vanno ad influenzare strettamente la loro distribuzione spaziale e di conseguenza anche la territorialità che è un aspetto dell'uso dello spazio; in particolare nelle femmine di specie granivore, come *A. flavicollis*, che dipendono da risorse distribuite in modo non uniforme, non stabili nello spazio e nel tempo e lentamente rinnovabili, è favorita la territorialità, proprio perché il cibo rappresenta una risorsa limitante. Invece, dal momento che per i maschi la risorsa limitante è rappresentata dalle femmine riproduttive, ci si aspetta che essi siano distribuiti in relazione alla distribuzione spaziale delle femmine, al fine di massimizzare il loro successo riproduttivo. Per verificare questa predizione, è stato valutato il grado di sovrapposizione degli home range e delle core area tra coppie di individui (i.e. coppie maschio-maschio, maschio-femmina e femmina-femmina) ed il pattern di utilizzo delle tane, aspettandosi sia una mancanza di sovrapposizione degli home range che una assenza di condivisione delle tane tra femmine;

b) Il sistema riproduttivo è promiscuo: per verificare ciò è stata valutata l'organizzazione spaziale di maschi e femmine, aspettandosi un alto grado di sovrapposizione degli home range tra esemplari appartenenti ai due sessi; inoltre ci si attende che lo home range di un maschio si sovrapponga a quello di più femmine e viceversa. Si suppone anche che i maschi abbiano home range di dimensioni maggiori rispetto alle femmine, in modo tale da massimizzare la probabilità di incontro con femmine in estro;

c) L'uso dello spazio è influenzato dalla densità di popolazione e dalla abbondanza di risorse trofiche: per determinare ciò sono state confrontate le dimensioni di home range e core area e le distanze percorse in due anni (i.e. 2005 e 2006) caratterizzati da condizioni di densità e disponibilità di risorse

contrastanti; ci si aspetta che gli spostamenti siano maggiori in condizioni di bassa densità e di scarsa disponibilità di risorse trofiche;

d) La dispersione autunnale degli adulti è influenzata dall'abbondanza di risorse: per verificare questa predizione, è stato confrontato il numero di eventi di dispersione tra il 2005 e il 2006, aspettandosi che questi, per entrambi i sessi, siano più frequenti in condizioni di scarse risorse trofiche;

e) L'eterogeneità sessuale nell'uso dello spazio determina l'eterogeneità sessuale nel grado di infestazione parassitaria: è noto che i maschi sessualmente maturi supportano un maggior carico parassitario da zecca rispetto alle femmine; per verificare ciò è stato determinato il carico parassitario individuale di entrambi i sessi ed è stato posto in relazione all'uso dello spazio, al fine di poter confermare l'ipotesi comportamentale secondo cui, i maschi, essendo più mobili delle femmine, andrebbero incontro ad una maggiore probabilità di contatto con i parassiti.

L'area di studio è una faggeta termofila posta a 750 m di quota, in località Dos Gaggio, nel comune di Cavedine (Valle dei Laghi – Trento). Sono stati impiegati due diversi metodi di raccolta dati: il metodo di cattura-marcatura-ricattura (CMR) e la telemetria con la tecnica dello "homing in". E' stata allestita una griglia di 324 trappole a vivo a cattura multipla (Ugglan II), poste ad una distanza di 15 m, in modo da formare un quadrato di 255x255 m, a coprire una superficie boscata di circa 6,5 ha; sia nel 2005 che nel 2006, tra maggio e novembre, sono state effettuate sessioni mensili di campionamento della durata di 6 giorni ciascuna. All'interno della griglia sono state collocate 140 trappole per la raccolta del seme di faggio, ai fini della stima della produttività primaria della faggeta. E' stata stimata la densità della popolazione adulta, sessione per sessione, con il programma CAPTURE. Sono stati marcati un totale di 412 individui (228 maschi e 184 femmine) nel 2005 e 66 individui (35 maschi e 31 femmine) nel 2006. I radio-collari utilizzati (modello: BD-2C, Holohil System Ltd.; peso: 1,8-2 g), della durata di circa 53 giorni, sono stati applicati ad un totale di 64 animali di cui 20 maschi e 12 femmine nel 2005 e 19 maschi e 13 femmine nel 2006; gli animali da radio-marcare sono stati scelti tra gli individui di peso adeguato a quello della trasmittente e residenti nell'area di studio. Le localizzazioni sono state organizzate in quattro sessioni (luglio-ottobre), ciascuna di 3 settimane, comprese tra due

sessioni successive di trappolaggio; gli animali sono stati seguiti prevalentemente nelle ore notturne, dal tramonto all'alba, per valutare gli spostamenti e nelle ore diurne per la localizzazione delle tane. Il numero medio di fix diurni/animale/sessione è stato di 12.4 ± 0.8 e di 11.4 ± 0.7 per il 2005 e 2006 rispettivamente, mentre il numero medio di fix notturni/animale/sessione è stato di 65.7 ± 2.2 e di 48.9 ± 2.6 per il 2005 e 2006 rispettivamente. Nel periodo autunno-inverno 2004-2005 si è verificata una alta produzione di seme di faggio (pasciona), pertanto il 2005 è stato caratterizzato da alta densità di popolazione e abbondanza di cibo nella prima parte dell'anno. Come ci si aspettava nell'autunno-inverno 2005-2006 non c'è stata produzione di seme e conseguentemente nel 2006 si è registrata una bassa densità di popolazione ed una scarsa disponibilità di cibo; quest'ultima è aumentata nell'autunno 2006 quando è stato registrato un incremento nella produttività della faggeta interessata da questo studio.

Gli home range e le core area dei maschi sono risultati largamente sovrapposti tra loro, al contrario di quanto registrato per le femmine le quali hanno evidenziato un certo grado di territorialità, manifestatosi nella monopolizzazione della core area; tale grado di territorialità femminile si è esplicitato anche nella difesa delle tane, tanto che non è mai stata osservata condivisione delle tane tra femmine. L'associazione più frequente in tana è stata rappresentata da coppie maschio-femmina.

La dimensione dello home range dei maschi è risultata significativamente maggiore di quella delle femmine, in entrambi gli anni; inoltre è stato osservato che lo home range di un maschio generalmente si sovrappone a quello di più femmine e che quello di una femmina si sovrappone allo home range di più maschi. Tale organizzazione spaziale sembra pertanto compatibile con un sistema riproduttivo di tipo promiscuo.

L'uso dello spazio è variato con la stagione e negli anni, indicando una dipendenza dalla distribuzione e dalla abbondanza delle risorse trofiche; in particolare è stato evidenziato un allargamento delle dimensioni dello home range nel 2006, in funzione della riduzione della disponibilità di risorse.

Nel 2005 tra la fine di settembre ed i primi di ottobre, la maggior parte degli animali monitorati sono andanti in dispersione, ovvero si sono definitivamente allontanati dall'area di studio, per trasferirsi in zone caratterizzate da maggior disponibilità di cibo; in particolare hanno colonizzato ambienti con elevata diversità di specie di piante da seme, con presenza di siepi stabili ed in vicinanza di coltivi. Al contrario, l'aumento della produzione di seme di faggio nel 2006, ha determinato una riduzione, rispetto al 2005, degli eventi di dispersione autunnale. Sembra pertanto che la dispersione degli adulti sia stata determinata proprio dalla scarsità di risorse disponibili, accentuata anche dalla alta densità di popolazione che ha caratterizzato il 2005.

I maschi, essendo risultati più mobili delle femmine sia in termini di dimensione dello home range che di distanze percorse, possono andare incontro ad una maggiore esposizione ai parassiti; pertanto l'eterogeneità sessuale nell'uso dello spazio sembra essere responsabile del maggior grado di infestazione da larve di zecca *I. ricinus* registrato per i maschi.

ABSTRACT

To date, the spatial behaviour of the yellow-necked mouse *Apodemus flavicollis* has been poorly investigated. I present the results of a two-year study on the spatial organization and mating system of adult *A. flavicollis*, monitored by radio-tracking (homing-in) in a beech woodland at 750 m above sea level in the eastern Italian Alps; I also used the CMR method (capture-mark-recapture) to estimate population density and structure. I observed the movements of 64 mice during the breeding season (i.e. from July to October) in 2005 (high population density, after a year of mast) and 2006 (low population density).

Female home ranges overlapped with those of other females much less than with male ones, whereas males widely shared their ranges with individuals of the same sex; moreover, female core areas were never (i.e. 2005) or very little (i.e. 2006) overlapped with those of other females. Consistently, I did not record communal nesting among females. These findings are consistent with the hypothesis of female territoriality, which results in the monopolization of core areas and nests.

Individual home ranges of males often overlapped with those of several females and, furthermore, individual home ranges of females overlapped with those of several males; in addition, male home ranges are larger than female ones. Furthermore, every mouse used many burrows sequentially or simultaneously with mixed sex pairs being the most common association. All these observations, support the hypothesis that male spatial behaviour in the breeding season is aimed at maximizing the number of potential matings, suggesting a promiscuous mating system.

The use of space changed seasonally and among years, likely indicating a dependence on resource abundance and distribution. Specifically, females exhibited reduced territorial exclusiveness and enlarged home ranges at a lower level of food availability. Males varied their spatial distribution accordingly.

After an evident decrease in habitat quality, I observed substantial and abrupt adult dispersal, both in males and females, from the end of September to early October 2005. The sudden abandonment of home ranges was a consequence of the low seed production and the high population density, which probably combined to escalate the competition for food in the study area. In a rodent species relying on patchy and slowly renewed resources, females showed a

flexible social and spatial behaviour, in response to variations in habitat quality and environmental constraints, whilst males appeared to consistently attempt to maximise encounters with receptive females.

Insight into the spatial ecology of this species helps to better understand its role in the transmission and dynamics of diseases, including zoonoses, and particularly to explain the sex-biased parasite burden. The sex-biased heterogeneity in parasitism rates could be explained by sexual differences in the use of space; in particular, wide ranging males enhance their probability to encounter questing ticks, as opposed to more sedentary females and this may result in a greater tick burden. In addition, the circulation of diseases is favoured by high contact rates between mice. Males with overlapping home ranges may induce this condition, whereas female territoriality may reduce the potential number of hosts exposed to the parasites they shed.

1. GENERAL CONTEXT (FORWARD)

This research belongs to a long term study, carried out by the Centre for Alpine Ecology, on rodents and some European emerging zoonoses; in particular it is a part of EDEN project (Emerging Diseases in a changing European environment) (*Proposal/Contract n° 010284-2, 6th Framework Programme, Sub-Priority 6.3, Sustainable Development, Global Change and Ecosystem*) that is an Integrated Project of the European Commission that aims to identify and catalogue those European ecosystems and environmental conditions which can influence the spatial and temporal distribution and dynamics of human pathogenic agents. The EDEN project takes as its starting point the idea that environmental change in Europe, and more generally globally, will make some parts of the greater European area more favourable for certain diseases, and other parts less favourable; its main research topic is the study of the ecology and epidemiology of wildlife diseases and emerging zoonoses. The theme is related to the growing concern of the impact of global change and biodiversity loss on human and animal quality of life and health with the need to adopt sustainable mitigation and control strategies. A number of zoonotic pathogens which include wildlife in their epidemiological cycle are in fact currently under constant monitoring and control by the international health organisations (WHO: world health organisations, OIE: the World Organization for Animal Health, formerly the Office International des Epizooties). An example is given by some vector borne diseases (e.g. diseases transmitted by the sheep tick *Ixodes ricinus*, such as Tick borne encephalitis, TBE, and Lyme disease) and by other pathogens, with a direct transmission, that seem still circulating only among wildlife but have the potential to spill over and infect humans (pox viruses as Cowpoxvirus and RNA viruses such as Hantavirus and Arenavirus). Some of them represents also a threat for biodiversity and endangered species survival. Among the indirectly transmitted diseases, those transmitted by the tick *I. ricinus*, are widespread and have the biggest impact on human health in Europe (Parola and Raoult, 2001; Randolph et al., 2002). TBE has been recorded in the human population of Italy since 1967 (Hudson et al., 2001); its causative agent is a flavivirus. In the last years there was an increased in the number of human cases in Trentino, with a mean of 7 cases per year (V. Tagliapietra, unpublished data).

Lyme disease is the most common bacterial infection transmitted in Europe by *I. ricinus* (Gray, 1998; Humair et al., 1999). In Italy, this pathology was first recorded in 1983 (Rizzoli et al., 2002); its causative agent is *Borrelia burgdorferi sensu lato*. The incidence rate of Lyme disease in the Trentino-Alto Adige region, one of the "hot-spots" of infection, was 8.02 human cases/100,000 inhabitants, estimated for the period 1986-1997 (Pavan et al., 2000).

Among the directly transmitted diseases, hantaviruses are the most significant rodent borne viruses in Europe and North America causing, in Europe, a mild to severe hemorrhagic fever with renal syndrome (HFRS) in humans, with the case fatality rate varying from 0.1 – 10%, depending on the specific virus (Saluzzo and Dodet, 1999; Zizi et al., 2002). Arenaviruses have so far only been known from the rodents in the New World and in Africa, with the exception of LCMV (lymphocytic choriomeningitis virus) in the house mouse *Mus musculus* in Europe (Saluzzo and Dodet, 1999); however, analyses of some recent samples have identified arenaviruses in wild rodents in Europe, including Italy (A. Rizzoli, unpublished data) and this may pose an important threat to humans in the future. Cowpox virus is now known to be endemic in rodents in large parts of Europe, and human infections have been diagnosed (Begon et al., 2003; Telfer et al., 2002).

The overall objective of the EDEN project is to develop a set of complementary, operational and standardized tools, methods and skills to allow member states to anticipate, prevent, mitigate or control the risk of antropozoonotic and animal diseases emerging due to global changes and ecosystem disturbances.

In particular, the province of Trento is characterised by an high degree of faunal diversity; this territory is also located across the main route of migration among Mediterranean areas and northern Europe for wildlife, goods and people. The territory is also affected by consistent land use changes and the effects of global warming are already visible; in this situation, the research on wildlife diseases ecology and epidemiology became strategic to allow the activation of early warning monitoring systems and to identify mitigation strategies to preserve and improve the quality of life and the conservation of biodiversity.

Some rodents species (i.e. *Apodemus sylvaticus*, *A. flavicollis*, *A. agrarius* and *Clethrionomys glareolus*) are known as main reservoirs of the above pathogens,

playing a crucial role in the ecology of several zoonoses (Hudson et al., 2002). This study focused on the yellow-necked mouse *Apodemus flavicollis*, as it is the main rodent species inhabiting the forests of Trentino and in particular it is widely distributed in the beech woodlands (Locatelli and Paolucci, 1998), which contextually are the main habitats for ticks.

Knowledge on rodents spatial behaviour is very important to assess the exposure of individuals to parasites and pathogens; moreover spatial behaviour and intra-specific interactions strictly affect contact rates and therefore the spatial and temporal dynamic of such diseases as the abundance and dynamics of rodent born viruses, and hence risk to humans, depends on the spatial distribution and population dynamics of the carrier rodents and on opportunities for exposure (Klingstrom et al., 2002).

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2. INTRODUCTION

2.1 Apodemus flavicollis: biological traits and behavioural ecology

Foto P. Paolucci

Phylum	**CORDATI**
Class	**MAMMALIA**
Sub Class	**THERIA**
Intra Class	**EUTHERIA**
Order	**RODENTIA**
Sub Order	**MYOMORPHA**
SuperFamily	**MUROIDAE**
Family	**MURIDAE Gray, 1821**
Genus	***Apodemus* Kaup, 1829**
Sub Genus	***Sylvaemus* Ognev, 1924**
Species	***Apodemus flavicollis***
Common name	**Yellow-necked mouse**

Tab. 2.1.1 Taxonomy of *A. flavicollis*

Taxonomy and phylogenesis

The yellow-necked mouse is a small mammal belongs to the *Rodentia* Order and *Muridae* Family; its taxonomy is reported in Table 2.1.1. The genus *Apodemus*

contains about twenty species distributed in broadleaf forests throughout the Palaearctic region (Michaux et al., 2002). Based on molecular studies, the genus has been estimated to have originated about eight million years ago, which is consistent with the presence of the fossil species *Apodemus primaevus* Hugueney and Mein, 1965, in Europe at the end of the Miocene (about seven million years ago) (Michaux et al., 2002). The majority of modern European *Apodemus* species were a later immigration, with their ancestor, *A. dominans* Kretzoi, 1959, arriving at the end of the Pliocene. During Pleistocene we can distinguish 3 *Apodemus* species: *A. dominans* ancestor of *A. sylvaticus* and *A. flavicollis*, *A. jeanteti* Michaux, 1967, ancestor of *A. mystacinus* Danford and Alston, 1877 and *A. leptodus* Kretzoi, 1956 ancestor of *A. agrarius* (Pasquier, 1974). Half of the 20 species of this genus show a geographic preference for Asia and half for Europe, with some having a global distribution. The various Asian species had split from each other earlier than the European species, which tend to be closely related to one another; Serizawa et al. (2000) inferred that this evidence may have reflected the different histories of broadleaf forest cover during the Pleistocene ice ages. Some broadleaf cover survived in Asia during the ice ages, allowing for the survival of wood mice over that time, while Europe became a broadleaf no-go zone.

Since the review of Musser et al. (1996) all but one of the *Apodemus* species have been divided into two subgenera: *Sylvaemus* (including most species with European and Near East distribution patterns) and *Apodemus* (excluding *A. argenteus* and including most species with East Asian distribution patterns and *A. agrarius*, which has a discontinuous Eurasian range). The remaining *A. argenteus* (a very particular Japanese species) seems to be distinct from the others. This hypothesis has been confirmed by Serizawa et al. (2000) based on sequences from the mitochondrial cytochrome b and the nuclear IRBP (interphotoreceptor retinoid-binding protein) genes. Moreover, these authors proposed a fourth monotypic group, *A. gurkha*, the Himalayan field mouse endemic to Nepal. According to several authors (i.e. Filippucci et al., 1989, 1996; Musser et al., 1996), 13 different species are presently recognized within the subgenus *Sylvaemus* in the western Palearctic region: *A. sylvaticus*, Linnaeus 1758; *A. flavicollis*, Melchior 1834; *A. alpicola*, Heinrich 1952; *A. uralensis*, Pallas 1881;

A. mystacinus, Danford and Alston 1877; *A. hermonensis*, Filippucci et al. 1989; *A. fulvipectus*, Ognev 1924; *A. mosquensis*, Orlov et al. 1996; *A. ciscaucasicus*, Orlov et al. 1996; *A. ponticus*, Sviridenko 1936; *A. hyrcanicus*, Vorontsov et al. 1992; *A. arianus*, Blanford 1881; and *A. wardi*, Wroughton 1908. Species within the subgenus *Sylvaemus* are phenotypically very similar, and traditional morphometrics are often at a loss to distinguish between them (Michaux et al., 2002). Although *A. sylvaticus* and *A. flavicollis* are closely related from a taxonomical point of view and have very similar morphology and distribution, they reacted and survived to the Quaternary glaciations in totally different ways. Indeed, from paleontological and genetic data, *A. flavicollis* did not survive, at least during the last glaciations (22000–16000 years ago), in the Iberian Peninsula, whereas *A. sylvaticus* persisted and recolonized almost all Europe from there at the end of the last glaciation. Conversely, the refuge region from which *A. flavicollis* recolonized Europe during the Holocene corresponds to the Balkan area where *A. sylvaticus* seems to have suffered a severe genetic bottleneck. According to the paleontological (Michaux and Pasquier, 1974) and molecular (Michaux et al, 2002) data, the differentiation between *A. flavicollis* and *A. sylvaticus* is probably the result of an allopatric speciation: the ancestors of *A. sylvaticus* were isolated in Spain and southern France, whereas those of *A. flavicollis* rather lived in Central Europe and in the Balkans. Each species could be more adapted to the environment of its ancestral region and, therefore, have had more chances of surviving there. However, as the differentiation between the two species is very old (4 My), both had time to establish across the European regions during the Quaternary and they probably had time enough to adapt themselves to the different European environments. Moreover, the differences between Western and Eastern European environments are probably not sufficient (Michaux et al., 2005) to support this hypothesis, particularly for such species characterized by strong ecological adaptability (Renaud and Michaux, 2003). Several ecological (e.g. Kaustuv et al., 2001; Holt, 2003) and paleontological (Barnosky et al., 2001) studies have suggested the importance of ecological factors in the changes of species ranges, particularly during climate variation. *A. sylvaticus* is characterized by a greater ecological plasticity than *A. flavicollis* which is more associated with forested habitat with a high canopy cover (Marsh and Harris, 2000). Thus, the

fragmentation of forests during the last glaciations in the Iberian peninsula may have played a role in its extinction in this region. Therefore, a more adaptable species like *A. sylvaticus* was probably more resistant to these factors than *A. flavicollis*. Finally, *A. flavicollis* shows poorer winter survival than *A. sylvaticus* (Montgomery, 1980b). Therefore, the harsher climatic conditions that characterized the Iberian peninsula during the last glaciations as compared to the Balkan region (Tzedakis et al., 1997) could also explain the extinction of the yellow-necked mouse in Western Europe during this period.

Geographic distribution

The distribution of *A. flavicollis* span from Finland to Turkey with a homogeneous distribution in central and eastern Europe, while in southern Europe the range is more reduced and fragmented due to the connection with mountain habitat. In Italy this species is present in all the forested and mountain areas of the peninsula but not in Sicily, Sardinia and Puglia and is rare in the Pianura Padana; in fact, this species avoids the plain areas. It is widespread in all Trentino province and we can find it in deciduous and mixed forests from the bottom of the valley to the upper tree limit (Figure 2.1.1) (Mitchell-Jones et al., 1999).

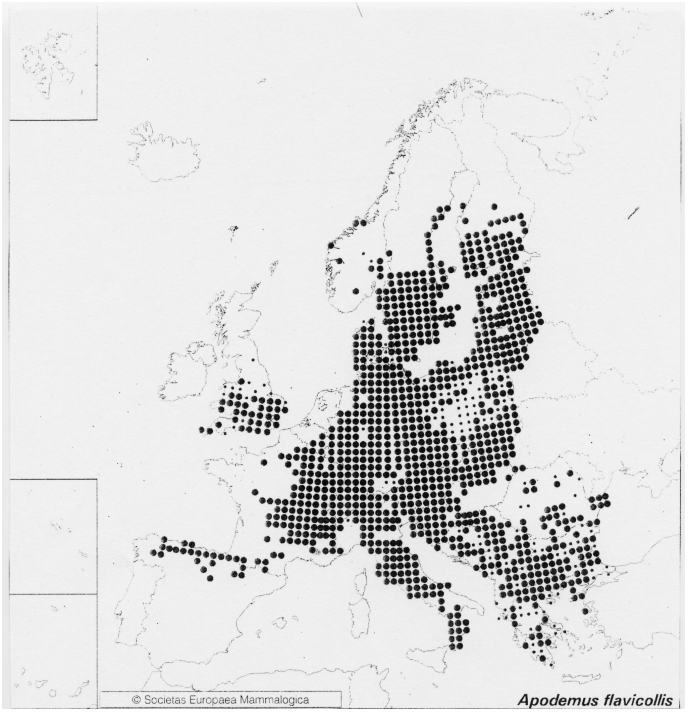


Fig 2.1.1 - Distribution of *A. flavicollis* in Europe (Mitchell-Jones et al., 1999)

Morphological features

Some distinctive morphological features of this species are the long tail (usually longer than the head-body length), the protruding eyes and ears, the reddish-brown colour of pelage on the back and the pale grey colour, mostly white, on the belly. Very distinctive and always present, is the unbroken yellow collar passing across the chest and lining the forelegs. Generally, body weights range from 20 to 48 grams, body length from 90 to 120 mm and tail from 80 to 134 mm (Toschi, 1965).

