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Annual home range and movement in freshwater turtles: management of the endangered European pond turtle (*Emys orbicularis*)

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Abstract: Movement in turtles can be considered spatially in intrapopulational or extrapopulational terms. Intrapopulational movements are primarily related to feeding, reproduction, basking, and hiding. Extrapopulational movements are primarily for migrating between seasonally variable habitats, nesting by females, and mate searching by males. The daily and seasonal timing of habitat use varies in response to environmental, physiological, and demographic conditions. We investigated the use of aquatic and terrestrial habitats by an endangered freshwater turtle, the European pond turtle (*Emys orbicularis*). We tested whether habitats were used differentially by turtle sexes and life stages over spatial and temporal scales. We monitored 10 female and 10 male turtles for two and half years in two different sites, using telemetry (over 13 000 locations). In addition, we trapped turtles (n = 790) over a three years period to supplement data on habitat use. Movement data based on telemetry and recaptures were analyzed for every individual. We compare the results of both methods and argue for the use of different protocols adapted to management questions. We conclude that every component of the annual cycle of freshwater turtles is at risk in human-dominated landscapes. The reliance of freshwater turtles on heterogeneous landscapes necessitates integrated conservation efforts. Failing to protect a single annual or life cycle stage will ultimately doom the entire population to extinction. We argue that it is essential for efficient management to choose the most adapted scale in the landscape.

Key words: conservation, *Emys orbicularis*, habitat management, habitat use, telemetry.

Resumen: Espacio vital en tortugas de agua dulce: gestión del amenazado galápagos europeo (*Emys orbicularis*). – La movilidad de los galápagos puede ser considerado espacialmente en términos intrapoblacionales o interpoblacionales. Los movimientos intrapoblacionales se relacionan con la alimentación, reproducción, termorregulación o refugio, mientras los interpoblacionales lo hacen con la migración en hábitats estacionalmente variables, la anidación de las hembras y la exploración del territorio de los machos. El uso del hábitat varía en respuesta a las condiciones medioambientales, fisiológicas, y demográficas. Se investiga el uso de hábitats acuáticos y terrestres por el amenazado galápagos europeo (*Emys orbicularis*), valorando si son usados diferencialmente por ambos sexos y fases de su ciclo vital a escala espacial y temporal. Usando técnicas de telemetría, se lleva a cabo el seguimiento de 10 machos y 10 hembras durante dos años y medio en dos lugares diferentes (mas de 13 000 datos), complementándose la información por medio de capturas efectuadas a lo largo de más de tres años (n = 790). Con información relativa a cada individuo, se comparan los resultados de ambos

métodos y se argumenta el uso de protocolos diferentes adaptados a cada situación concreta. Se concluye que cada fase del ciclo anual de los galápagos está amenazada en los entornos de influencia humana, lo que aconseja esfuerzos de conservación integrados en paisajes heterogéneos. Descuidando un solo ciclo anual o una sola fase del mismo se pone en riesgo de extinción a la población entera, por lo que una gestión eficaz es esencial.

Palabras clave: conservación, *Emys orbicularis*, gestión del hábitat, uso del hábitat, telemetría.

INTRODUCTION

Management of wildlife populations to conserve threatened species generally entails habitat management (CADI, 2003). Habitat management presupposes some understanding of the species needs. To assess a species needs, researchers commonly study habitat use and, based on the results, infer selection and preference. In all probability, species should reproduce or survive better (i.e. their fitness should be higher) in habitats they prefer. Managers can then manipulate landscapes to contain more habitats that are suitable and thus increase the efficiency of their conservation actions (GARSHELIS, 2000; JOYAL *et al.*, 2001). Two basic assumptions are inherent to this approach: that habitat selection can be inferred from observations of habitat use and that such selection relates to fitness and hence to population growth rate.

Freshwater turtles usually inhabit lentic and lotic habitats with stable hydroperiods. These aquatic habitats are used for basking, feeding, mating, and overwintering (SERVAN, 1986, 1988; LEBBORONI & CHELAZZI, 1991; ERNST *et al.*, 1994; DALL'ANTONIA *et al.*, 2001). The annual cycles of some species are well documented (*Trachemys scripta*, GIBBONS, 1990). Males of most species rarely leave these habitats other than to emigrate, search for females, or overwinter terrestrially (TUBERVILLE *et al.*, 1996, DUGUY & BARON, 1998). Females may leave the home wetland to emigrate, overwinter, and spawn, which occurs once to several times a year (GIBBONS

et al., 1990, ROVERO & CHELAZZI, 1996; MEESKE, 1997, DALL'ANTONIA *et al.*, 2001). Hatchlings, after emergence from terrestrial nests, migrate to the wetland to feed, grow, and