Habitat

A. flavicollis is regarded primarily as a mature deciduous woodland species and generally its abundance decreases moving from broadleaf to coniferous woods (Debernardi et al., 2003); this species appears to prefer woodlands with a high level of canopy cover probably because they offer a good tree seed crop. Moreover forests with hard seed/fruit diversity and abundant fallen timber, seem to provide the best habitat for this rodent. In particular it is known that all tree species show an irregular pattern of annual seed production, thus a seed specialist as *A. flavicollis* could be restricted to areas where sufficient plant diversity occurs to ensure an adequate food supply each year from one source or another (Angelstam et al., 1987; Marsh et al., 2001; Miklos and Ziak, 2002); on the other hand the presence of fallen ligneous vegetation creates cover and good nesting sites, and it is also indicative of a low level of woodlands management (Marsh and Harris, 2000).

Diet

This species may be referred to as typically granivorous; although its diet is also based on invertebrates, green plants and fungi, seeds represent its favourable food. The proportion of seed consumption may vary seasonally and generally it is greater in autumn and winter, whereas in spring and summer the scarcity of seeds availability is compensated for by increase in both animal and fungal food consumption (Obrtel and Holisova, 1983; Hansson, 1985; Abt and Bock, 1998).

Activity

A. flavicollis is a nocturnal rodent (Andrzejewski and Olszewski, 1963). A biphasic pattern occurs during long winter nights with peaks two to four hours after sunset and before dawn, whereas during summer nights one peak in activity

in the middle of the night is usual (Buchalczyk, 1964; Montgomery and Gurnell, 1985); however a great individual variability in the circadian rhythm was found (Wolton, 1983). Kotzageorgis and Mason (1996) found that, during the breeding season, males spend no time in their nests during night, whilst females spend at least two hour in the nest each night.

Burrow system

All species of *Apodemus* live in underground burrow systems; tunnel systems are excavated at a depth of 70-180 mm or more, and are typically 30-40 mm in diameter. Generally tunnel systems show a circular pattern around the base of a tree, with many entrances, the nest chamber and the chamber for food storage (Flowerdew, 1984; Montgomery and Gurnell, 1985). There are evidences that the same burrow systems are used over many generations, moreover it seems that females make deeper and more sophisticated burrows than males (Montgomery and Gurnell, 1985). *A. flavicollis* is known to use several nests, climb to 25 m and to use nest boxes or nests of birds (Truszkowski, 1974).

Reproductive cycle and mating system

The length of the breeding period vary accordingly to geographic and climatic features, but generally the breeding season begins in late February and ends in October-November; however mating season can extend into fall and winter in years of plentiful forest crop (Adamczewska, 1961; Flowerdew, 1984). Gestation is 25-26 days with a mean litter size of 5.5 sons. Small mice born blind and without fur and at 3 days old they are able to move quickly and their ears are opened; fur appears at the 7^{th} day of life, eyes open at about 13 days and weaning occurs at 18-22 days from birth, so mice are independent at about 21 days. The weight at weaning is 6-8 g (Flowerdew, 1984; Fracasso, 1990). Spring-summer born individuals grow slowly and commonly become sexually active during the year of birth, whereas autumn born individuals grow rapidly but develop mature the year following their birth (Adamczewska, 1961). The mating system of nocturnal and elusive rodents is difficult to study, and it is typically derived from spatial distribution of males and females (e.g. Ribble and Millar, 1996); in particular, for this species, mating tactics are not well understood and in the literature there are some contrasting results (e.g. Kotzageorgis and Mason, 1996). Basing on data inferred from studies on *Peromyscus* spp (Ribble and Millar,

1996), commonly regarded as ecologically similar to *Apodemus* spp., and on *A. sylvaticus* (Wolton, 1985; Tew and Macdonald, 1994; Polechova and Stopka, 2002), it is expected that during breeding season *A. flavicollis* has a promiscuous mating system.

Population dynamics

It is impossible to establish the effect of a single factor influencing the population dynamics; in fact, there is a combination of several components, such as food availability, predation pressure, social organisation (e.g. presence or absence of territoriality), and climatic conditions, acting together in a positive or negative way or counteracting each other (Bergstedt, 1965). However, trophic resource abundance seems the main factor influencing population growth (Mazurkiewicz and Rajska-Jurgiel, 1998). Intra-annual demographic fluctuations are well-known in this species and, in particular, density of *A. flavicollis* populations increases normally between spring and fall (Gosálbez and Castién, 1995), so that the autumnal peak is followed by a rapid decrease in population size. This species also show inter-annual demographic fluctuations, which are more marked at high latitudes than low ones; specifically the year with the highest mice density is typically preceded by heavy mast crop and so by winter breeding (Mazurkiewicz and Rajska-Jurgiel, 1998).

Ranging movements

Home range is a concept that attempts to describe the spatial context of an animal's behaviour. Home range was formally defined by Burt (1943) as that area traversed by the individual in its normal activities of food gathering, mating and caring for young; occasional sallies outside the area should not be considered part of the home range. Moreover, very few, if any, species of mammal use their home range in a uniform manner; most have preferred areas, defined as core areas, which are areas of particularly home range usage (Harris et al., 1990). Home range size of mammals is affected by several factors, such as sex, age, social and reproductive status, season, population density and habitat quality (Burt, 1943; Bergstedt, 1966; Corp et al., 1997); furthermore, home range estimates can vary significantly according to the method used for calculation (Lawson and Rodgers, 1997). Scarce and not so detailed are studies on *A. flavicollis* space use (i.e. home range and territoriality); however, Mazurkiewicz and Rajska-Jurgiel (1998) noted

that the spatial behaviour of yellow-necked mice is high flexible and can change under various environmental conditions. In particular they found that home range size increases at low population density and low resource abundance as the strategy increasing fitness (survival and breeding) is to possess the largest amount of resources within the smallest area; moreover, dispersal rates decline with increasing availability of food. These authors found that year to year differences in home range are greater for mice, more dependent on specific food resources than for less food selective species as *Clethrionomys glareolus* and other voles species; in particular, not only the site tenacity of individuals *A. flavicollis* is very low, but also they have a high capacity to colonize rapidly new territories.

It seems that males move wider than females, so that their home ranges are greater than those of females (Wolton and Flowerdew, 1985; Kotzageorgis and Mason, 1996); Schwartzenberger and Klingel (1995) observed an high degree of home range overlap among males and among males-females, whilst females showed intra-sexual territoriality. Males tend to be more aggregated than females and a great aggregation between two sexes is evident during breeding season (Montgomery, 1980a).

Predators

Mice are at the base of the food chain, so their predation rate is very high, in fact several animals consider rodents as prey. In the forests of Trentino-Alto Adige region, the main mice predators are carnivores such as fox (*Vulpes vulpes*), badger (*Meles meles*), stone marten (*Martes foina*), weasel (*Mustela nivalis*); other predators include nocturnal birds as long-eared owl (*Asio otus*), tawny owl (*Strix aluco*), and little owl (*Athene noctua*) and reptiles as asp viper (*Vipera aspis*), adder (*Vipera berus*), Aesculapian snake (*Elaphe longissima*) and grass snake (*Coluber viridiflavus*).

Most studies on spatial behaviour of *Apodemus* spp. have focused on the common wood mouse *Apodemus sylvaticus*, whereas many gaps in the knowledge of mating systems, space use and ranging movements of *A. flavicollis* still remain. These two rodent species are morphologically very close and they are often sympatric, especially in western Europe (Bergstedt, 1965; Montgomery, 1980b); so that in the past, they were frequently mismatched and some of the behavioural

features of *A. sylvaticus* were presumed to be similar in the two species and therefore assigned to *A. flavicollis*. Thus, the main part of this research is aimed to improve knowledge on spatial and social organisation of this little known rodent species.

2.2 A mouse in an unstable habitat: reasons for a study

I monitored a *A. flavicollis* population living in a suboptimal patchy environment, with seed production mainly due to one plant species. I used two different methods to collect data; in particular, I applied the capture-mark-recapture (CMR) method by live-trapping technique and telemetry method by homing-in technique. The former allowed to assess temporal patterns of population density, population structure and individual parasite load, while the latter method allowed to evaluate specifically the use of space and ranging movements.

CMR vs radiotracking: how to track those tiny creatures in the wild?

Capture–recapture methods are useful research tools for animals that are elusive, nocturnal, or simply difficult to observe in their natural habitat, like small mammals.

Population structure in terms of fluctuations of mice number, sex ratio and age structure is generally affected by breeding, survival and dispersal and it seems influenced by immigrations (Rajska-Jurgiel, 1992); this author also noted that the high turnover rate in population of *A. flavicollis* is a feature of this species, resulting from high mobility and low residency. Furthermore, the age structure seems density dependent and, in particular, in low density years the population typically consist mainly of mature individuals, whereas in high density years immature individuals prevail (Mazurkiewicz and Rajska-Jurgiel, 1998).

Grid trapping using live traps is a common method for studying populations of small rodents in the field (Gurnell and Gipps, 1989); however, for estimating density, the trapping grid is assumed to be demographically and geographically closed. The requirement of demographic closure is not difficult to meet because the trapping interval can be kept short enough to preclude most, if not all, mortality (White and Shenk, 2001) and juveniles can be recognized and excluded from the sample. However, geographic closure is more difficult to handle. In particular, one problem frequently encountered with this method is that traps in the outer sector of the grid catch more animals than those near the centre (Dice,

1938; Tanaka, 1972). This so-called "edge effect" is a result of trap bait attracting individuals neighbouring the outer rings of the grid (Pelikán et al., 1972), and overlap between the grid boundary and the home ranges of the sampled population (Tanaka, 1980), which rarely correspond with one another. As a consequence, the edge effect leads to an overestimation of the population size. In an attempt to account for the edge effect and obtain unbiased estimates of density, the effective trapping area A(W) (or ETA) was introduced, that is the actual area to which the trapping data refers to (Bondrup-Nielsen, 1983). W, the width of a boundary strip, substantially increases the area of the trapping grid, TGA. The method first proposed by Dice (1938) to estimate boundary strip width was to add a strip equal to half the home range of the species, calculated from trapping data, to the outermost line of traps. In other studies, the effective area has been calculated by simply adding a strip equal to the distance or half the distance between traps (Grodzinski et al., 1966; Aulak, 1967; Faust et al., 1971; Stafford and Stout, 1983). This arbitrary method is somewhat unsatisfactory, however, because it has no theoretical, behavioural or ecological basis (Stenseth et al., 1974). Instead, Brant (1962) concluded that a strip equal to the mean distance moved by individuals between successive captures (MDM) would lead to a more accurate estimate. More recently, Wilson and Anderson (1985) proposed the MMDM method, where strip width is defined as the mean of the maximum distance between recaptures for all animals caught at least twice. Seber (1986) regarded the use of radio-telemetry as a major technological advancement relevant to population estimation because the true location of the animals can be determined. Bias of population size estimates can be reduced because radio-transmitters allow correction for immigration and emigration from the study area and provide efficient ways to correct other biases inherent in traditional population size estimators. Despite these advantages, few studies have used ranging parameters estimated from radio-tracking in assessing density (e.g. Powell et al., 2000; White and Shenk, 2001). Attuquayefio et al. (1986) referred to the mean home range radius from radio-tracking data for calculating the width of the boundary strip.

Live - trapping techniques have severe limitations in the assessment of spatial behaviour, especially in wide – ranging rodents (Montgomery, 1980b;

Montgomery and Bell, 1981; McShea and Madison, 1992); in fact there are many factors influencing the catches. In particular there is a great capture frequency heterogeneity due to:

- new traps are less attractive than those that have been in use for some time (Curry-Lindahl, 1956; Bergstedt, 1965; Jensen, 1975; Montgomery, 1979a);
- if natural food in the mice habitat is abundant their trapping frequency is poor (Curry-Lindahl, 1956; Bergstedt, 1965; Jensen, 1975; Montgomery, 1979a);
- a trapped animal appears to attract individuals of its own family-group as well as repel other individuals (Bergstedt, 1965; Jensen, 1975);
- some animals tend to avoid traps and others tend to frequent traps more than commonly: phenomena known as "trap-shy" and "trap-happy", respectively (Montgomery, 1979a);
- rodents seem to return to the same traps; generally a male mouse is caught in a trap previous frequented by a female of the same species (Wolton and Flowerdew, 1985; Rajska-Jurgiel, 2001).

Moreover the grid size used for trapping rodents may heavily affect the estimation of home range size and site tenacity of mice, in particular home range size of wide ranging males may be underestimated in small grids (Rajska-Jurgiel, 2001).

On the opposite, radio-telemetry is considered more appropriate (Bubela et al., 1991; Ribble et al., 2002) and particularly, radio-collars have been shown to have no apparent effects on small rodents activity (Ormiston, 1985; Pouliquen et al., 1990; Berteaux et al., 1996), on their survival rate (Johannesen et al., 1997), or on predation risk (Korpimäki et al., 1996), and the presence of human trackers seemed to negligibly affect their behaviour (Prosser et al., 2004). Nevertheless, most studies concerning the behaviour of *A. flavicollis* were based on live – trapping (Todorović et al., 1968; Radda, 1969; Montgomery, 1979b; Mazurkiewicz and Rajska-Jurgiel, 1998) and only very few on radio-tracking (Schwartzenberger and Klingel, 1995; Kotzageorgis and Mason, 1996), none of which have been carried out in the Italian Alps.

An interesting triangle: resources vs population density vs reproduction

Social and spatial organisation of mammal species may vary in relation to ecological (resource-related), demographic and reproductive constrains. Common behavioural patterns may be recorded as responses to certain environmental constrains, as well as behavioural plasticity as consequence of resource availability or habitat quality variations. In particular, spatial organisation of females depends on abundance, distribution and renewal rates of resources, because mammals present inter-sexual differences in parental investment, although at different degree across mammalian orders (Trivers, 1972; Davies, 1991). Mature females of species relying on sparse, patchy and slowly renewed resources are expected to express intra-sexual territoriality, as the costs-benefits balance should favour the defence of trophic rich but restricted areas (Ostfeld, 1985; Ostfeld, 1990). Conversely, homogeneous distribution of resources should elevate the costs to maintain a territory, thus promoting group-living. Rapid changes in food availability and habitat quality may result in a blend of these behavioural patterns, as females would be likely to occupy home ranges that represent the minimum economically defensible area, but which are large enough to fulfil their metabolic needs and those of their offspring (Reiss, 1988; Maher and Lott, 2000). In turn, male spatial organisation is driven by access to females, and therefore by their distribution, rather than by acquisition of nutrients (Ostfeld, 1990; Ribble and Millar, 1996). For example, when females are territorial, defending clumped resources, males will be unable to monopolize them by defending territories and therefore their reproductive success will be enhanced by searching widely for receptive females (Madison, 1980; Ostfeld, 1990). This should result in a promiscuous mating system, with males having larger, extensively overlapping home ranges (Heske and Ostfeld, 1990).

In mammal species with short life-histories and high reproductive rates, variation in food availability heavily affects survival rate, thus generating fluctuating patterns of population density (Krebs and Davies, 1978; Ostfeld et al., 1996b; Wolff, 1996), with evident consequences on space use and sexual interaction. For this reason, small rodents are ideal model organisms to investigate the dependence of social and spatial organisation on habitat quality, variation in resource availability and demographic parameters.

Parasites or not parasites? This is the question

Where locally abundant, *A. flavicollis* plays a crucial role in the ecology of some tick-borne diseases, acting as reservoir host of the immature stages of the sheep tick, *I. ricinus* (Randolph et al., 1999; Perkins et al., 2003). In particular, there is evidence of sex-biased heterogeneity in parasitism rates of rodents (Wilson et al., 2002; Perkins et al., 2003; Ferrari et al., 2004; Skorping and Jensen, 2004) which depends both on physiological (Hughes and Randolph, 2001) and ecological (Ostfeld et al., 1996a; Stanko et al., 2002) mechanisms. Moreover, some authors found that the host density affects their parasite burden, and in particular tick burden per mouse decrease with increasing density of mice (Ostfeld et al., 1996a; Rosà et al., 2007); this phenomenon is known as "dilution effect" (Rosà and Pugliese, 2007). Epidemiological studies would considerably benefit from improved knowledge of spatial behaviour of *A. flavicollis*. In fact, social and spatial behaviour may heavily affect disease dynamics and transmission (Stanko et al., 2002).

3. AIMS

This study therefore aims at testing the following hypotheses:

(a) Females of *A. flavicollis* are territorial, i.e. they show a certain degree of exclusiveness of their home ranges, as it is a granivorous species relying on sparse, patchy and slowly renewed trophic resources (Ostfeld, 1990). To assess this hypothesis, I evaluated the degree of home range overlap among sexes and the pattern of communal nesting. In particular, I predict lack of nest sharing and home range overlap between adult females;

(b) during the breeding season, *A. flavicollis* shows a promiscuous mating system. To assess this hypothesis, I investigated the sexual differences in the use of space. In particular, I predict the home ranges of the two sexes to extensively overlap, with the males' ones larger (Gaulin and Fitzgerald, 1988; Ribble and Millar, 1996);

(c) use of space by *A. flavicollis* is affected by population density and resource abundance. To assess this hypothesis, I estimated ranging movements in two years, the first following a year of masting (high population density, decreasing resources throughout the season), and the successive one (low population density, increasing resources throughout the season). In particular, I predict larger ranging movements at low population density (Wolton and Flowerdew, 1985) and scarce trophic resources (Mares and Lacher, 1987; Corp et al., 1997);

(d) autumnal adult dispersal is affected by resource abundance and is not sex-biased. To assess this hypothesis, I calculated the dispersal distance in sexes, in two years with different autumnal resource abundance. In particular, I predict the events of dispersion to be more frequent at low resource availability (Gliwicz, 1988), in both sexes (Greenwood, 1980);

(e) sexual differences in the use of space result in a sex-biased heterogeneity in parasitism rate. In particular, I predict that the tick burden is male-biased, likely depending both on physiological (Hughes and Randolph, 2001) and ecological (Ostfeld et al., 1996a; Stanko et al., 2002) mechanisms.

The CMR data are necessary:

- to monitor population structure over time;
- to estimate population density corrected for edge effect;

- to assess the sex-biased heterogeneity in parasitism rate.

4. STUDY AREA

Fieldwork was carried out on an isolated calcareous ridge (750-800 m above sea level) located in Valle dei Laghi, Trentino, in the north-eastern Italian Alps (10°57'47''E 45°58'50''N). The Valle dei Laghi is south-western located from Trento (Figure 4.1) and delimited at north side by the Garda lake, at east by the mountain group connecting Monte Stivo with Monte Bondone and at north-west by the end of the Brenta mountain group and Monte Casale. The study grid (Figure 4.2) is characterize by a mixed broadleaf woodland dominated by mature beech *Fagus sylvaticus* and with a very thin under-storey; the canopy cover is dominated by the hazel *Corylus avellana* and by the manna ash *Fraxinus ornus*, while the grass layer is characterized by felci (*Dryopteris filix-mas,* Schott), and various species of gram and geophytes as ivy (*Hedera helix,* Linneo) and cyclamen (*Cyclamens purpurascens,* Linneo).

The woodland area was selected as representative of *A. flavicollis* habitat, which was the predominant rodent species in 4 years trapping records (A. Rizzoli, Centre of Alpine Ecology, unpublished report).

4.1 Geomorphology

The area is located in the central part of Trentino mountains and in particular it belongs to the Bondone mountain group which is mainly formed by sedimentary rocks and shaped by the quaternary glatiations. (Zanella et al., 2001).

The hilly areas are characterized by calcareous or clay-calcareous bedrock soils derived from the decomposition of rocks of geologic periods going from the Jurassic to the Eocene. The Valle dei Laghi soils are usually rich in see bed skeleton and are usually quite dry; their pH is neutral or sub-alkaline due to the presence of calcareous rocks (Zanella et al., 2001).

The kinds of humus found in this area are Mull, Oligo-Dysmull and Amphimull (Zanella et al., 2001).

4.2 Climate

Although surrounded by a wide area with a continental climate, the study area has sub-mediterranean climate, due to the thermoregulation effects of the Garda lake and the presence of mountain chain delimiting the valley. The climate is generally

mild and temperate: the mean annual temperature is about 12°C - 12,5°C, the solar exposure is optimal and the winters are mild so that the temperature rarely goes under 0°C.

The annual rainfall is about 900 mm, and it is uniformly distributed throughout the seasons.

4.3 Vegetation

The beech tree is the most abundant canopy species in this area; although this plant is able to adapt to various environmental conditions, it prefers cold winters, rainy springs, and soils with good physic features. It needs high water availability because of its superficial roots, and it is present both in carbonatic and silicatic soils (Odasso, 2002).

The flora of this area is typically Mediterranean with the presence of grape-vine (*Vitis vinifera*), olive tree (*Olea europaea*), holm oak (*Quercus ilex*) and cypress (*Cupressus* spp.). The main factors affecting the distribution of the beech woodlands in Trentino are: macroclimate, nature of the soil, altitude and soil fertility (Odasso, 2002).

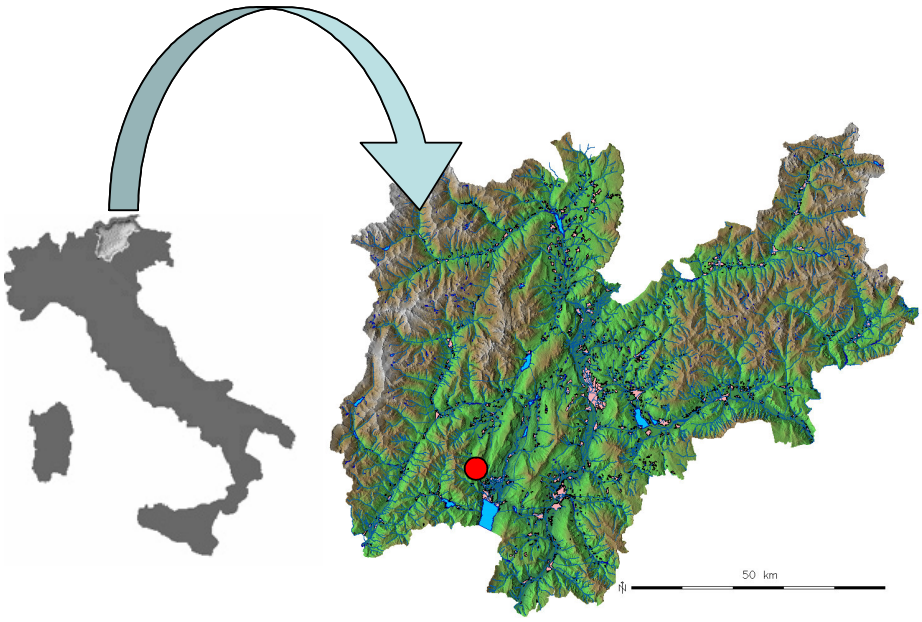


Fig. 4.1 - Trentino-Alto Adige region; in red the location of the study area

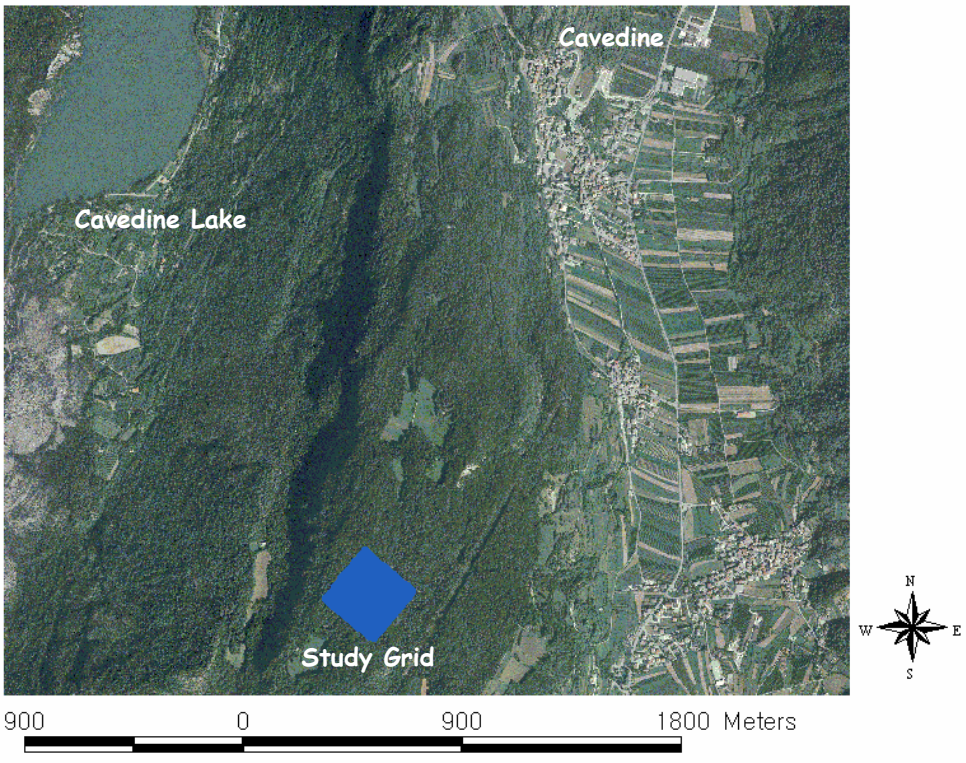


Fig. 4.2 - The location of the study grid

5. MATERIALS AND METHODS

5.1 Seed production

From 2004 to 2006, I collected data on beech seed production. Every year, 140 cone shaped litter traps with a diameter of 80 cm were placed within the trapping grid and checked fortnightly from the end of July to the middle of November (Fig. 5.1.1 and 5.1.2). I counted the number of beech seeds per trap and then I put seeds on a drying oven at 105 °C for 48 hour to determine their dry weight.

5.2 Capture-mark-recapture

From May to November 2005 and from April to November 2006 (2005: 8-13 May; 8-13 July; 7-12 August; 4-9 September; 3-9 October; 2-7 November and 2006: 23-28 April; 21-26 May; 18-23 June; 16-21 July; 13-18 August; 10-15 September; 8-13 October; 4-9 November) I carried out rodent live-trapping for 5 consecutive nights/month in an 18 X 18 trapping square grid, for a total effort of 9976 and 12960 trap nights for 2005 and 2006, respectively. Trap interval was 15 m, therefore the hypothetical grid size was 6,67 ha. Many authors recommend a minimum of 5 days of consecutive trapping for a robust and precise estimation of population size, survival rate, recruitment and good performance of closed population models (Otis et al., 1978; White et al., 1982; Nichols et al., 1984; Williams et al., 2002). In general, the trapping grid should be as large as feasibly possible to reduce the edge effect to close to zero (Faust et al., 1971). In order to estimate small mammal densities, Otis et al. (1978) recommended a grid of r (number of rows) and c (number of columns) between 9 X 9 and 15 X 15, while White et al. (1982) suggested $r + c > 25$ and Jones et al. (1996) a square grid of at least 10 X 10 traps.

Some terrain features (such as hills and rocks) caused small shifts in individual trap alignments, therefore all traps were mapped with Global Positioning System (GPS: GeoExplorer3 Trimble, Crisel, Roma, Italy) units using post-processed differential correction (accuracy of 1-5 m). I used these data to derive accurate area estimates and the exact position of fixes and traps. I used live and multiple-capture traps (Special Mouse Trap 2, Ugglan, Grahnab, Sweden; Figure 5.2.1), baited with pieces of potato of regular size as a source of water and sunflower seeds for food. I provided hay for bedding and shelter. I checked traps once a day only so as not to introduce time variation in density estimates, and to minimize

handling time, thereby avoiding trap-shy behaviour. On initial capture, I injected an implantable subcutaneous passive induced transponder (PIT) tag (Trovan ID 100, Ghislandi and Ghislandi, Covo, Bergamo, Italy) into each individual, and I recorded sex (the method to identify the sex is indicated in Figure 5.2.2), pelage color, breeding condition, body mass and ecto-parasite burden (ticks, mites and fleas); I took a 75 µl blood sample and a 3 mm biopsy from the tip of the tail for additional epidemiological and molecular analyses. In particular each blood sample was sent to a laboratory partner of the Centre for Alpine Ecology, to test also for TBE antibodies using a standard ELISA test; the antibody titre was compared to a TBE-free population of *A. sylvaticus* from Ireland. An antibody dose unit level higher than the highest level observed in the TBE-free population was taken to be TBE seropositive.

All animal manipulations were performed in accordance with EU and national laws and approved by the Wildlife Committee of the Autonomous Province of Trento.

5.3 Radio-tracking

From July to October of both years, I fitted resident adult individuals (i.e. with brown pelage, Flowerdew, 1984) of *A. flavicollis*, weighing at least 29 g, with VHF radio-transmitters (BD-2C: Holohil System Ltd., Carp, Ontario, Canada), mounted on nylon cable-tie collars (Figure 5.3.1); the weight of the complete transmitter package was less than 2 g (i.e. collar weight < 8% of animal weight, Wolton and Trowbridge, 1985). To minimize the monitoring of transient mice, I radio-collared individuals only if they were trapped a minimum of 3 times in more than 1 trapping session (Rajska-Jurgiel, 2001). Before collaring, mice were injected with light anaesthesia (Zoletil, Virbac, Milano, Italy; dose used: 140 mg/kg). Collared individuals were maintained in a terrarium overnight to allow them to recover from the anaesthetic and adapt to the collar; I released them at their point of capture the following morning. The transmitter batteries had an average life-span of 53 days; when possible, individuals were re-trapped to change the radio-collar before battery exhaustion. In 2005 I radio-collared a total of 20 individual males and 12 females: among them, 19 individuals were followed for 1 month, 6 for 2 months, 6 for 3 months and 1 male was tracked for the whole study period; in 2006 I collared 19 males and 13 females: among them 14

individuals were followed for 1 month, 7 for 2 months, 9 for 3 months and 1 male and 1 female were tracked for the whole study period. I aimed at marking a similar number of males and females in each session, but this was not possible in October 2005 (Table 5.3.1).

Every year, I completed four radio-tracking sessions in the period between successive trapping sessions (2005: 14 July – 5 August; 13 August – 2 September; 10 September – 1 October; 10 October – 31 October: 2006: 22 July – 11 August; 19 August – 8 September; 16 September - 6 October; 14 October - 7 November).

Radio-tracking was performed using ATS receivers (Model R2000: Advanced Telemetry System, Isanti (Minnesota), USA) in conjunction with a 4-element flexible Yagi antenna (Biotrack Ltd., Dorset, UK). I radio-tracked mice by homing-in (precision 3.5 m) (Wolton, 1985), referring to a field grid marked using canes with reflective tape for an accurate data collection at night, obtained dividing each square of the trapping grid, delimited by 4 traps, into 21 points, as in Figure 5.3.2. Localizations which fell out of the study grid were mapped by GPS. I recorded animal movements from dusk to dawn, so that the time interval between successive fixes was not less than 50 minutes, considered sufficiently short to follow movements of each mouse (Wolton, 1985) and long enough to avoid autocorrelation of the data (Swihart and Slade, 1985; Rooney et al., 1998; Otis and White, 1999). I also recorded one fix/animal/day in daylight, to localize burrows. At the moment of localization, I recorded date, time, meteorological conditions, status of the individual (i.e. active/inactive, below or above ground), and any specific behaviour; field form for data collection as in Figure 5.3.3.

I could not estimate the home range of all animals, as some individuals were predated early after the beginning of the session. I therefore performed the home range analysis only on animals which showed an asymptotic curve of number of fixes *vs* home range size (Harris et al., 1990). This was the case for 21 mice, 14 males and 7 females in 2005 and for 21 mice, 11 males and 10 females in 2006 (Table 5.3.1). Both sexes reached asymptotes when more than 50 fixes were recorded (Figure 5.3.4).

All animal handling procedures were carried out in accordance with the protocols approved by the scientific Committee of the Research Fund of the Autonomous Province of Trento.

Tab. 5.3.1 Proportion of radio-collared *A. flavicollis* with sufficient number of fixes for monthly home range analysis.

Year	Month	Males	Females	Total
2005	July	4/6	4/5	8/11
	August	7/7	6/7	13/14
	September	6/10	4/8	10/18
	October	4/7	0/3	4/10
2006	July	4/9	4/9	8/18
	August	7/12	7/10	14/22
	September	6/7	7/9	13/16
	October	3/5	3/4	6/9

5.4 Density estimation

Previous research (Parmenter et al., 1998) has shown that handling procedures have no significant effects on rodent recapture rates or mortality, therefore I used data from CMR and radio-tracking exercises to assess density estimates.

Density estimates were limited to the adult population, in order to put the radio-tracked sample in context and meet the assumption of demographic closure (White and Shenk, 2001).

In each primary trapping session, I classified the individuals as “adults” or “juveniles” according to the following criteria:

1) capture history: I classified as adult any recaptured individual already trapped in a previous trapping session;

2) individual parameters: for each session, I tested individual weights at trapping for differences in relation to sex, pelage color and interaction among the two factors (Flowerdew, 1984; Marsh, 1999);

3) breeding status, where sexual maturity was defined by presence of descended testes for males and perforated vagina, pregnancy or lactation for females (Gurnell and Flowerdew, 1990).

I used the Program Capture (CAPTURE 2 version <050810.1025>, 2005) (White et al., 1978; Rexstad and Burnham, 1991) to perform a closure test for each trapping session.

I entered capture histories of all animals in an "xy-reduced" format into the program to perform the model selection procedure. CAPTURE then computed population size according to all models with an available population estimator, i.e.:

1) the null model M_0 (Otis et al., 1978) that assumes equal capture probabilities among individuals;
2) the time model M_t (Darroch, 1958) that assumes capture probabilities to vary with time;
3) two heterogeneity models: jackknife estimator, M_h (Otis et al., 1978) and M_h-Chao (Chao, 1987) that assume capture probabilities to vary independently among individuals;
4) the behavioural model M_b (Zippin, 1956, 1958) that assumes capture probabilities to vary with trap experience (i.e. "trap-happy" or "trap-shy");
5) the generalized removal model M_{bh} (Otis et al., 1978) that assumes capture probabilities to vary with heterogeneity and behavioural response to capture;
6) the model M_{tb} (Otis et al., 1978) that assumes capture probabilities to vary with time and behavioural response to capture.

To density estimates I took into account only the best estimator choose by the software; in particular, M_{bh} was the best model in most sessions of 2005, whereas M_0 was the best one in most sessions of 2006. The naïve density was calculated as M_{t+1} divided by the raw trapping grid area (TGA) (Otis et al., 1978), while M_0 and M_{bh} were divided by two estimates of the effective trapping area, i.e. the trapping grid area plus a boundary strip of width W, to account for the edge effect (Bondrup-Nielsen, 1983).

In particular, density estimates ($\hat{D}$) were derived from population size ($\hat{N}$) calculated using the two best estimators (i.e. M_{bh} for 2005 and M_0 for 2006) and three definitions of effective trapping area A(W) or ETA:

1) trapping grid area (TGA);

2) TGA plus W equal to MMDM calculated from trapping data, i.e. the mean of the maximum distance between recaptures for all animals caught at least twice (Wilson and Anderson, 1985);
3) TGA plus W equal to the mean radius of monthly home ranges (Dice, 1938) defined as: $r = \sqrt{(P^2/4) - 2A}/2$ where A and P are the area and perimeter of home ranges, calculated as Kernel at 95%.

I calculated TGA and MMDM using the Program DENSITY (DENSITY version 3.3 Release 2, 2005) (Efford et al., 2004), where data were entered in trapID format (individual ID, trapping session and trap coordinates).

5.5 Population structure

I checked the temporal variation on population structure assessing the monthly age class composition of the population under study, both for 2005 and 2006; moreover, I evaluated the monthly sex ratio, the capture frequency and the seasonal pattern of individual body weight both for males and females. To compare mean monthly body weight among sexes, I applied the non parametric Mann-Whitney test, whilst to compare the numbers of adult males and females caught in every trapping session, I applied the chi-square test.

5.6 Analysis of radio-tracking data

I tested all response variables for normality using the Shapiro-Wilk test and for homogeneity of variance using the Bartlett test; if data were not normally distributed, I determined the actual distribution of errors, testing the empirical values of the response variable *vs* the theoretical distributions (Crawley, 2002). Where appropriate, response variables were log transformed or arcsine transformed. Response variables were modelled for dependence on predictor variables using the all-subset model selection method based on the Akaike information criterion (AIC) corrected for small sample size, AICc (Burnham and Anderson, 2002). I calculated AIC for all possible models starting from an *a priori* full model, and ranked the models accordingly. From the AICc differences (ΔAICc), I calculated AICc weights (ω) and the relative evidence ratios (Burnham and Anderson, 2002). When differences in AICc values were less than two, indicating approximately equal parsimony of models, I ranked all variables considered in the full model according to their importance (predictor weights $\omega_+(j)$, Burnham and Anderson, 2002). Parameter estimates were evaluated for the

best model or by model averaging, in case of equal parsimonious models, weighting estimates from each model according to their Akaike weight. When comparing datasets of the two sampling years, I considered as full model that including all variables selected in the best model of either year, and their biologically meaningful interactions.

Data were presented as means ± SE.

All statistical analysis were carried out with the software R version 2.3.1 (2006), R package nlme version 3.1-77 (2006), R package lme4 version 0.995-2 (2006) and R package fBasics version 240.10068.1 (1996). Spatial analysis were carried out with the software ArcGIS 9.0 (2006).

5.6.1 Ranging movements

I estimated monthly home range size using 2 methods: the minimum convex polygon at 100% (*MCP*) and the fixed Kernel at 95% (*HR*) applying least squares cross validation to select the smoothing parameter (Kernohan et al., 2001). MCP is the most widely used deterministic technique, and therefore useful for comparison, but its restrictions are well known (Laver, 2005), whilst the latter is a probabilistic method that provides a more robust home range estimate (Harris et al., 1990; Seaman and Powell, 1996). To estimate core area size (*CA*), the area within a home range that is overused compared to a uniform distribution (Samuel et al., 1985), I applied the Kernel function at 50% (Harris et al., 1990). Kernel probability distributions (i.e. utilization distributions, or UDs, geographically represented by raster maps) and their relative 95% and 50% probability surfaces (geographically represented by polygons) were calculated using the software R version 2.3.1 (2006) and the R package Adehabitat version 1.5-1 (2006).

I tested the response variables *MCP*, *HR*, *CA* for variation associated with *sex*, *month* and *weight* in each year and for variation associated with *year*, *sex* and *month* for the two pooled datasets by means of linear mixed models, with *individual* as random effect to account for pseudoreplication (Crawley, 2002) **(Hypotheses b and c)**.

I determined the centre of maximum activity of each mouse as the maximum probability value of the UD; I calculated the distance between such points (maximum activity distance, *MAD*) among males (MM), females (FF) and sexes (MF) and I tested the response variable *MAD* for variation associated with *year*,

sex and *month* for the two pooled datasets by means of a generalized linear model with gamma distributed error **(Hypotheses c)**.

In the radio-tracked sample population, I recorded adult animal dispersal. To distinguish between excursions and "true dispersal" movements (McShea and Madison, 1992), I calculated the spatial distance between fixes of the same animal recorded in successive nights after a known time interval (*ΔT*); I grouped the distances into 2 binary variables according to the 75th and 98th percentiles, which corresponded to 60 m and 210 m, respectively, in 2005 and to 95 m and 400 m, respectively, in 2006 (*DM75* equals 0 if interfix distance < 60 m in 2005 and 95 m in 2006, otherwise 1; *DM98* equals 0 if interfix distance < 210 m in 2005 and 400 m in 2006, otherwise 1). I tested variables *DM75* and *DM98* for variation associated with *sex*, *month*, *ΔT* and *dispersion* by means of generalized linear mixed models with binomial error, fitting *individual* as random effect, both for 2005 and for 2006; the explanatory variable *dispersion* indicated whether the individual permanently moved away from the trapping grid **(Hypotheses b and d)**.

5.6.2 Home range overlap

The simplest method for quantifying static overlap between individuals is to calculate the percentage of overlapping ranges relative to the number of potential such overlaps (Chambers et al., 2000; Tristiani et al., 2003); however, this calculation ignores the relative probability of space use by individuals. Instead, Fieberg and Kochanny (2005) suggested two overlap indices that are a function of the product of the UDs of overlapping animals: the utilization distribution overlap index (*UDOI*), for quantifying the pattern of space use, and the Bhattacharyya's affinity (*BA*), which quantifies the degree of similarity among UD estimates. *UDOI* can range from 0 to infinite and, in particular, it is equal to 0 for UDs that do not overlap, to 1 if UDs are uniformly distributed and completely overlapped, and greater than 1 if the UDs are not uniformly distributed with an high degree of overlap. Applying this index to an individual with itself, I assessed the uneven use of space of such individual. *BA* can range from 0 to 1 and, in particular, it is equal to 0 with no overlap and to 1 when home ranges totally overlap. I applied BA index to all possible pairs of individuals to define their degree of overlap. I tested the response variables *UDOI* for variation associated with *sex*, *month* and *weight*

in each year by means of linear mixed models, with *individual* as random effect **(Hypothesis c)**. I investigated the effect of *sex* (in this case, pair composition, i.e. male-male, male-female, female-female) and *month* on *BA* for each year and the effect of *year* and *sex* for the two pooled datasets by means of generalized linear models with gamma error **(Hypotheses a and b).**

In addition, for the pairs of animals actually overlapping, I estimated the probability of animal j being located in animal i's home range/core area and *vice versa*; this procedure is directional, so 2 values quantify the overlap of a pair ($PHR_{i,j}$ and $PHR_{j,i}$). I transformed these quantities into 2 binary variables (*PHR50* and *PHR95*), that define the presence (*PHR* = 1) or absence (*PHR* = 0) of overlap at 50% and 95% probability contours. I tested the effect of *sex* (in this case, pair composition, i.e. male-male, male-female, female-female) on *PHR50* and *PHR95* by generalized linear models with binomial error **(Hypotheses a and b)**.

5.6.3 Use of the burrow system

For every radio-tracking session, I established the mean number of burrows used by all males and females (compared by Mann-Whitney non parametric test) and the presence of shared burrows. For individuals with UD estimates, I calculated the distance between each burrow and their centre of maximum activity, i.e. the maximum probability value of the UD (*BD*).

I investigated the effect of *year*, *sex* and *month* on *BD* for the pooled datasets (2005 and 2006) by means of a linear mixed model, fitting *individual* as random effect **(Hypotheses a and b)**.

5.6.4 Parasite burden

For both years, I monitored the temporal pattern and the sexual heterogeneity of the individual larvae load by testing tick burden of the whole marked population for variation associated with *sex* and *month* by generalized linear models with negative binomial error; moreover I compared the individual larval load amongst the two study years, evaluating the response variable (*TB*: tick burden) for variation associated with *year*, *sex* and *month* for the two pooled datasets by means of generalized linear model with negative binomial error **(Hypothesis e)**.

Fig. 5.1.1 – Cone shaped litter traps

Fig. 5.1.2 – Beech seeds

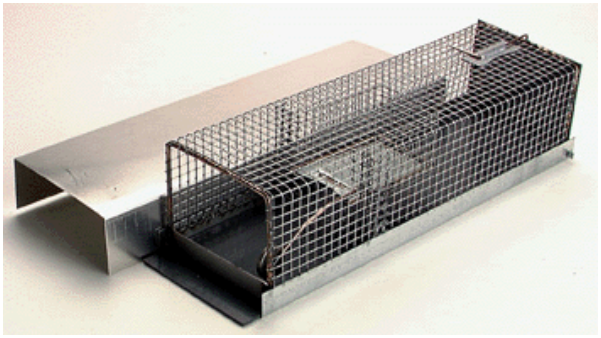


Fig. 5.2.1 – Ugglan multiple capture live trap

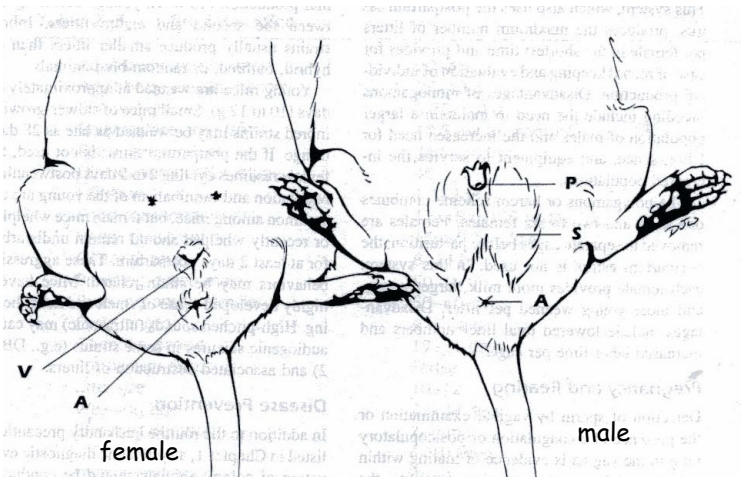


Fig. 5.2.2 – Method to identify sex in small rodents
(V: vaginae; A: anus; P: penis; S: testis)

Fig. 5.3.1 – Radiocollar

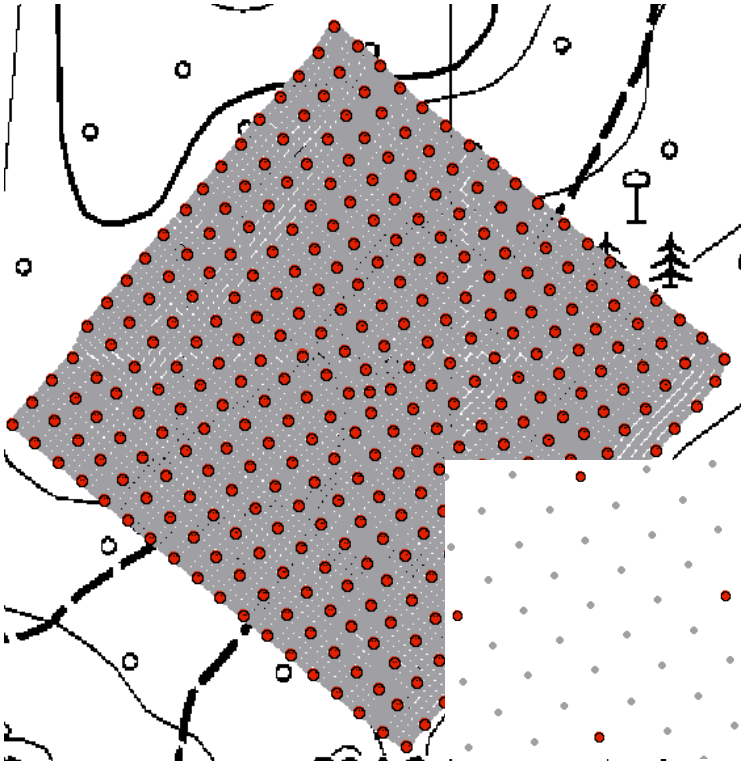


Fig. 5.3.2 – Trapping grid; each square delimited by 4 traps (large circles) was divided into 21 points (small circles) with 3.5 m spacing

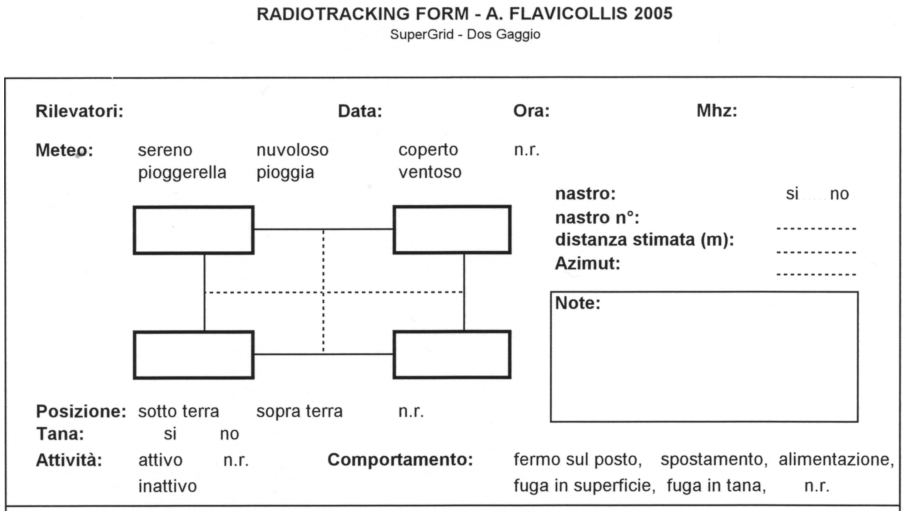


Fig. 5.3.3 – Field form for radio-tracking data collection

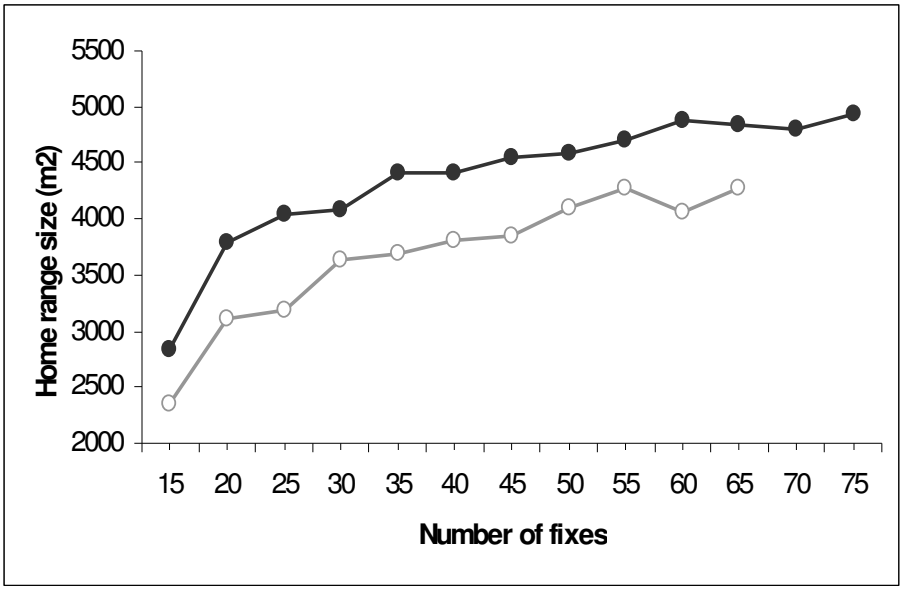


Fig. 5.3.4 Asymptotic curve achieved by plotting home range size *vs* number of fixes for female (open circles) and male (closed circles) *A. flavicollis*

6. RESULTS

6.1 Seed production

In 2004 beech seed mast was recorded, as 15164 seeds were collected; on the opposite, as expected, in 2005 no forest primary productivity was recorded (i.e. zero seeds were collected). Finally, in 2006 there was an increase in the beech tree productivity as 657 seeds were collected. The number of seeds collected every year and their dry weight are shown in Table 6.1.1.

Tab. 6.1.1 – Number of beech seeds collected every year and their dry weight

Year	N° beech seeds	Dry weight (g)
2004	15164	1806.03
2005	-	-
2006	657	79.22

6.2 Density estimation

Capture probability was between 0.39 and 0.64 for 2005 and between 0.20 and 0.51 for 2006 and the assumption of population closure was met in all sessions, except in September 2005 (closure test: z = -1.65, p= 0.048). No rodents escaped during the handling and data recording procedures. Rodent mortality due to trapping was extremely low (i.e. 1.5%), and dead animals were eliminated from the data set (Otis et al., 1978). In 2005, juveniles were mainly captured in May, with very few such captures in the other sessions, whilst in 2006 they were caught only in November (see paragraph 6.3). No individuals lost their marks during the experiment.

In general, ETA increased when behavioural parameters were used in its estimation. In particular, when W was equal to the mean radius of home ranges calculated with Kernel at 95%, a buffer area exceeding 100% of TGA was added in all sessions (Table 6.2.1), thus leading to the smallest density values (Table 6.2.2). The Program CAPTURE selected model M_{bh} as best one in all trapping sessions of 2005 and M_0 as second choice; in 2006, the model M_0 was selected as the first choice in all sessions. In 2005, density estimates for each trapping session were consistent when calculated by the two different estimators (Table 6.2.2). I

selected M_0 to compare density estimates amongst the two years. Both in 2005 and 2006, population density was maximum in July and August and started to decrease in September (Table 6.2.2). In 2005, the population density reached mean to high values when compared to other similar areas (e.g. Montgomery, 1980b; Rajska-Jurgiel, 1992; Mazurkiewicz and Rajska-Jurgiel, 1998) and was higher than in 2006 for all trapping sessions (Table 6.2.1, Figure 6.2.1 and Figure 6.2.2).

Tab. 6.2.1 - Effective trapping area (E.T.A., ha) calculated from May to November 2005 with 2 different values of boundary strip (W) and relative area values added (in %) to the trapping grid area (TGA)

			MAY		JUNE		JULY		AUGUST		SEPTEMBER		OCTOBER		NOVEMBER	
YEAR	W	TRAPPING GRID	E.T.A.	% Area added	E.T.A.	% Area added	E.T.A.	% Area added	E.T.A.	% Area added	E.T.A.	% Area added	E.T.A.	% Area added	E.T.A.	% Area added
2005	TGA + MMDM	6.67	8.96	34.33	-	-	9.47	41.98	9.87	47.98	11.83	77.36	14.1	111.39	13.61	104.05
	TGA + radius Kernel	6.67	-	-	-	-	18.17	172.41	20.99	214.69	22.99	244.68	33.82	407.05	-	-
2006	TGA + MMDM	6.67	13.12	96.7	9.57	43.33	9.82	47.23	12.53	87.86	14.56	118.29	12.19	82.76	9.94	49.03
	TGA + radius Kernel	6.67	-	-	-	-	38.69	480.06	33.66	404.65	34.96	424.14	39.53	492.65	-	-

Table 6.2.2 - Density estimates of the adult population of *A. flavicollis*, based on the CMR experiment

Year	Month	Naïve density (N/ha) M_{t+1}/TGA[a]	Density (N/ha±SE) M_0[b]/(TGA+MMDM[d])	Density (N/ha±SE) M_0/(TGA+r[e])	Density (N/ha±SE) M_{bh}[c]/(TGA+MMDM)	Density (N/ha±SE) M_{bh}/(TGA+r)
2005	May	13.34	10.05 ± 2.46	-	10.49 ± 2.52	-
	July	16.79	11.93 ± 3.23	6.22 ± 5.79	13.09 ± 3.39	6.82 ± 6.09
	August	18.29	12.46 ± 2.88	5.86 ± 3.15	12.56 ± 2.90	5.91 ± 3.16
	September	11.54	6.51 ± 3.03	3.35 ± 1.89	6.76 ± 3.08	3.48 ± 1.93
	October	5.40	2.55 ± 4.13	1.06 ± 1.46	3.48 ± 4.82	1.45 ± 1.83
	November	4.65	2.28 ± 3.34	-	2.42 ± 3.44	-
2006	May	0.90	0.85 ± 10.20	-	-	-
	June	2.25	1.69 ± 3.35	-	-	-
	July	3.30	2.27 ± 4.19	0.57 ± 1.56	-	-
	August	4.20	2.50 ± 3.72	0.93 ± 1.74	-	-
	September	2.10	1.11 ± 4.09	0.46 ± 1.14	-	-
	October	1.35	0.83 ± 1.92	0.25 ± 1.37	-	-
	November	0.60	0.41 ± 7.28	-	-	-

Density estimates refer either to the trapping grid area (Naïve density) or to the effective trapping area (Density), obtained adding a boundary strip to the trapping grid area, to account for edge effect.

[a] TGA: trapping grid area

[b] M_0: N estimated according to the null model

[c] M_{bh}: N estimated according to the generalized removal model

[d] MMDM: boundary strip calculated as Mean Maximum Distance Moved

[e] r: boundary strip calculated as mean radius of home range, estimated as kernel 95%.

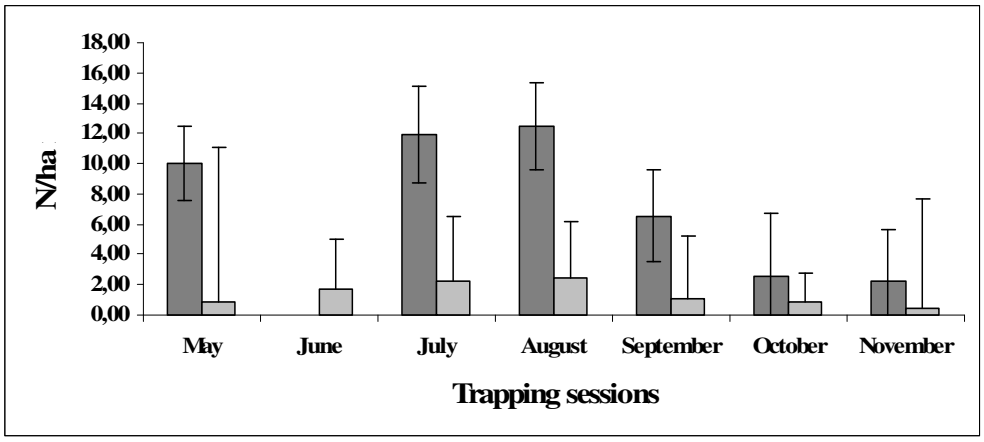


Fig. 6.2.1 - Density values calculated as M_0/(TGA+MMDM), where M_0 is N estimated according to the null model, TGA: trapping grid area and MMDM: boundary strip calculated as Mean Maximum Distance Moved derived from trapping data; data from 2005 (black bars) and 2006 (grey bars) are shown

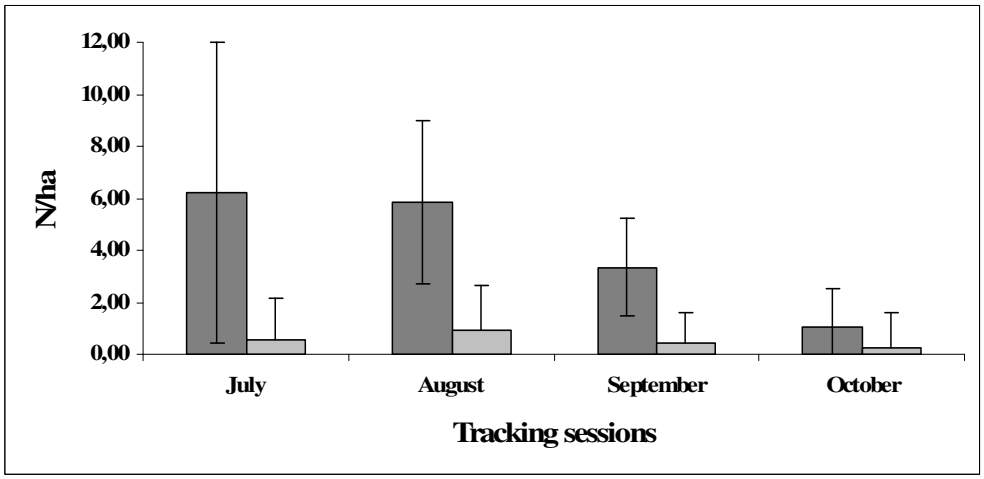


Fig. 6.2.2 - Density values calculated as M_0/(TGA+r), where M_0 is N estimated according to the null model, TGA: trapping grid area and r: boundary strip calculated as mean radius of home range, estimated as kernel 95%; data from 2005 (black bars) and 2006 (grey bars)
are shown

6.3 Population structure

I registered a total of 2023 and 274 mice captures and recaptures in 2005 and 2006, respectively. In 2005, 417 individual *A. flavicollis* were marked with PIT-tags; among these 228 were males, 184 females and 5 indeterminate. During 2006, only 68 individuals were marked; of these 35 were males, 31 females and 2 indeterminate.

Table 6.3.1 and 6.3.2 show, session by session, the number of daily recapture and capture (i.e. recapture plus new capture), and the daily percentage of new caught, for 2005 and 2006, respectively. In 2005, from the first trapping day to the last one there was a decrease in the percentage of new animal caught, and this value, at the 5th trapping day never exceeded 13% (Tab 6.3.1); on the opposite, in 2006, within each trapping session, the pattern of variation of the percentage of new mice captured was not so clear as in 2005, so that there was a great fluctuation in the number of new captures, as shown in Table 6.3.2. This great variability may be due to the mice high mobility that occur typically during year of low population density and scarce food abundance (Mazurkiewicz and Rajska-Jurgiel, 1998).

Tab. 6.3.1 - Number of daily mice recapture, capture (i.e. recapture plus new capture) and percentage of new daily mice caught, during trapping session of 2005

Trapping session	Trapping day	N° daily recaptures	N° daily total capture	% new captures
May	1	-	95	100
	2	55	101	45.5
	3	88	111	20.7
	4	100	121	17.4
	5	133	146	8.9
July	1	20	66	54.5
	2	51	74	31.1
	3	55	67	17.9
	4	75	86	10.5
	5	67	77	12.9
August	1	67	77	12.9
	2	69	77	10.4
	3	70	76	7.9
	4	75	78	3.8
	5	67	71	5.6
September	1	28	34	17.7
	2	41	47	12.8
	3	50	57	12.3
	4	53	57	7.0
	5	48	50	2.0
October	1	14	25	44
	2	12	17	29.4
	3	24	26	7.7
	4	32	35	8.6
	5	31	32	3.1
November	1	16	18	11.1
	2	16	17	5.9
	3	16	16	-
	4	22	26	15.4
	5	24	26	7.7

Tab. 6.3.2 - Number of daily mice recapture, capture (i.e. recapture plus new capture) and percentage of new daily mice caught, during trapping session of 2006

Trapping session	Trapping day	N° daily recaptures	N° daily total capture	% new captures
May	1	1	1	-
	2	-	2	100
	3	1	1	-
	4	2	5	60
	5	2	2	-
June	1	3	7	57.1
	2	6	8	25
	3	7	8	12.5
	4	7	7	-
	5	8	11	27.3
July	1	8	12	33.3
	2	4	5	20
	3	7	11	36.4
	4	11	13	15.4
	5	11	12	8.3
August	1	14	16	12.5
	2	7	10	30
	3	14	17	17.6
	4	16	17	5.9
	5	12	15	20
September	1	7	8	12.5
	2	4	4	-
	3	8	10	20
	4	9	9	-
	5	8	10	20
October	1	5	5	-
	2	1	1	-
	3	5	5	-
	4	5	5	-
	5	4	4	-
November	1	1	3	66.6
	2	3	7	57.1
	3	4	8	50
	4	8	9	11.1
	5	7	8	12.5

In 2005, the spring population (i.e. May) was mainly formed by juvenile *A. flavicollis*, whilst during the others trapping sessions, the number of juveniles caught was very low and decreased from May to November (Figure 6.3.1). In 2006, juveniles occurred only in November, whilst during the year I never trapped individuals of such age class (Figure 6.3.2).

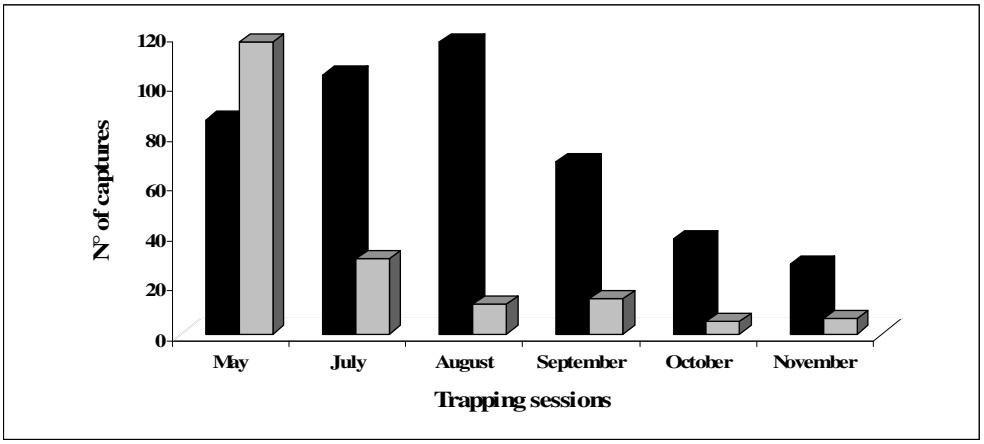


Fig. 6.3.1 – Number of adults (black bars) and juveniles (grey bars) caught per trapping session in 2005

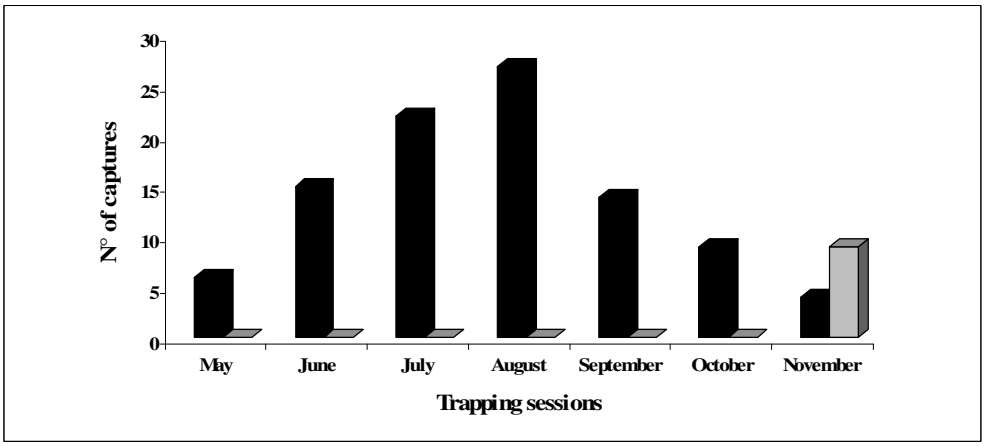


Fig. 6.3.2 – Number of adults (black bars) and juveniles (grey bars) caught per trapping session in 2006

In 2005, the number of males and females trapped in every trapping session, decreased gradually throughout the year and in particular it reached the minimum values in November; moreover the sex-ratio was significantly deviated from 1:1 only in November (χ^2 = 4.24, p< 0.05), it was nearly constant from May to September and then it had a quick and abrupt increase between October and November (Figure 6.3.3). Differently, in 2006, the number of captures increased from spring to summer, reaching the peak in August, and then decreased since September; furthermore, the pattern of sex ratio was not so clear as in 2005, fluctuating throughout the seasons (Figure 6.3.4), but it was not significantly different from 1:1.

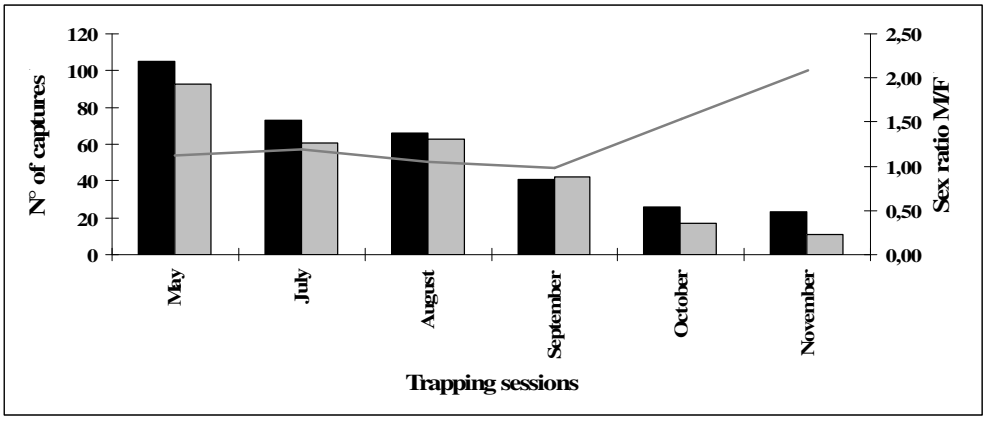


Fig. 6.3.3 – Number of male (black bars) and female (grey bars) *A. flavicollis* caught per trapping session in 2005 and sex ratio (M/F) (grey line)

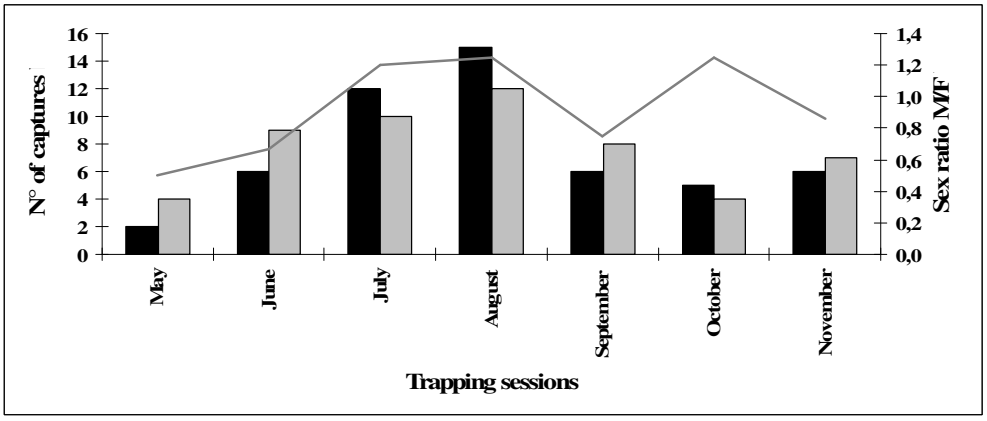


Fig. 6.3.4 – Number of male (black bars) and female (grey bars) *A. flavicollis* caught per trapping session in 2006 and sex ratio (M/F) (grey line)

Table 6.3.3 show the mice capture frequency, both for 2005 and 2006, calculated in the whole study period; in 2005, the animals caught 1 or 2 times (i.e. individuals classified as transient - Rajska-Jurgiel, 2001) was 32.8% of the marked population, whilst in 2006 it increased at 50%.

Tab. 6.3.3 Mice capture frequency for 2005 and 2006

Year	N° captures	N° individuals	Year	N° captures	N° individuals
2005	1	87	2006	1	22
	2	50		2	12
	3	73		3	11
	4	57		4	5
	5-10	90		5-10	13
	>10	60		>10	5

In 2005, I registered an increase of the mean body weight from spring to summer, particularly for males, followed by a decrease during October and November (Figure 6.3.5); in all but one trapping sessions the mean body weight of males was higher than females one (July: U= 9701, p= 8.06E-06; August: U= 2235.5, p= 1.46E-11; September: U= 1335.5, p= 2.73E-08; October: U= 362.5, p= 1.83E-03; November: U= 232.5, p= 0.004); in May, this was not true probably because of the great number of pregnant females found in this month.

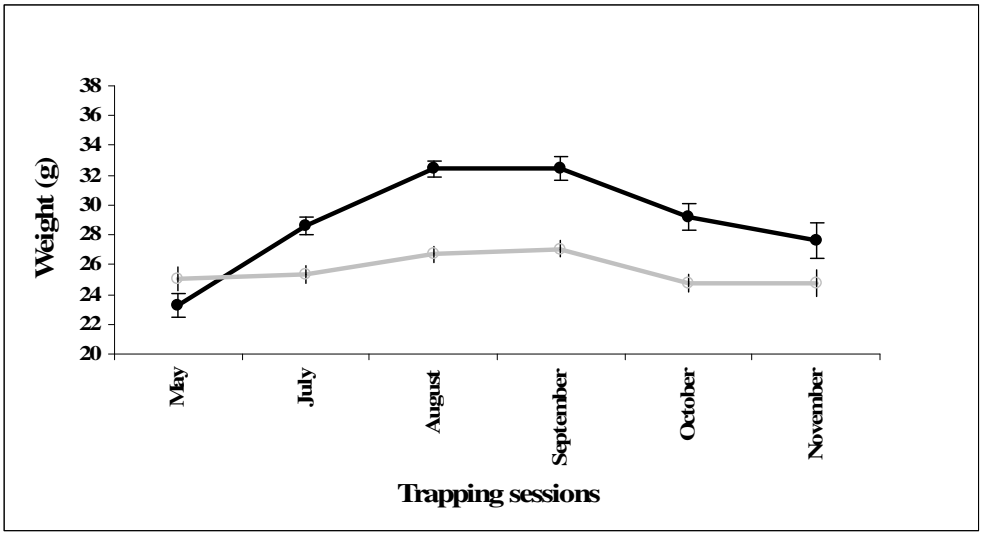


Fig. 6.3.5 – Seasonal pattern of male (closed circle) and female (open circle) *A. flavicollis* mean body weight (g) in 2005

In 2006, the mean female body weight reached a peak in October, then followed by a quick decrease, whereas mean male body weight got to the maximum value

on July and remained constant from July to October, decreasing rapidly in November, as observed for females (Figure 6.3.6). The mean male body weight resulted higher than female one only during July and August (July: U= 15, p= 0.003; August: U= 25, p= 0.0005).

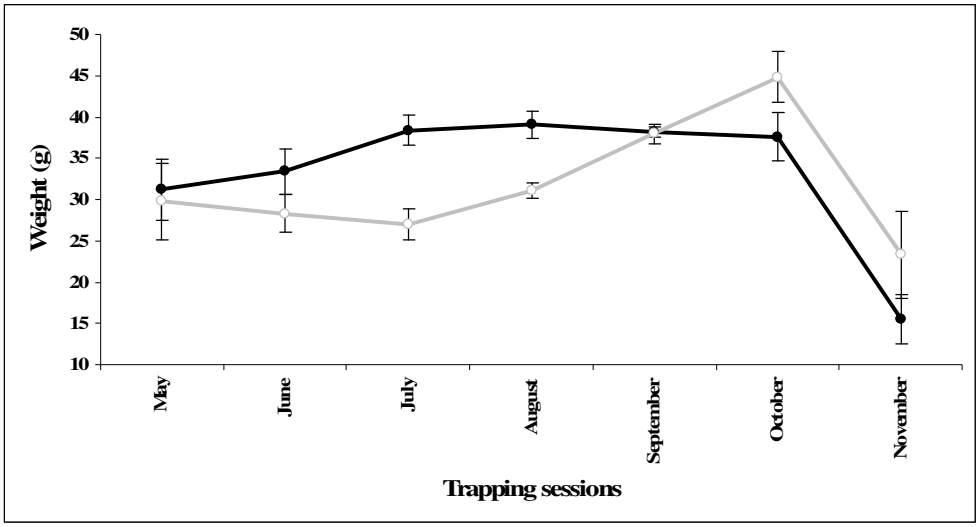


Fig. 6.3.6 – Seasonal pattern of male (closed circle) and female (open circle) *A. flavicollis* mean body weight (g) in 2006

6.4 Radio-tracking data

6.4.1 Ranging movements

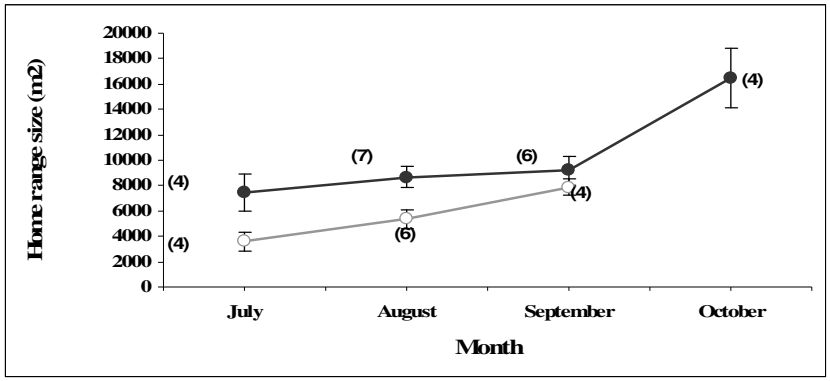
The mean number of radio-tracking localizations per animal per session was 12.4 ± 0.8 and 65.7 ± 2.2, for diurnal and nocturnal fixes respectively, in 2005, and it was 11.4 ± 0.7 and 48.9 ± 2.6, for diurnal and nocturnal fixes respectively, in 2006. The mean values of home range size, calculated as kernel at 95% and MCP, and core area size, are shown in Figure 6.4.1.1 and 6.4.1.2 for 2005 and 2006, respectively.

In 2005, the two primary predictor variables for home range size (*HR* and *MCP*) were *sex* and *month* (predictor weights for *HR*: *sex*=0.83, *month*= 0.58; for *MCP*: *sex*= 0.77, *month*= 0.34), included in either equal parsimonious model (Table 6.4.1.1a). Male home ranges were larger than those of females, as shown by the model averaged coefficients (Table 6.4.1.1b: *MCP* coefficients were also model averaged for homogeneity with *HR*). Moreover, home range size increased throughout the study period (Table 6.4.1.1b and Figure 6.4.1.1). In 2006, the best

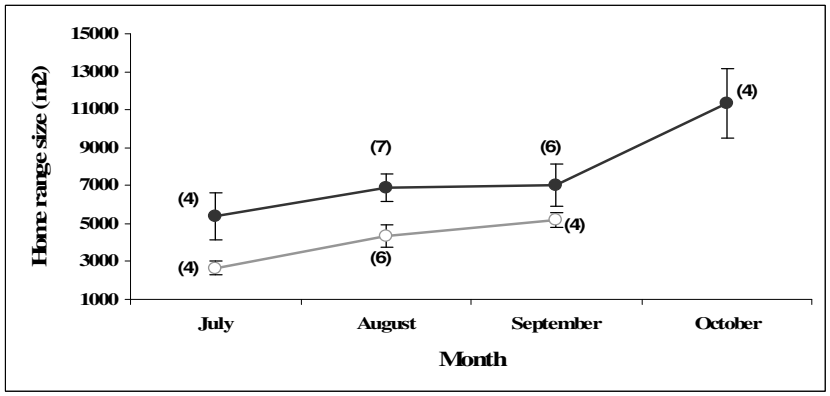
model for home range size (*HR* and *MCP*) included only *sex* as explanatory variable (Table 6.4.1.2a). Male home ranges were larger than those of females, as shown by the best model coefficients (Table 6.4.1.2b); during this year we did not observe any temporal effect on the home range size (Figure 6.4.1.2). When all data were pooled, home range size (*MCP* and *HR*) was influenced by *year* and *sex* (Table 6.4.1.3a); in particular, the home range size was greater in 2006 than in 2005 as shown by the best model coefficients (Table 6.4.1.3b). Both in 2005 and 2006, home range size was not influenced by individual *body weight* (Table 6.4.1.1a and 6.4.1.2a, respectively).

In 2005, core area size (*CA*) was affected by *sex* and *month* (predictor weights: *sex*= 0.93, *month*= 0.35) (Table 6.4.1.1a); in particular, male core areas were larger than those of females and core area size increased throughout the season (Table 6.4.1.1b and Figure 6.4.1.1). In 2006, the primary predictor variable for *CA* was *sex* (Table 6.4.1.2a; predictor's weight: *sex*= 0.63), and specifically males had larger core area than females (Table 6.4.1.2b); no effect of *month* was detected, as for *HR* and *MCP* in the same year (Figure 6.4.1.2, Table 6.4.1.2a). For pooled data, I found that the best model was affected by *year* and *sex* (Table 6.4.1.3a), with the core area size greater in 2006 than in 2005, as shown by the best model coefficients (Table 6.4.1.3b).

(a)



(b)



(c)

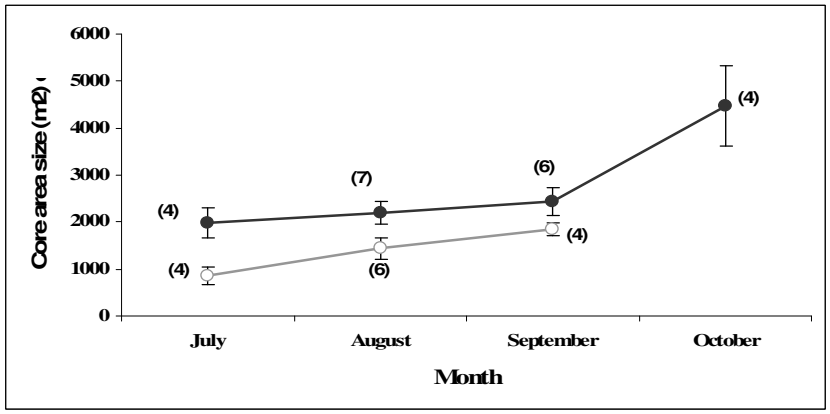


Fig. 6.4.1.1 - Mean home range size ± SE of *A. flavicollis* in 2005, calculated using kernel at 95% (a) and the minimum convex polygon at 100% (b), and mean core area size, calculated using kernel 50% (c). Closed circles: males; open circles: females. Sample size in parentheses

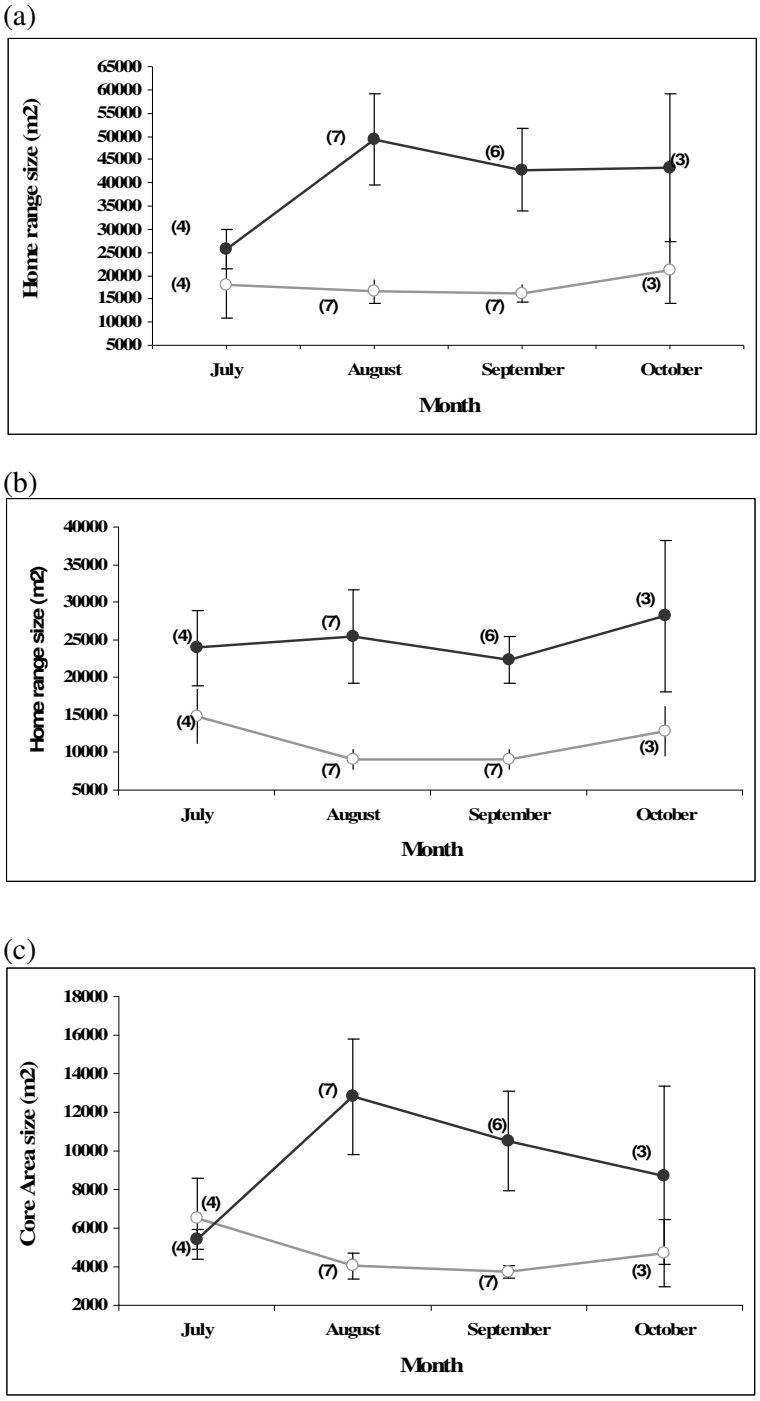


Fig. 6.4.1.2 - Mean home range size ± SE of *A. flavicollis* in 2006, calculated using kernel at 95% (a) and the minimum convex polygon at 100% (b), and mean core area size, calculated using kernel 50% (c). Closed circles: males; open circles: females. Sample size in parentheses

When data from the two years were pooled, I observed that the primary predictor affecting the distance between centres of maximum activity (*MAD*) was *year*, followed by *month* and *sex* (predictor weights: *year*= 1, *month*= 0.77, *sex*= 0.52) (Table 6.4.1.3a). In particular, there was a positive correlation between the response variable and *year*, as *MAD* increased from 2005 to 2006 (Table 6.4.1.3b and Figure 6.4.1.3).

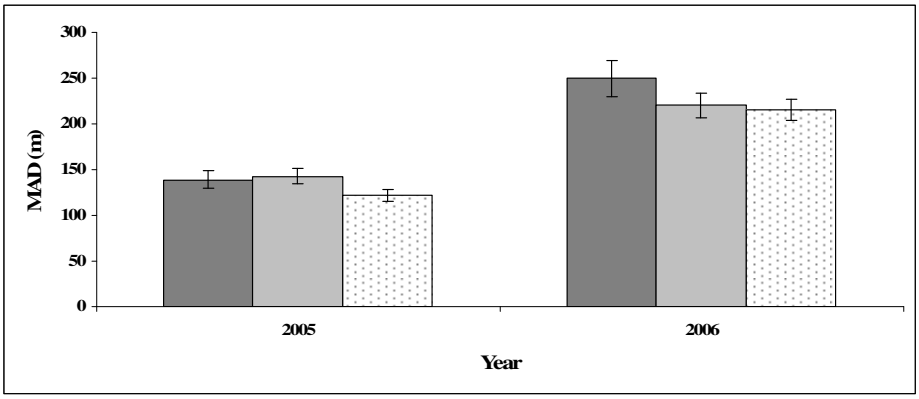


Fig. 6.4.1.3 – Mean distance between centres of maximum activity, calculated in 2005 and 2006, for male-male pairs (black bars), female-female pairs (grey bars) and male-female pairs (dot bars)

In 2005, from the end of September to early October, 8 out of 13 collared mice (4 males and 4 females) moved permanently away from the trapping grid. The dispersion was abrupt and, for most individuals, occurred during a single night. The main predictor variables of *DM75* were *dispersion*, *sex* and *month* (predictor weights: *dispersion*=1, *sex*=0.99, *month*=0.45, ΔT=0.21) (Table 6.4.1.1a). The proportion of long daily distances travelled increased in October and it was greater in males than in females, as indicated by the model averaged coefficients (Table 6.4.1.1b, Figure 6.4.1.4a: e.g. daily distances travelled greater than 120 m, with the exception of dispersion events, occurred only in September and October, in males). The most parsimonious model for *DM98* included only *dispersion* as fixed effect (Table 6.4.1.1a), indicating that outlier daily distances travelled (i.e. greater than 300 m) were strictly associated to dispersion events, and occurred in September and October only, in both sexes (Figure 6.4.1.4a). Among dispersed individuals, the mean total distance travelled during the dispersion event was 1540

m ± 322.8 for males and 1476 m ± 356.7 for females; figure 6.4.1.5 show the locations of mice after dispersal, in 2005.

In 2006, from the end of September to early October, 3 out of 16 collared mice (1 male and 2 females) moved permanently away from the trapping grid. *DM75* was affected by *Time interval* (*ΔT*), *sex* and *dispersion* (Table 6.4.1.2a); in particular, males moved wider than females, but no clear monthly pattern was recorded, apart for dispersion events (Table 6.4.1.2b and Figure 6.4.1.4b). *Dispersion* and *ΔT* were the two main predictor variables of *DM98* (predictor weights: *dispersion* = 1, *ΔT* = 0.59, *sex*=0.27), included in either equal parsimonious model (Table 6.4.1.4a). As in 2005, outlier daily distances travelled (i.e. greater than 510 m) were associated to dispersion events, and occurred from the end of September to October in both sexes (Figure 6.4.1.4b). Among dispersed individuals the mean total distance travelled during the dispersion event was 1104.5 m ± 231.6.

Moreover, the daily distance travelled, apart from dispersion events, was generally longer in 2006 than in 2005 (up to 500 m and 200 m, respectively, Figure 6.4.1.4).

Tab. 6.4.1.1a - Model selection for the response variables computed from the 2005 radio-tracking data of *A. flavicollis*. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
HR[a] ~ W[b]+M[c]+S[d]+(1/I)[e]	HR ~M+S+(1/I)	7	-4.83	0.00	4.38E-01	1.00
	HR ~S+(1/I)	4	-4.60	0.22	3.92E-01	1.12
	HR ~M+(1/I)	6	-2.60	2.22	1.44E-01	3.04
	HR ~1+(1/I)	3	1.29	6.12	2.05E-02	21.34
MCP[f] ~W+M+S+(1/I)	MCP ~S+(1/I)	4	-5.44	0.00	5.89E-01	1.00
	MCP ~M+S+(1/I)	7	-3.07	2.36	1.81E-01	3.26
	MCP ~M+(1/I)	6	-2.83	2.61	1.60E-01	3.68
	MCP ~1+(1/I)	3	-1.07	4.37	6.62E-02	8.89
CA[g] ~ W+M+S+(1/I)	CA ~S+(1/I)	4	-0.99	0.00	6.37E-01	1.00
	CA ~M+S+(1/I)	7	0.59	1.58	2.90E-01	2.20
	CA ~M+(1/I)	6	3.89	4.88	5.56E-02	11.46
DM75[h] ~S+ΔT[i]+D[l]+M+ (1/I)	DM75 ~S+D+(1/I)	4	453.69	0.00	5.08E-01	1.00
	DM75~S+D+M +(1/I)	7	454.94	1.26	2.71E-01	1.87
	DM75~S+ΔT+D+M +(1/I)	8	455.91	2.23	1.67E-01	3.04
	DM75~S+D+ΔT+ (1/I)	5	458.83	5.14	3.88E-02	13.09
DM98[m] ~S+ ΔT +D+M+(1/I)	DM98 ~D+(1/I)	4	6.05	0.00	6.00E-01	1.00
	DM98~ΔT +D+(1/I)	7	8.09	2.03	2.00E-01	2.77
	DM 98~S+D+(1/I)	8	8.09	2.03	2.00E-01	2.77
	DM 98~D+M+(1/I)	5	12.18	6.13	3.00E-02	21.44

[a] HR: home range size calculated by kernel 95%;
[b] W: body weight
[c] M: month,
[d] S: Sex (male or female)
[e] 1/I: individual as random effect
[f] MCP: home range size calculated by MCP 100%
[g] CA: core area size calculated by kernel 50%
[h] DM75: daily distance moved (0 if interfix distance < 60 m, 1 otherwise)
[i] ΔT: exact time interval between successive fixes for calculation of DM75 and DM98
[l] D: daily distance moved associated to dispersion
[m] DM98: daily distance moved (0 if interfix distance < 210 m, 1 otherwise)

Tab. 6.4.1.1b - Parameter estimates relative to the best model ($\Delta AIC_c > 2$) or evaluated by model averaging, in case of equal parsimonious models, for the response variables computed from the 2005 radio-tracking data of *A. flavicollis*; in the latter case, only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.1.1a, otherwise indicated below

Best model or full model	Coefficients	Estimate mean ± SE	t	p
(**) HR ~ W+M[a] +S[b]+(1/I)	Intercept	3.66 ± 0.08		
	S (M)	0.22 ± 0.05	-	-
	M(2)	0.13 ± 0.03	-	-
	M(3)	0.22 ± 0.04	-	-
	M(4)	0.45 ± 0.06	-	-
(**) MCP ~W+M +S+(1/I)	Intercept	3.57 ± 0.07		
	S (M)	0.24 ± 0.06	-	-
	M(2)	0.17 ± 0.02	-	-
	M(3)	0.18 ± 0.02	-	-
	M(4)	0.45 ± 0.04	-	-
(**) CA ~ W+M +S+(1/I)	Intercept	3.07 ± 0.07		
	S (M)	0.26 ± 0.07	-	-
	M(2)	0.14 ± 0.02	-	-
	M(3)	0.22 ± 0.03	-	-
	M(4)	0.45 ± 0.04	-	-
(**) DM75 ~S+ΔT+D+M +(1/I)	Intercept	-2.45 ± 0.42		
	D	17.69 ± 1223.09	-	-
	ΔT	0.05 ± 0.01	-	-
	S(M)	1.23 ± 0.28	-	-
	M(2)	0.73 ± 0.17	-	-
	M(3)	0.66 ± 0.17	-	-
	M(4)	1.36 ± 0.20	-	-
(*) DM98 ~D+(1/I)	Intercept	-11.87 ± 8.16	-1.45	0.15
	D	24.05 ± 165.94	0.15	0.89

(*) Best model
(**) Full model
[a] M: Month: (2)= August; (3)= September; (4)= October. Reference level is July
[b] S: Sex (M)= male; reference level is female.

Tab 6.4.1.2a - Model selection for the response variables computed from the 2006 radio-tracking data of *A. flavicollis*. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown. a-m as in Table 6.4.1.1a

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
HR[a] ~ W[b]+M[c]+S[d]+(1/I)[e]	HR ~S+(1/I)	4	7.06	0.00	9.10E-01	1.00
	HR ~1+(1/I)	3	11.83	4.77	8.40E-02	10.84
	HR ~W+S+(1/I)	5	17.57	10.52	4.74E-03	192.02
MCP[f] ~ W+M+S+(1/I)	MCP ~S+(1/I)	4	4.00	0.00	9.35E-01	1.00
	MCP ~1+(1/I)	3	9.49	5.49	6.01E-02	15.57
	MCP ~W+S+(1/I)	5	14,80	10.80	4.22E-03	221.43
CA[g] ~ W+M+S+(1/I)	CA ~S+(1/I)	4	29.12	0.00	6.22E-01	1.00
	CA ~1+(1/I)	3	30.16	1.04	3.70E-01	1.68
	CA ~W+S+(1/I)	5	39.33	10.21	3.77E-03	165.11
DM75[h]~ S+ΔT[i]+D[l]+M +(1/I)	DM75~S+ΔT +D+(1/I)	5	648.30	0.00	8.88E-01	1.00
	DM75~S+ΔT+D+M+(1/I)	8	652.53	4.24	1.07E-01	8.31
	DM75 ~S+D+(1/I)	4	658.66	10.37	4.97E-01	178.39
DM98[m]~S+ΔT +D+M+(1/I)	DM98 ~ ΔT+D+(1/I)	4	48.37	0.00	4.00E-01	1.00
	DM98 ~ D+(1/I)	3	49.12	0.74	2.76E-01	1.45
	DM98~S+ ΔT+D+(1/I)	5	50.41	2.03	1.45E-01	2.76
	DM 98~S+D+(1/I)	4	51.08	2.71	1.03E-01	3.88
	DM98~ΔT+D+M+(1/I)	7	53.24	4.87	3.51E-02	11.39

Tab. 6.4.1.2b - Parameter estimates relative to the best model ($\Delta AIC_c > 2$) or evaluated by model averaging, in case of equal parsimonious models, for the response variables computed from the 2006 radio-tracking data of *A. flavicollis*; in the latter case, only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.1.1a

Best model or full model	Coefficients	Estimate mean ± SE	t	p
(*) HR ~S[a]+(1/I)	Intercept	4.23 ± 0.06	75.49	0
	S (M)	0.31 ± 0.08	3.90	<0.01
(*) MCP ~S+(1/I)	Intercept	4.07 ± 0.06	73.48	0
	S (M)	0.31 ± 0.08	3.95	<0.01
(**) CA ~ W+M+S+(1/I)	Intercept	3.68 ± 0.09	-	-
	S (M)	0.28 ± 0.06	-	-
(*) DM75 ~S+ΔT+D+(1/I)	Intercept	-2.04 ± 0.18	-11.43	<0.01
	S(M)	1.12 ± 0.20	5.48	<0.01
	ΔT	0.12 ± 0.04	3.44	<0.01
	D	17.20 ± 946.12	0.02	0.99
(**) DM98 ~S+ ΔT +D+M+(1/I)	Intercept	-8.94 ± 3.45	-	-
	ΔT	0.22 ± 0.09	-	-
	D	23.75 ± 515.91	-	-
	S(M)	0.24 ± 1.28	-	-

(*) Best model
(**) Full model
[a] S: Sex (M)= male; reference level is female.

Table 6.4.1.3a - Model selection for the response variables computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
HR[a] ~ S[b]+M[c]+Y[d]+S*Y+M*Y +(1/I)[e]	HR ~S+Y+(1/I)	5	-5.62	0.00	9.14E-01	1.00
	HR~S+Y+S*Y +(1/I)	6	-0.86	4.76	8.50E-02	10.80
MCP[f] ~ S+M+Y+S*Y+M*Y +(1/I)	MCP ~S+Y+(1/I)	5	-10.25	0.00	9.13E-01	1.00
	MCP~S+Y+S*Y +(1/I)	6	-5.53	4.73	8.60E-02	10.62
CA[g] ~ S+M+Y+S*Y+M*Y +(1/I)	CA ~S+Y+(1/I)	5	24.11	0.00	9.15E-01	1.00
	CA~S+Y+S*Y +(1/I)	6	28.95	4.84	8.10E-02	11.25
MAD[h]~ S+M+Y+S*Y+M*Y	MAD ~M+Y	6	278.93	0.00	2.14E-01	1.00
	MAD ~S+M+Y	8	279.00	0.07	2.07E-01	1.03
	MAD~M+Y +M*Y	9	279.50	0.57	1.61E-01	1.33
	MAD~S+M+Y +M*Y	11	279.94	1.01	1.30E-01	1.65
	MAD ~S+Y	5	280.27	1.33	1.10E-01	1.95
	MAD ~Y	3	280.37	1.43	1.05E-01	2.05
	MAD~ S+M+Y+S*Y	10	282.71	3.78	3.24E-02	6.63
	MAD~S+M+Y +S*Y+M*Y	13	283.53	4.59	2.16E-02	9.94
	MAD~S+Y+S*Y	7	283.81	4.88	1.87E-02	11.46

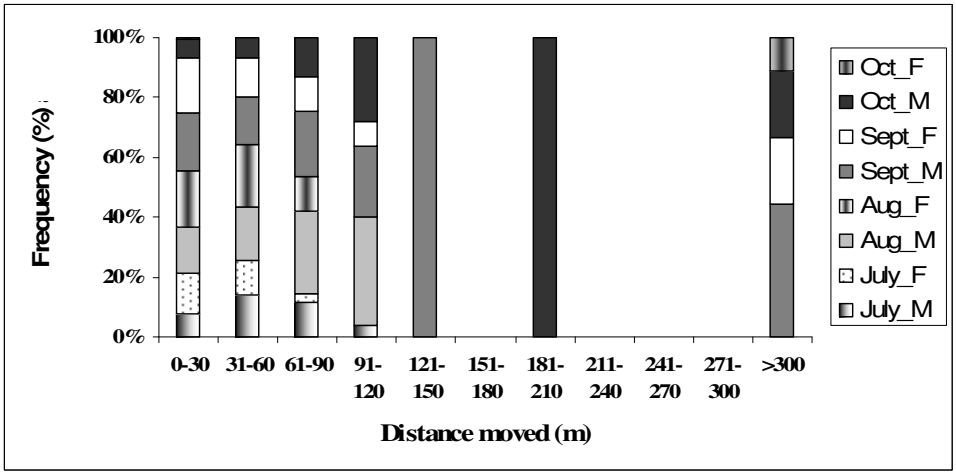
[a] HR: home range size calculated by kernel 95%
[b] S: Sex (male or female)
[c] M: month
[d] Y: year (2005 or 2006). Reference level is 2005
[e] 1/I: individual as random effect
[f] MCP: home range size calculated by MCP 100%
[g] CA: core area size calculated by kernel 50%
[h] MAD: distance between centres of maximum activity

Tab. 6.4.1.3b - Parameter estimates relative to the best model ($\Delta AIC_c > 2$) or evaluated by model averaging, in case of equal parsimonious models, for the response variables computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006; in the latter case, only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.1.3a

Best model or full model	Coefficients	Estimate mean (± SE)	t	p
(*) HR ~Y+S[a]+(1/I)	Intercept	0.96 ± 0.29	3.33	<0.01
	Y	0.55 ± 0.05	10.75	<0.01
	S (M)	0.29 ± 0.05	5.65	<0.01
(*) MCP ~Y+S+(1/I)	Intercept	1.01 ± 0.29	3.45	<0.01
	Y	0.51 ± 0.05	9.91	<0.01
	S (M)	0.28 ± 0.05	5.45	<0.01
(*) CA ~Y+S+(1/I)	Intercept	0.46 ± 0.32	1.42	0.16
	Y	0.53 ± 0.06	9.24	<0.01
	S (M)	0.28 ± 0.06	4.95	<0.01
(**) MAD ~S+M[b]+Y+S*Y+M*Y	Intercept	0.70 ± 0.04	-	-
	S (MF)	0.02 ± 0.01	-	-
	S (MM)	0.004 ± 0.01	-	-
	M(2)	-0.01 ± 0.01	-	-
	M(3)	0.01 ± 0.01	-	-
	M(4)	-0.03 ± 0.02	-	-
	Y	0.14 ± 0.01	-	-

(*) Best model
(**) Full model
[a] S: Sex (M)= male; reference level is female
[b] M: Month: (2)= August; (3)= September; (4)= October. Reference level is July

(a)



(b)

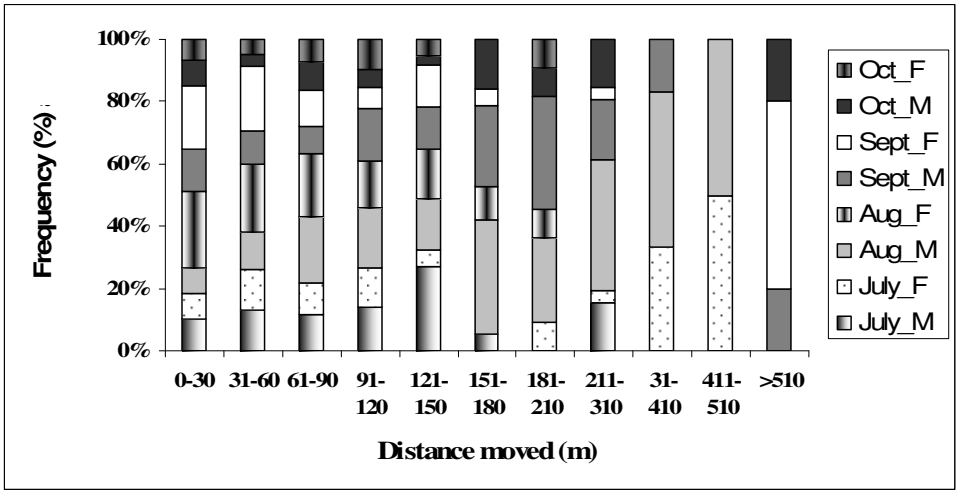


Fig. 6.4.1.4 - Distance moved by collared mice between successive monitoring nights in 2005 (a) and 2006 (b). Events are classified by sex (M: males, F: females) and month (July, August, September and October)

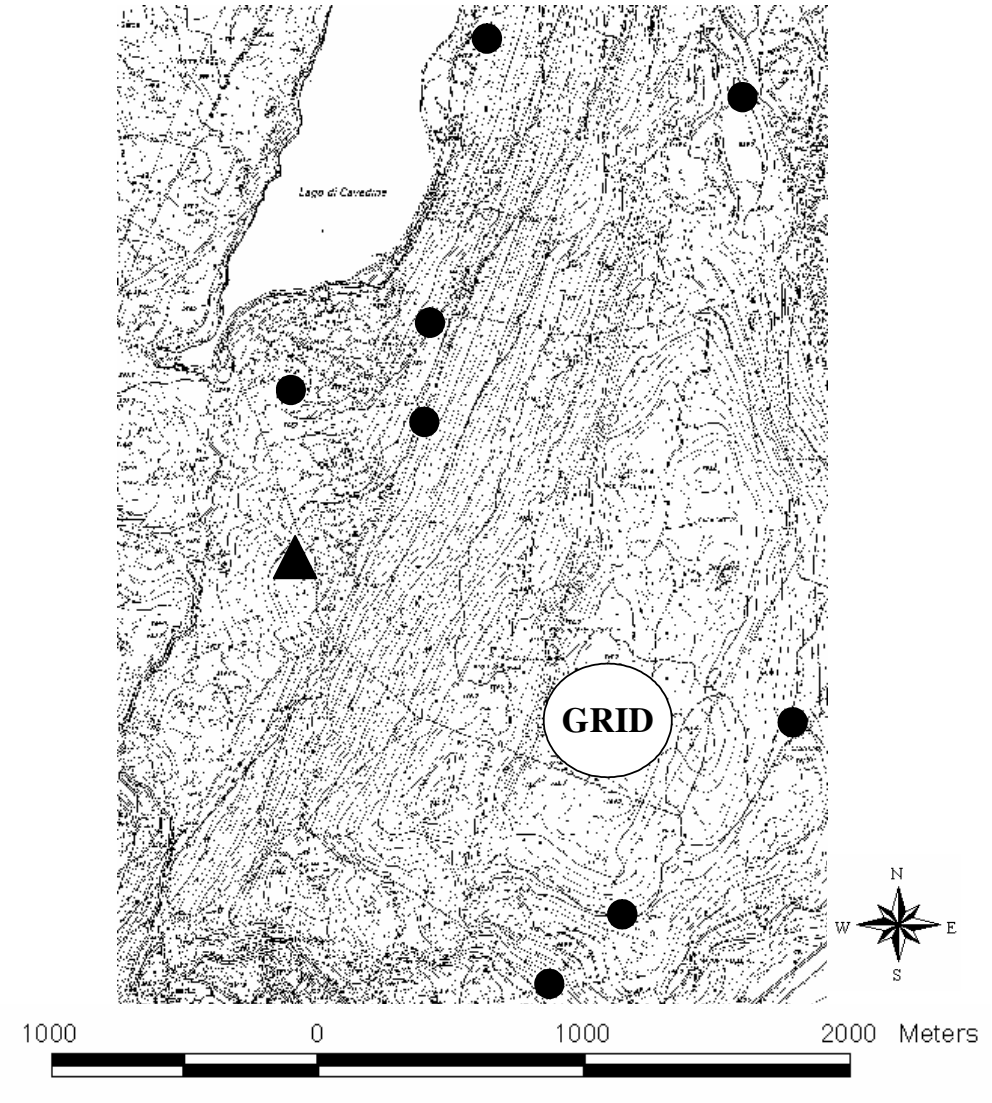


Fig. 6.4.1.5 – New locations of mice after dispersal, in 2005; every point indicate an individual *A. flavicollis* dispersed, triangle indicates the excursion of an individual male which returned on the study grid after one night

6.4.2 Home range overlap

The values of *UDOI* (Table 6.4.2.1) were much greater than 1 indicating an uneven use of space both for males and females in the two years. Both for 2005 and 2006, the best model for *UDOI* did not include any fixed effect and only individuals as random effect (Table 6.4.2.2a and 6.4.2.3a for 2005 and 2006, respectively).

BA had gamma distributed errors in all cases (empirical values did not significantly differ from the theoretical distribution, 2005: χ^2= 8.04, df= 5, p=0.09; 2006: χ^2= 6.52, df= 5, p= 0.26; pooled datasets: χ^2= 11.17, df= 8, p= 0.23). In 2005, *BA* index was primary influenced by *sex* (predictor weight: *sex* = 0.62) (Table 6.4.2.2a), with a larger degree of overlap between male-male and male-female than between female-female pairs, as shown by the model averaged coefficients (Table 6.4.2.2b). In 2006, the best model for *BA* did not include any fixed effect (Table 6.4.2.3a). When all data were pooled, *sex* and *year* were the main predictors of *BA* (predictor weights: *sex*= 0.70, *year*= 0.52), included in either equal parsimonious model (Table 6.4.2.4a); in particular, the degree of overlap among animals was greater in 2006 than in 2005 (Table 6.4.2.4b).

The mean proportion of events of overlap among home ranges and core areas (kernel at 95% and 50%, respectively) of animal pairs is illustrated in Figure 6.4.2.1 and Figure 6.4.2.2, for 2005 and 2006, respectively. In 2005, *PHR95* was affected by *sex* (predictor weight: *sex*= 0.50) (Table 6.4.2.2a): overlap among male-male and male-female pairs was more common than among female-female pairs, as showed by the model coefficients (Table 6.4.2.2b). Conversely, in 2006, the best model for *PHR95* did not include any fixed effect (Table 6.4.2.3a).

In 2005, very few core areas overlapped, and none among females (Figure 6.4.2.1). The best model for *PHR50* included *sex* as fixed effect (Table 6.4.2.2a). As all female-female cases were 0 (no overlap), model coefficients could not be properly estimated (Table 6.4.2.2b). In 2006, *PHR50* was affected by *sex* (predictor weight: *sex*= 0.62) (Table 6.4.2.3a), with male-male and male-female pairs overlapping more frequently than female-female pairs (Table 6.4.2.3b and Figure 6.4.2.2).

Some examples of the distribution and overlap among home ranges of male-male pairs, female-female pairs and male-female pairs are shown in figures 6.4.2.3,

6.4.2.4 and 6.4.2.5, respectively. The degree of home range overlap was higher between male-male pairs than between female-female pairs (Figure 6.4.2.3 and Figure 6.4.2.4); furthermore, the home range of an individual male typically overlapped with those of more than one females and the home range of an individual female can overlapped with those of several males (Figure 6.4.2.5).

Tab. 6.4.2.1 - Mean UDOI values calculated for males and females for each tracking sessions. N indicates sample size

Year	Month	Male N	Male (mean ± SE)	Female N	Female (mean ± SE)
2005	July	4	7.40 ± 0.39	4	8.69 ± 1.31
	August	7	7.55 ± 0.43	6	6.85 ± 0.67
	September	6	7.50 ± 0.59	4	8.30 ± 0.61
	October	4	7.84 ± 0.31	0	-
2006	July	4	11.29 ± 0.83	4	8.39 ± 0.82
	August	7	8.92 ± 0.41	7	9.30 ± 0.70
	September	6	9.53 ± 0.91	7	9.84 ± 0.96
	October	3	13.58 ± 1.67	3	10.14 ± 0.16

Tab. 6.4.2.2a - Model selection for the response variables computed from the 2005 radio-tracking data of *A. flavicollis*. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
UDOI[a]~ W[b]+M[c]+S[d]+(1/I)[e]	UDOI ~1+(1/I)	3	-63.93	0.00	9.76E-01	1.00
	UDOI ~S+(1/I)	4	-56.11	7.82	1.95E-02	49.91
BA[f] ~M+S+M*S	BA ~S	4	-1165.73	0.00	5.77E-01	1.00
	BA ~1	2	-1164.82	0.91	3.65E-01	1.58
	BA ~M+S	7	-1160.24	5.50	3.69E-02	15.61
PHR50[g] ~S	PHR50 ~S	3	28.99	0.00	7.80E-01	1.00
	PHR50 ~1	2	31.52	2.53	2.20E-01	3.55
PHR95[h] ~S	PHR95 ~1	2	43.99	0.00	5.00E-01	1.00
	PHR95 ~S	3	44.03	0.03	5.00E-01	1.02

[a]UDOI: utilization distribution overlap index
[b]W: body weight
[c]M: month
[d]S: Sex (M: male; F: female; MM: male-male pairs; MF: male-female pairs; FF: female-female pairs)
[e]1/I: individual as random effect
[f]BA: Bhattacharyya's affinity overlap index
[g]PHR50: presence/absence of overlap at 50% probability contour of animal pairs, where S: Sex (MM: male- male, FF: female-female and MF: male-female)
[h]PHR95: presence/absence of overlap at 95% probability contour of animal pairs, where S: Sex (MM: male- male, FF: female-female and MF: male-female)

Tab. 6.4.2.2b - Parameter estimates relative to the best model ($\Delta AIC_c > 2$) or evaluated by model averaging, in case of equal parsimonious models, for the response variables computed from the 2005 radio-tracking data of *A. flavicollis*; in the latter case, only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.2.2a

Best model or full model	Coefficients	Estimate mean ± SE	t	p
(*) UDOI ~1+(1/I)	Intercept	0.88 ± 0.014	63.87	0
(**) BA ~M +S+M *S	Intercept	14.92 ± 8.86		
	S(MF)	15.569 ± 4.34	-	-
	S(MM)	15.357 ± 4.37	-	-
(*) PHR50 ~S	Intercept	-21.97 ± 6891.14	-0.003	0.99
	S(MF)	20.39 ± 6891.14	0.003	0.99
	S(MM)	19.82 ± 6891.14	0.003	0.99
(**) PHR95 ~S	Intercept	-1.19 ± 0.68	-	-
	S(MF)	1.25 ± 0.30	-	-
	S(MM)	1.33 ± 0.19	-	-

(*) Best model
(**) Full model

Tab. 6.4.2.3a - Model selection for the response variables computed from the 2006 radio-tracking data of *A. flavicollis*. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown. a-h as in Table 6.4.2.2a

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
UDOI[a]~ W[b]+M[c]+S[d]+(1/I)[e]	UDOI ~1+(1/I)	3	-66.40	0.00	9.54E-01	1.00
	UDOI ~S+(1/I)	4	-60.22	6.18	4.33E-02	22.03
BA[f] ~M+S+M*S	BA ~1	2	-2534.54	0.00	7.52E-01	1.00
	BA ~S	4	-2530.81	3.74	1.16E-01	6.47
	BA ~M	5	-2530.71	3.83	1.11E-01	6.80
PHR50[g] ~S	PHR50 ~S	3	51.00	0.00	6.20E-01	1.00
	PHR50 ~1	2	51.98	0.98	3.80E-01	1.63
PHR95[h] ~S	PHR95 ~1	2	46.97	0.00	8.05E-01	1.00
	PHR95 ~S	3	49.81	2.84	1.95E-01	4.14

Tab. 6.4.2.3b - Parameter estimates relative to the best model ($\Delta AIC_c > 2$) or evaluated by model averaging, in case of equal parsimonious models, for the response variables computed from the 2006 radio-tracking data of *A. flavicollis*; in the latter case, only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.2.2a

Best model or full model	Coefficients	Estimate mean ± SE	t	p
(*) UDOI ~1+(1/I)	Intercept	0.98 ± 0.02	67.39	0
(*) BA ~1	Intercept	5.07 ± 0.49	10.34	<0.01
(**) PHR50 ~S	Intercept	-2.07 ± 0.66	-	-
	S(MF)	1.23 ± 0.35	-	-
	S(MM)	1.31 ± 0.25	-	-
(*) PHR95 ~1	Intercept	0.13 ± 0.14	0.96	0.34

(*) Best model
(**) Full model

Tab. 6.4.2.4a - Model selection for the response variables computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
BA^a~S^b+Y^c+S*Y	BA~S	4	-3690.9	0.00	4.80E-01	1.00
	BA~Y	3	-3689.9	0.96	3.00E-01	1.61
	BA~S+Y	5	-3688.8	2.06	1.70E-01	2.80
	BA~S+Y+S*Y	7	-3686.7	4.20	6.00E-02	8.17

[a]BA: Bhattacharyya's affinity overlap index
[b]S: Sex (M: male; F: female)
[c]Y: year (2005 or 2006). Reference level is 2005

Tab. 6.4.2.4b - Parameter estimates evaluated by model averaging for the response variable computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006; only estimates of primary predictors are shown, as ranked by predictor weights. Explanatory variables as in Table 6.4.2.4a

Full model	Coefficients	Estimate mean (± SE)	t	p
BA~S+Y+S*Y	Intercept	14.27 ± 10.69	-	-
	S (MF)	10.82 ± 9.14	-	-
	S (MM)	10.56 ± 9.43	-	-
	Y	2.10 ± 1.57	-	-
	S(MF)*Y	13.09 ± 0.39	-	-
	S(MM)*Y	13.55 ± 0.40	-	-

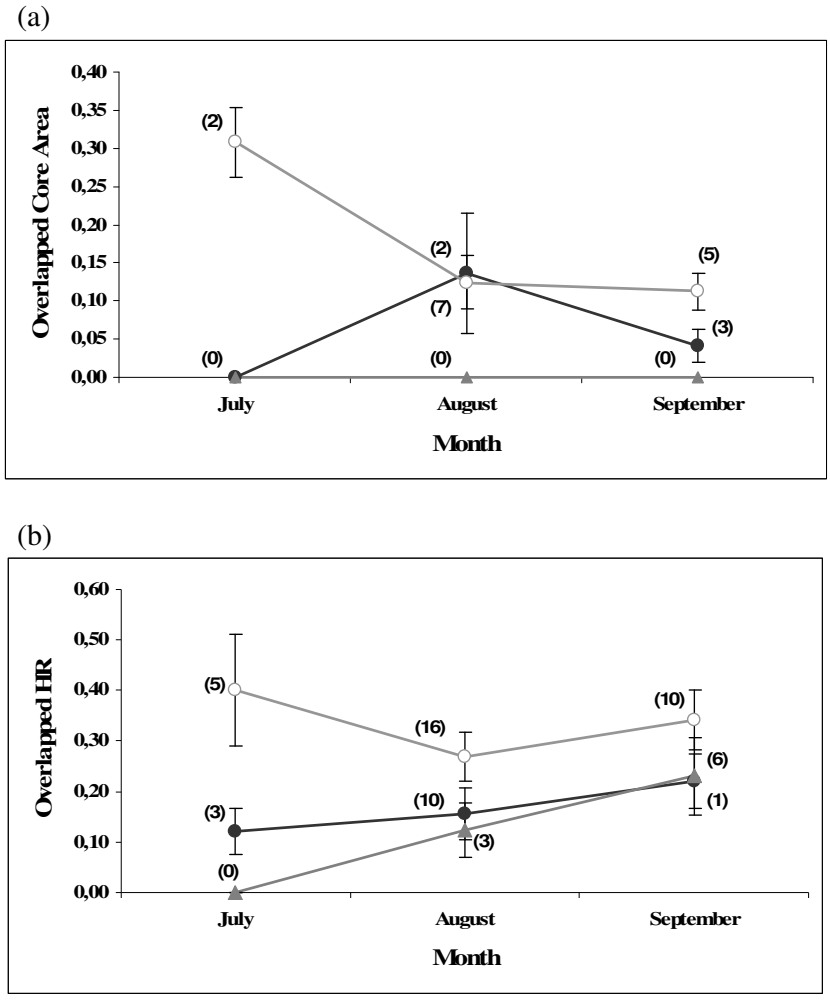
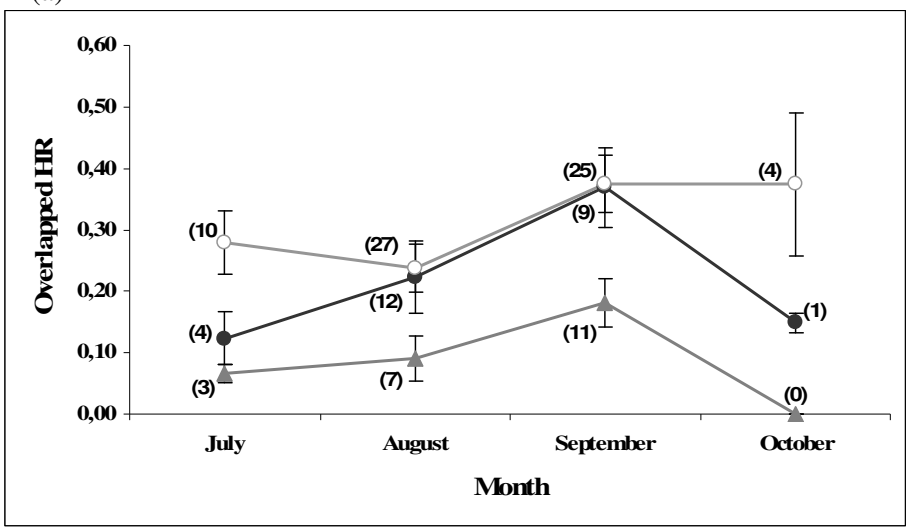


Fig. 6.4.2.1 - Mean proportion ± SE of home range (a) and core area (b) overlapped among animal pairs, in 2005. Open circles: male-female pairs; closed circles: male-male pairs; closed triangles: female-female pairs. Sample size in parentheses

(a)



(b)

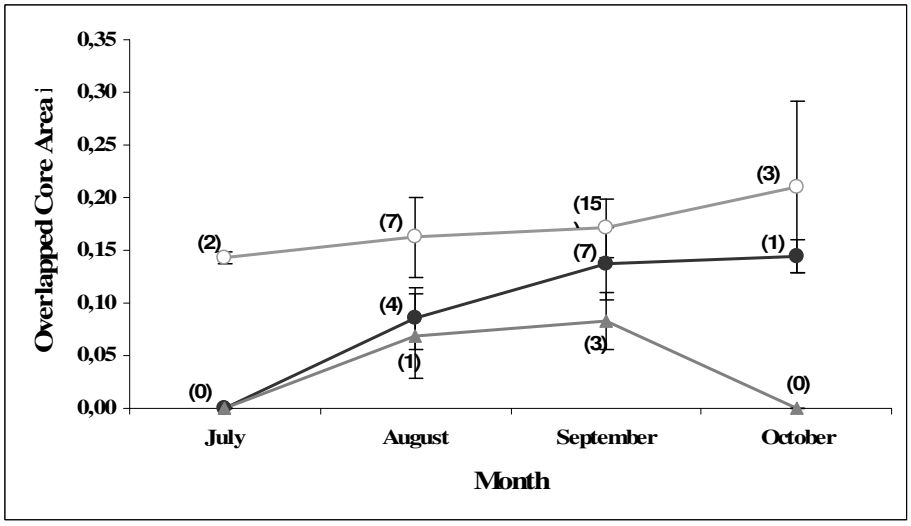


Fig. 6.4.2.2 - Mean proportion ± SE of home range (a) and core area (b) overlapped among animal pairs, in 2006. Open circles: male-female pairs; closed circles: male-male pairs; closed triangles: female-female pairs. Sample size in parentheses

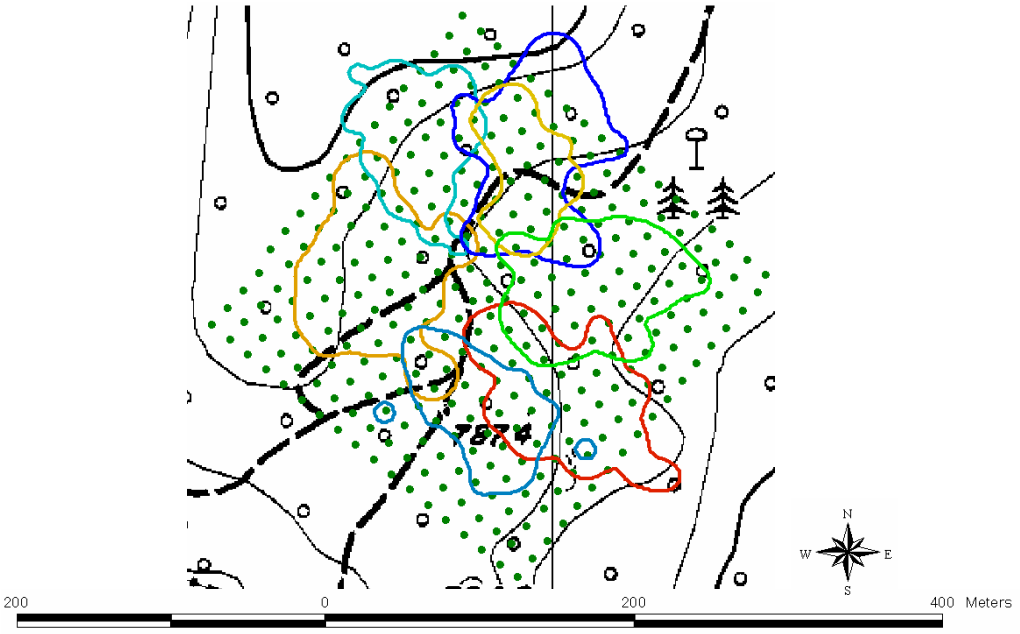


Fig. 6.4.2.3 – Examples of home ranges distribution and overlap amongst male-male pairs. Data are from the 2nd tracking session of 2005

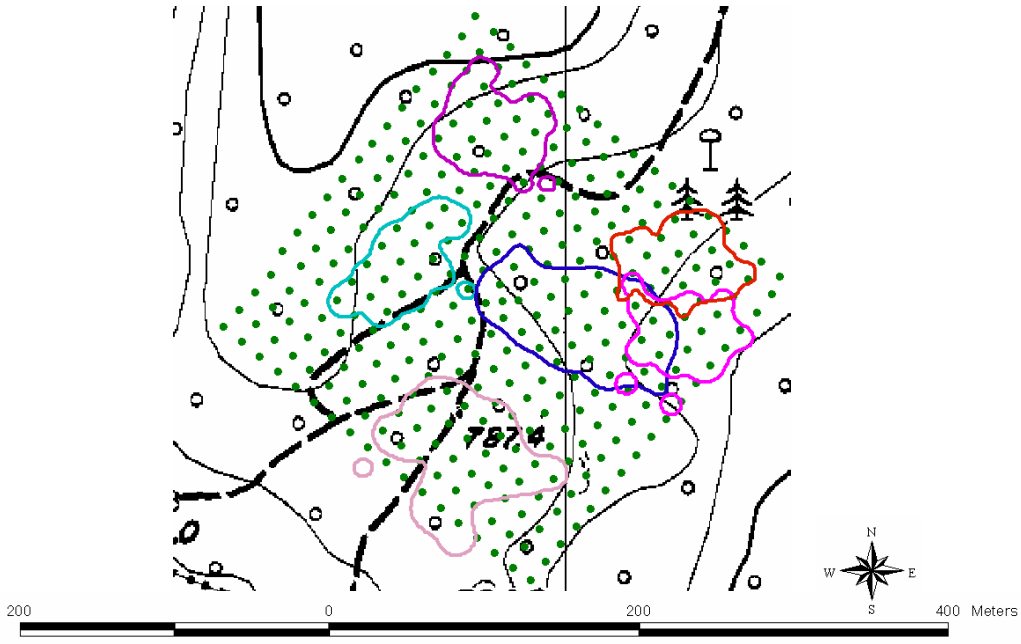


Fig. 6.4.2.4 – Examples of home ranges distribution and overlap amongst female-female pairs. Data are from the 2nd tracking session of 2005

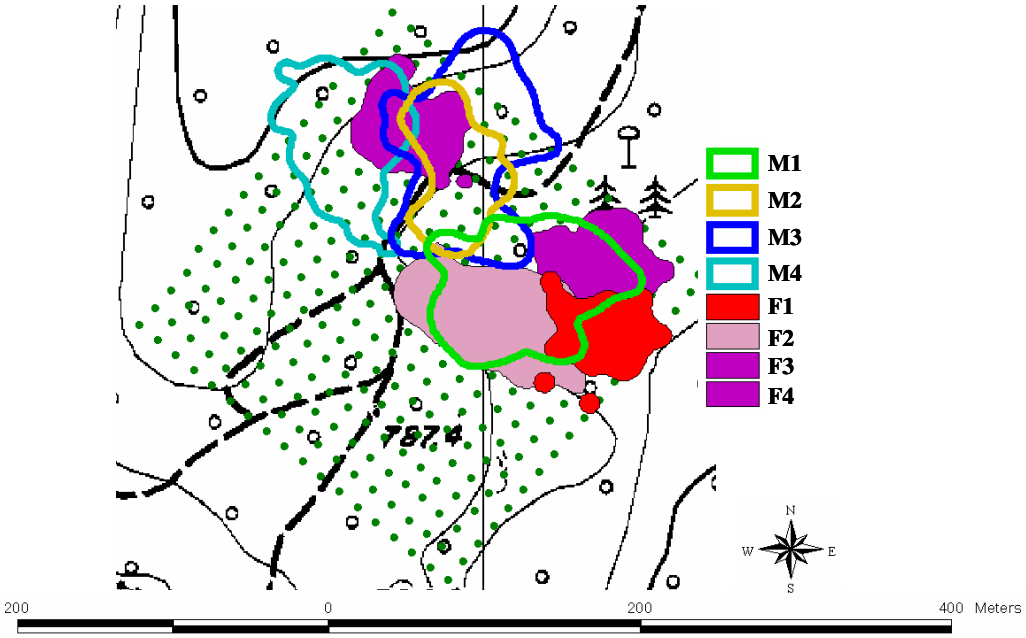


Fig. 6.4.2.5 – Examples of home ranges distribution and overlap amongst male-female pairs. Data are from the 2nd tracking session of 2005; M: males; F: females

6.4.3 Use of the burrow system

The mean number of burrows used per tracking session per individual was 3.57 ± 0.31 for males and 4.91 ± 0.39 for females in 2005 and it was 3.47 ± 0.31 for males and 4.33 ± 0.46 for females in 2006. These values did not significantly differ among sexes (Mann-Whitney test; July 2005: U= 8, p=0.20; August 2005: U= 15.5, p=0.15; September 2005: U= 24, p=0.25; July 2006: U= 43.5, p=0.90; August 2006: U= 41, p=0.21; September 2006: U= 24, p=0.25; October 2006: U= 6.5, p= 0.39). The distance between burrows and the centre of maximum activity of individuals (*BD*) was affected by *year* only (Table 6.4.3.1a): *BD* increased from 2005 to 2006 (Table 6.4.3.1b and Figure 6.4.3.1). 16 out of 32 and 13 out of 32 collared mice shared burrows in 2005 and 2006, respectively. From July to October 2005, I monitored 194 nests occupied at least once by collared individuals; among these, none was shared by female-female pairs, 13 were shared by male-female pairs, 2 by male-male pairs and 1 by a female and 2 males. From July to October 2006, I individuated 222 nests, none shared by female-female pairs, 13 shared by male-female pairs and 1 by a male-male pair. Within each session of 2005, when male-female burrow-sharing was detected, it was exclusive for males, i.e. each individual male shared one or more of its nests always with the same female, whereas in 2006 I found that a single male shared its burrows with more than one female during the same radio-tracking session and that a single female shared nests with no more than one male. Figure 6.4.3.1 shows an example of the location of the burrows inside the home range and core area of an individual male and female.

Tab. 6.4.3.1a - Model selection for the response variables computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown.

FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
BD[a]~ S[b]+M[c]+Y[d]+S*Y+M*Y+(1/I)[e]	BD ~Y+(1/I)	4	180.62	0.00	9.38E-01	1.00
	BD ~S+Y+(1/I)	5	186.47	5.86	5.01E-02	18.71

[a]BD: distance between burrows and centre of maximum activity of each animal
[b]S: Sex (M: male; F: female)
[c]M: month
[d]Y: year (2005 or 2006). Reference level is 2005
[e]1/I: individual as random effect

Tab. 6.4.3.1b - Parameter estimates relative to the best model (ΔAIC_c >2) for the response variable computed from the radio-tracking data of *A. flavicollis*, pooled over 2005 and 2006. Explanatory variables as in Table 6.4.3.1a.

Best model	Coefficients	Estimate mean (± SE)	t	p
BD ~Y+(1/I)	Intercept	-0.29 ± 0.32	-0.91	0.37
	Y	0.35 ± 0.06	6.04	<0.01

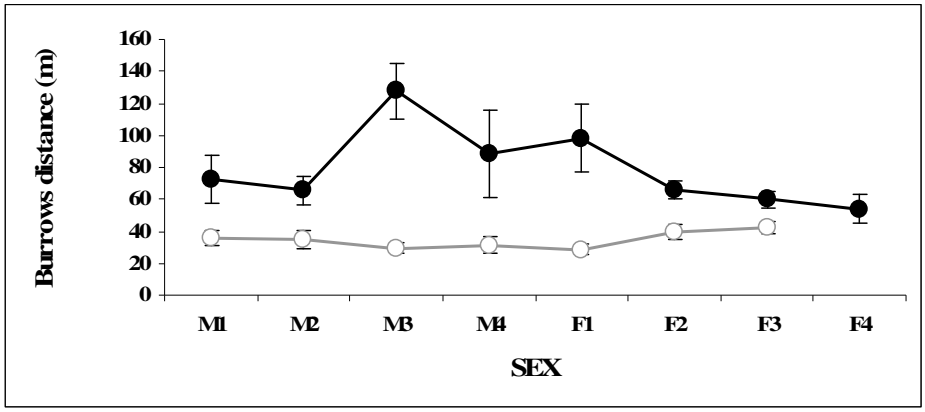


Fig. 6.4.3.1 - Mean distance between burrows and centre of maximum activity of *A. flavicollis* calculated for sex and session (M1: males in July; M2: males in August; M3: males in September; M4: males in October; F1: females in July; F2: females in August; F3: females in September; F4: females in October). Open circles: data from 2005; closed circles: data from 2006

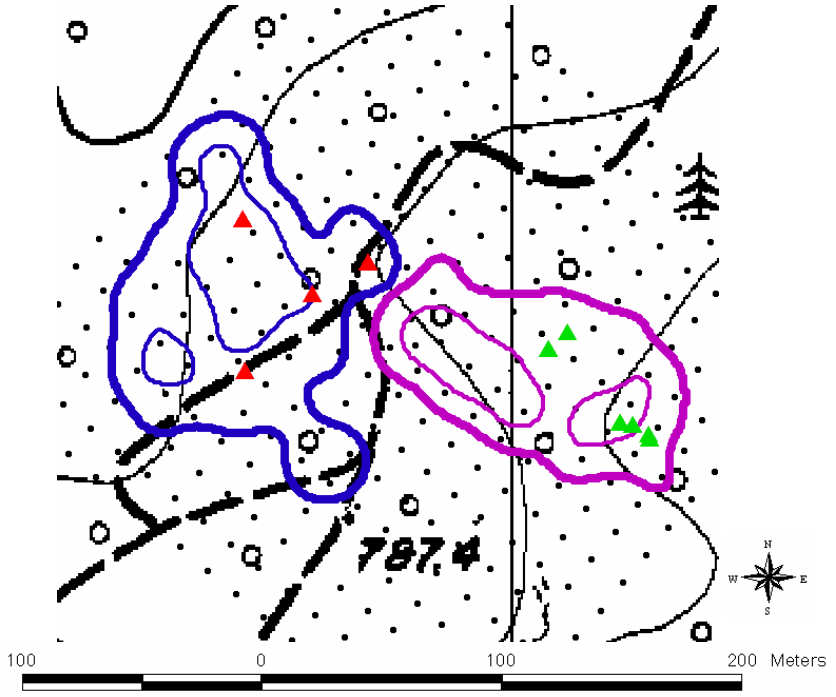


Fig. 6.4.3.1 – Home ranges of a male and a female (blu and pink line, respectively), their core areas (blu and pink thin lines) and location of their burrows (red triangles for male and green ones for female)

6.4.4 Parasite burden

In both years the tick burden was affected by *sex* and *month* (Table 6.4.1a), and in particular males supported an higher larvae load than females, as shown by the best model coefficients (Table 6.4.4.1b; Figure 6.4.4.1 and 6.4.4.2 for 2005 and 2006, respectively). Moreover, in 2005, the individual tick burden increased throughout the study period (Table 6.4.4.1b), whereas in 2006 it showed the opposite pattern, decreasing from August to November (Table 6.4.4.1b). The temporal pattern of the rodent larvae load, both for males and females, is shown in Figure 6.4.4.1 and 6.4.4.2 for 2005 and 2006, respectively. The increase in the individual larvae load recorded from September to November 2005 was probably due to the decrease of the number of mice on the trapping grid; it is well known that the host density influences the individual tick burden, and in particular it is lower at high host density than at low host density (Rosà and Pugliese, 2007). In 2005, the mean number of larvae/individual was 3.2 ± 0.2 for males and 2.5 ± 0.2

for females, while in 2006 it was 16.4 ± 2.5 for males and 9.3 ± 1.5 for females, with a clear increment of the individual larvae load from 2005 to 2006. In fact, when all data were pooled, tick burden (*TB*) was influenced by *year*, *sex* and *month* (Table 6.4.1a); in particular, individual tick load was significantly greater in 2006 than in 2005 as shown by the best model coefficients (Table 6.4.4.1b).

Tab. 6.4.4.1a - Model selection for the response variables computed from the 2005, 2006 and pooled radio-tracking data of *A. flavicollis*. The selection method was based on the Akaike information criterion (AIC) corrected for small sample size, AICc, starting from an *a priori* full model (ΔAIC_c = difference in AIC_c between the best and the actual model; ω_I = Akaike's weight; Evidence ratios = ratio of the Akaike's weights of the best and the actual model). Only the best ranked models are shown

YEAR	FULL MODEL	MODEL STRUCTURE	*K*	AIC_c	ΔAIC_c	ω_i	E. Ratios
2005	**TB[a]~M[b]+S[c]**	TB ~M+S	7	2587.30	0.00	8.80E-01	1.00
		TB ~M	6	2591.37	4.07	1.20E-01	7.64
2006	**TB~M+S**	TB ~M+S	8	654.22	0.00	9.99E-01	1.00
		TB ~M	7	669.68	15.46	4.00E-04	2275.16
Pooled data	**TB~ M+S+Y[d]**	TB ~M+S+Y	9	3336.06	0.00	9.97E-01	1.00
		TB ~M+Y	8	3347.41	11,35	3.42E-03	291.19

[a] TB: tick burden (larvae)
[b] M: month
[c] S: Sex (male or female)
[d] Y: Year (2005 or 2006). Reference level is 2005

Tab. 6.4.4.1b - Parameter estimates relative to the best model, for the response variables computed from the 2005, 2006 and pooled radio-tracking data of *A. flavicollis*

Year	Best model	Coefficients	Estimate mean ± SE	t	p
2005	**TB~M[a] +S[b]**	Intercept	0.38 ± 0.11	3.46	< 0.01
		S(M)	0.25 ± 0.09	2.51	0.01
		M(2)	0.37 ± 0.14	2.70	<0.01
		M(3)	0.29 ± 0.15	1.98	0.05
		M(4)	1.21 ± 0.16	7.75	<0.01
		M(5)	0.99 ± 0.20	4.89	<0.01
		M(6)	1.19 ± 0.22	5.47	<0.01
2006	**TB~M +S**	Intercept	2.69 ± 0.302	8.90	<0.01
		S(M)	0.71 ± 0.16	4.41	<0.01
		M(2)	0.01 ± 0.35	0.01	0.99
		M(3)	0.04 ± 0.34	0.11	0.91
		M(4)	-1.03 ± 0.34	-3.08	<0.01
		M(5)	-1.31 ± 0.38	-3.44	<0.01
		M(6)	-2.05 ± 0.43	-4.80	<0.01
		M(7)	-3.26 ± 0.49	-6.72	<0.01
Pooled data	**TB~M +S+Y[c]**	Intercept	-6.57 ± 0.68	-9.63	<0.01
		S(M)	0.34 ± 0.09	3.70	<0.01
		M(2)	1.05 ± 0.32	3.31	<0.01
		M(3)	0.46 ± 0.13	3.47	<0.01
		M(4)	0.18 ± 0.14	1.25	0.21
		M(5)	1.02 ± 0.15	6.65	<0.01
		M(6)	0.69 ± 0.19	3.58	<0.01
		M(7)	0.76 ± 0.20	3.75	<0.01
		Y (2006)	1.40 ± 0.13	10.49	<0.01

[a] M: Month: (2)= July; (3)= August; (4)= September; (5)= October; (6)= November, for 2005 and (2)= June; (3)= July; (4)= August; (5)= September; (6)= October; (7)= November for 2006 and for pooled data. Reference level is May
[b] S: Sex (M)= male. Reference level is female
[c] Y: Year. Reference level is 2005

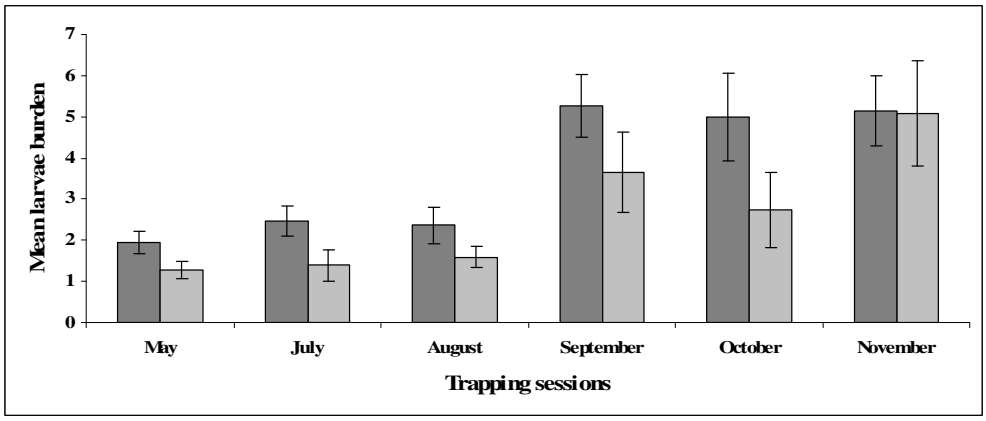


Fig. 6.4.4.1 – Mean tick burden (larvae) calculated, session by session, for males (black bars) and females (grey bars), in 2005. SE is shown

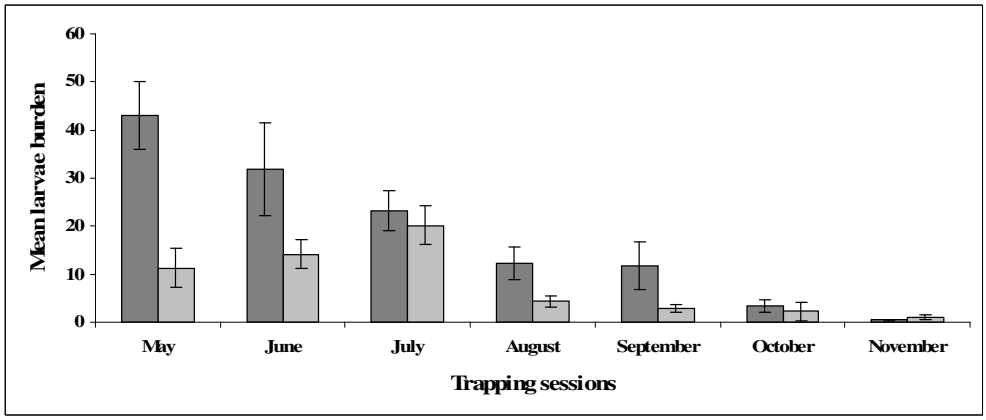


Fig. 6.4.4.2 – Mean tick burden (larvae) calculated, session by session, for males (black bars) and females (grey bars), in 2006. SE is shown

7. DISCUSSION

7.1 Density estimation

The factors that may affect CMR density estimate include population size, capture probability, duration of trapping sessions and grid size, both in terms of area covered and number of traps used (Otis et al., 1978; White et al., 1982), as well as behavioural responses such as trap shyness, bait attraction (Pelikán et al., 1972), conspecific smell attraction during the reproductive season (Montgomery, 1979a; Stoddart and Smith, 1984) and more general ecological constrains such as food availability and habitat suitability.

In this study, capture probability was constantly high. I used a large trapping grid and 5 trapping nights/session directed at catching a large proportion of animals in the sampled area to ensure good performance of closed population models and more robust and precise estimates of population size (Nichols et al., 1984; Williams et al., 2002).

Bondrup-Nielsen (1983) showed that when the size of the live trapping grid used in censuses was less than about four times the average home range size, marked overestimates of population size occur, and a ratio of grid size to home range size of less than 16 requires correction for edge effect. In this case, the ratio of trapping grid to average home range size was less than that measure, therefore, it is likely that edge effect occurred in this grid; if home range size or more in general animal movements had been negligible with respect to grid size, I would have expected ETA not to heavily influence density values. Lack of populations closure in September 2005 could indicate alteration of population closure, either for permanent immigration/emigration of individuals or for bait attraction effect after food scarcity, or both.

Parmenter et al. (2003) suggested that the primary objective in defining the ETA is to determine “the maximum distance from which animals outside the grid boundaries are moving onto the grid” (i.e. W). Home range radius calculated from telemetry observations made at the same time as the CMR studies suit this definition, as it refers to the actual movement distances of the individuals undergoing density estimates. While the use of TGA or ETA obtained by adding a fix value (such as trap interval) are clearly unrelated to rodent movement patterns, Parmenter et al. (2003) experimentally found that the use of MMDM based on

trapping data resulted in the best performance, but they warned against the difficulty of meeting the theoretical assumptions on animal movements it involves. One of the main problems they noted is that the upper limits of MMDM values are constrained by the grid itself, so they expected the "real" movement distances to be greater; MMDM is expected to be negatively biased as a consequence of the truncation of the observations at the edge of the grid. Consistent with this prediction, in this study, the radius of home range (Kernel) led to the largest values of ETA, and consequently to the lowest density estimates. Behavioural knowledge of the species, such as home range size and ranging distances, are necessary to improve the information of CMR studies, as indicated by Powell et al. (2000) for other taxa and by Tioli et al. (submitted). However, because of spatial behaviour of rodents is dependent on very contextual and unstable factors, such as resource availability and population density itself, I therefore agree with Parmenter et al. (2003) that only parameters estimated from telemetry observations that are in good agreement with grid trapping studies are adequate for density estimates; however, this is clearly unfeasible in most cases. These considerations should foster new methods to estimate density, which are independent of trap layout, as that proposed by Efford (2004) and Efford et al. (2004, 2005). However, these results suggest caution in assuming stable home ranges, especially under certain behavioural or ecological constrains (e.g. reproduction or food availability).

Density of *A. flavicollis* populations increases normally between spring and early autumn, with an autumnal peak, followed by an abrupt decrease from autumn till spring of the following year, as observed by Banach (1987) and Andrzejewski (1963). Similarly, other authors observed that the numbers of *A. flavicollis* increased after the onset of breeding in spring and the high density of population occurred during late summer and autumn with a decrease during winter months (Montgomery, 1980a; Rajska-Jurgiel, 1992). Yalden (1971) noted that this species is rare in spring and winter, whereas it is abundant in early summer. Consistently with these observations, I found the highest mice density during July and August, in both years.

Long-term population dynamics of various rodent species largely reflects the pattern of availability of their resources, so that differential food abundance from

year to year may influence the density and the spatial behaviour of rodents (Flowerdew, 1985; Pucek et al., 1993; Wolff, 1996); accordingly, this study showed a great population density decrease from 2005 to 2006, especially in spring. Large food supply, has that observed in a year of masting (2005 in this study), promotes mice survival during winter months (Montgomery, 1980a). The mating season can extend to fall and winter (Gosálbez and Castién, 1995), thus leading to a large spring population which in turn governs population size in early summer (Watts, 1969; Wolff, 1996).

7.2 Population structure

In 2005 the number of adult males and females captured in each trapping session, showed that the sex ratio in *A. flavicollis* changed seasonally and in particular males prevailed in autumn; this is in agreement with Montgomery (1980a) and Rajska-Jurgiel (1992) who found that the lowest proportion of males of this rodent species generally occurs in spring or early summer, whereas its highest proportion occurs in autumn. Rajska-Jurgiel (1992) noted that the *A. flavicollis* sex ratio was mainly connected with immigration so that the great number of adult males caught during autumn may be the consequence of their high mobility in this period; these observation finds evidence in this study during October 2005, when males enlarged their home range size, possibly in search for food.

Several studies showed intra-annual body weight fluctuations, in particular Montgomery (1980a) found an increase of mean body weight in the pre-reproductive period with a peak around the mid point of the breeding season, proving that this increase was earlier and greater in males; as a consequence, the difference between male and female weights was most noticeable at the peak of the breeding season. I only partly confirm these observations, as in this study the mean male body weight reached a maximum in August. Moreover, this author observed that the decrease in mean body weight during the second half of the breeding season probably resulted from the disappearance of heavier and therefore older animals and the maturation of animals born early in the breeding period; these animals are presumably lighter and thus the mean adult weight decline. Pelikán (1967) suggested that weight increase in males is due to the development of the gonads and secondary sex characters, while females gain weight later as a consequence of the development of the uteri and the mammary glands.

Accordingly, in this study I found a mean body weight decrease at the end of the breeding season, both in 2005 and 2006.

In May 2005, juveniles constituted the largest part of the population as likely consequence of winter reproduction. In fact, the great food abundance and the warm weather registered in the autumn-winter 2004-2005 probably caused a high mice winter survival. In agreement with Mazurkiewicz and Rajska-Jurgiel (1998), the age structure of the spring population at high density differed from that at low density; in particular, in 2006 juveniles were absent in all trapping sessions, except in November, indicating the lack of the spring peak in reproduction which only started in November, after the falling of seeds.

Moreover, the proportion of transient animals (i.e. individual with 1 or 2 captures) trapped in 2005 was lower than in 2006, probably because of the great mobility of mice in the year of low population density and scarce seed availability.

7.3 Radio-tracking data

In this study, I investigated the spatial organisation of *A. flavicollis*, a granivorous rodent species relying on unstable and clumped resources, i.e. seeds undergoing mast cycles (Pucek et al., 1993), that largely determine the population density fluctuation (Jensen, 1982; Ostfeld et al., 1996b; Mazurkiewicz and Rajska-Jurgiel, 1998). In such species relying on slowly renewed food resources, females are expected to utilize exclusive ranges, whereas males are expected to occupy larger home ranges than females to maximize the probability of encountering oestrous females (Eisenberg 1966; Ostfeld 1985). Consistently with predictions, these results showed female territoriality and home range overlap between sexes and among males, suggesting a promiscuous mating system. Use of space of both sexes was affected by food availability and population density, in terms of ranging movements and autumnal adult dispersal. Sex dependent spatial behaviour likely affected parasite burden (i.e. ticks), which was male-biased.

Home range estimates can vary significantly according to the method used for calculation (Lawson and Rodgers, 1997), as well as with season, sex, age, population density and habitat quality (Wolton and Flowerdew, 1985). Mean home range size was considerably larger than those reported for *A. flavicollis* by Zejda and Pelikán (1969) (inclusive boundary strip: 0.32 ha for males and 0.13 ha for females) and by Montgomery (1979b) (95% ellipse: 0.22 ha and 0.19 ha for

males and females, respectively), both based on trapping data. Instead, home ranges calculated in this study (i.e. data from 2005) were comparable to those determined by radio-telemetry for *A. sylvaticus* by Wolton (1985) (MCP: 1.07 ha and 0.40 ha for males and females respectively) and by Tattersall et al. (2001) (concave polygon: 1.03 ha and 0.32 ha for males and females, respectively) and for *A. flavicollis* by Schwartzenberger and Klingel (1995) (1.5 ha for males and 0.38 ha for females, during breeding season). Bubela et al. (1991) assumed for other rodent species that since the core area encompasses the minimum required resources, it may not significantly vary in size with sex and season. Conversely, in this study, I found that core area size was affected, as was home range size, by sex.

Hypothesis a

In agreement with Schwartzenberger and Klingel (1995), these data indicated that female home ranges overlapped with those of other females much less than with male ones (especially in 2005), whereas males widely shared their ranges with individuals of the same sex. Moreover, female core areas were never (i.e. 2005) or very little (i.e. 2006) overlapped with those of other females. Consistently, I did not record communal nesting among females, in contrast with de Mendonça (2003). These findings are consistent with the hypothesis of female territoriality, which results in the monopolization of core areas and nests. Following Ostfeld's (1990) hypothesis that females of small mammal species which use clumped and perennial trophic resources are likely to compete for food, several studies reported that females of *A. sylvaticus* defend territories against conspecifics of the same sex during the breeding season (Tew and MacDonald, 1994; Montgomery et al., 1997). The results of the present study suggest that the same is true for *A. flavicollis* females.

In the study area, nests were not necessarily located near the centre of maximum activity or inside the individual core area. For females, this confirms the use of exclusive core areas for the defence of trophic resources rather than nest sites, which however seem to be defended against other females, possibly to prevent infanticide (Wolff and Cicirello, 1989; Ostfeld, 1990). In agreement with Truszkowski (1974), Schwartzenberger and Klingel (1995) and de Mendonça (2003), I found that *A. flavicollis* used several dwelling places sequentially or in

parallel; these changes in nest site position could be explained by interactions with conspecifics and/or avoidance of predators or parasites (Wolton and Flowerdew, 1985). In particular, this behaviour could decrease the risk of predation, by reducing the time required to return to a shelter or, for females, prevent infanticide, by confounding the predator on the location of juveniles. Alternatively, as suggested by Wolton (1985) for *A. sylvaticus*, this could be because mice prefer to use pre-existent burrow systems rather than digging their own.

Hypothesis b

Few studies have included observations on sex bias in *A. flavicollis* ranging behaviour (e.g. Schwartzenberger and Klingel, 1995; Kotzageorgis and Mason, 1996). This research indicated that spatial behaviour was affected by sex, where males ranged wider than females both in terms of home range size and daily distance travelled.

As predicted I observed that individual home ranges of males often overlapped with those of several females and, furthermore, individual home ranges of females overlapped with those of several males; in addition male home ranges are larger than female ones. Communal nesting has been observed in various small mammal species (Fedyk, 1971; Ribble and Salvioni, 1990; Manning et al., 1995; de Mendonça, 2003); it is an important phenomenon to study as it can give information about social behaviour and mating system and it may play a central role in disease transmission. The strict spatial association between males and females during the mating season, already observed for *A. sylvaticus* (e.g. Randolph, 1977; Wolton, 1985; Tew and Macdonald, 1994) was also confirmed, in this study, by frequent male-female pairs when communal nesting was recorded (de Mendonça, 2003). I assume that nest sharing during summer and early autumn was not due to social thermoregulation as hypothesized by Fedyk (1971) for such rodent species during winter, given the seasonal favourable climatic conditions in the study area. All these observations, support the hypothesis that male spatial behaviour in the breeding season is aimed at maximizing the number of potential matings (Madison, 1980), suggesting a promiscuous mating system (Ribble and Millar, 1996), that in turn would be the response to the high costs of monopolizing territorial, asynchronous females (Ostfeld, 1990; Tew and Macdonald, 1994).

Kotzageorgis and Mason (1996) reported contrasting results, either supporting monogamy or promiscuity. However, in monogamous species, mated pairs usually have largely exclusive home ranges (Gaulin and Fitzgerald, 1988; Ribble and Salvioni, 1990), which was not the case in this study. I conclude that more information on reproductive success determined by genetic analyses are required to confirm promiscuous mating in *A. flavicollis*.

Hypothesis c

Gorman and Zubaid (1993) pointed out that seeds are typically patchily distributed and are highly clumped both in terms of space and time; therefore, granivorous species, such as *A. flavicollis*, may tend to concentrate their activity in specific areas within the home range boundaries. In fact, as hypothesized by these authors, I found an uneven use of space inside the home range in both sexes.

In small mammals, home range estimates can vary significantly according to season, sex, age, population density and habitat quality (Wolton and Flowerdew, 1985). As the variation in size of home range is probably a function of food availability and population density, home ranges are expected smaller in favourable habitat than in a poor one (Taitt, 1981; Wolff, 1985); furthermore home ranges also appeared to be smaller at high than low density (Stickel, 1960; Zejda and Pelikán, 1969; Taitt, 1981).

Wilson et al. (1993) indicated an inverse correlation between the home range size of *A. sylvaticus* and the population density, similarly to what observed for *A. flavicollis* in this study between 2005 (high population density) and 2006 (low population density). In 2005, home range size showed a seasonal trend, increasing towards the end of summer/beginning of autumn. As changes in spatial patterns with density and forest productivity are well documented on rodents species (Wolff, 1985; Ims, 1987; Wolff, 1996; Mazurkiewicz and Rajska-Jurgiel, 1998; Juškaitis, 2002), I suggest that this temporal variation could be related to resource availability and population density. In the study area, beech seed mast occurred in autumn 2004 and, in accordance with the prediction of Ostfeld et al. (1996b), the following year I registered high density of *A. flavicollis*. Besides, in autumn 2005 no beech seed production was recorded, causing very scarce food availability in spring-summer 2006 and low population density.

As food requirements are dependent on parental care investment, I expect trophic resource variation to mainly condition female spatial behaviour and particularly the degree of territory exclusiveness (Ostfeld, 1990). In turn, males would adequate their distribution to females' one, to keep mating possible. In spring 2005, at high population density and abundant resources, females showed a clear territory exclusiveness, resulting in an evident sex-biased home range and core area overlap. In autumn 2005, the high population density and scarce resources availability probably exacerbated the competition for food, resulting in increased home range size and daily distance moved of both sexes as noted by other authors (Mares and Lacher, 1987; Rogers and Gorman, 1995; Corp et al., 1997) and adult dispersal. In spring-summer 2006, at low population density and scarce resources, home range size and daily distance moved of both males and females was as double as much than in 2005; females showed a lower degree of territory exclusiveness than in 2005, as core area overlap was sex-biased, but home range overlap was not. In autumn 2006, a minimal seed production was recorded. Although a decrease in home range size and increase in female territory exclusiveness could be expected, these analyses could not confirm a statistically significant effect, but anecdotal field observations were consistent with this prediction.

Hypothesis d

Dispersal is a unidirectional movement away from individual home ranges (Lidicker and Stenseth, 1992) requiring complex behaviour that can differ between individuals and circumstances (Lin and Batzli, 2004). In small mammals, many authors reported that a deficiency in food resources caused a dispersal rate increase (Wolton and Flowerdew, 1985; Gliwicz, 1992; Mazurkiewicz and Rajska-Jurgiel, 1998); it is a phenomenon driven by a large set of factors such as age, sex, population density, social status, breeding conditions and habitat quality. Long distance movements in short periods had been already reported both for *A. sylvaticus* and *A. flavicollis* (Bergstedt, 1966; Wolton and Flowerdew, 1985; Kozakiewicz et al., 1999; Marsh and Harris, 2000). Gliwicz (1988) found that *A. flavicollis* dispersal had a seasonal pattern with two distinct peaks: the first in spring and early summer and the second in autumn. In this case, I hypothesize that adult dispersal was a result of seasonal change in habitat quality (Bondrup-

Nielsen, 1985; Wolton and Flowerdew, 1985; Gliwicz, 1992) and thus not expected to be sex biased, as this would occur mainly in species inhabiting stable and predictable habitats (Greenwood, 1980). Under such environmental conditions, the benefits arising from reaching new resources have presumably exceeded the costs in terms of increased predation risk. In support to this theory, I observed that dispersers occupied areas of higher resource quality and abundance than the original beech woodland and in particular they colonized patches with high seed production and established hedgerows. I conclude that adult *A. flavicollis* that departed from their stable home ranges could be categorized as "involuntary dispersers" as defined by Lidicker and Stenseth (1992). This is further supported by the more frequent dispersion of individuals in the year of low resource availability, as observed in the present study and by Gliwicz (1988).

Hypothesis e

Information provided by behavioural studies on rodents are of particular interest for wildlife epidemiology and specifically the dynamics of zoonoses, for the significance to human health. The sex-biased spatial organisation of *A. flavicollis* may affect parasite transmission and persistence. Males occupying larger home ranges than females both at high and low population density, may be more exposed to pathogens, as noted by Skorping and Jensen (2004). This would be particularly relevant for ectoparasites with indirect transmission, i.e. mediated by the environment, such as ticks. Wide ranging male rodents enhance their probability to encounter questing ticks, as opposed to more sedentary females and this may result in a greater tick burden, as here recorded; this evidence supports the behavioural hypothesis described by Stanko et al. (2002) on sex-biased heterogeneity in parasitism rates of rodents. Host density also affects individual tick load (e.g. Rosà et al., 2007), as clearly showed by the comparison between 2005 and 2006 and by the temporal pattern of individual larvae load in 2005. In the case of parasites with direct transmission or mediated by free-living stages (e.g. larvae of the endoparasite *Heligmosomoides polygyrus*), the circulation of the disease is favoured by high contact rates. Males with overlapping home ranges may induce this condition (Ferrari et al., 2007), whereas female territoriality may reduce the potential number of hosts exposed to the parasites they shed. Other aspects of mice behaviour that I observed may exert a central role in disease

transmission, for example the use of common burrows may increase contact rates. In addition, the relatively large dispersal distances recorded here for *A. flavicollis* points to this species as being potentially crucial also to disease spatial dynamics. These hypotheses could be supported by experimental assessments of disease dynamics among sexes, as those proposed by Ferrari et al. (2004).

8. CONCLUSIONS

Much like rodent populations in other environments, *A. flavicollis* populations may influence ecosystem processes at several trophic levels in Alpine forests. For example, their role in the transport, manipulation and accumulation of seeds may be a determinant of vegetation composition; forest renovation, for example, can be enhanced by the activity of rodents, but also depressed by excessive exploitation in low productivity years (Jensen, 1982). Furthermore, as a potentially important source of food, they may influence the dynamics of predator populations.

As a potential vector of tick-borne diseases, *A. flavicollis* may influence the dynamics of disease spread, including zoonotic pathogens. In particular, this study supports the hypothesis that the sex-biased parasitism rate may depend on different spatial organization and ranging movements of sexes (Ferrari et al., 2004; Ferrari et al., 2007). Furthermore, in the study of disease dynamics the assessment of host contact rate is of main importance, as it is involved in the pathogen transmission (McCallum, 2000). A number of techniques are used to interpret the social interactions between individuals in a population, from which we can make an estimate of host contact networks; among those, telemetry method, providing data of high temporal resolution, seems to better capture the dynamics of parasites, especially those with short infectious periods (Perkins et al., submitted).

The present study illustrates that *A. flavicollis* is a valuable model species for investigating the interactions between social and spatial behaviour, resource availability and population dynamics. These results indicate that heterogeneous distribution of resources resulted in sex-biased patterns of space use, which rapidly adapted to the changes imposed by seasonal and annual variations in habitat quality, in turn determining population density and structure. In particular, this research demonstrated that males *A. flavicollis* move wider than females, both in terms of home range size and distances travelled, and that male home ranges tend to overlap with those of several females to maximize their reproductive success; also female home ranges tend to overlap with those of several males, but females, monopolizing their core areas and nests, showed a certain degree of territoriality against conspecific of the same sex. Such a spatial organisation of

males and females *A. flavicollis* also suggests a promiscuous mating system. In addition, the enlargement of the home range size noted in 2006 and the high number of dispersers found in 2005, indicate that the use of space is dependent on resource availability and population density. Finally, the sexual differences in the use of space, showed in this study, can explain the sex-biased heterogeneity in the parasitism rate.

Further investigations to determine the genetic structure of the population would be useful to confirm the promiscuous mating system (e.g. Ribble and Millar, 1996), and manipulations of food availability would allow experimental evaluation of the effects of food resources on spatial structure and demographic trends (e.g. Watts, 1970; Flowerdew, 1972; Ims, 1987; Akbar and Gorman, 1993).

Knowledge of the absolute densities of small mammal populations is of crucial importance in conservation and epidemiological applications of demographic studies; for example, in the management of threatened species or for monitoring the role of small-mammal density in zoonotic disease outbreaks.

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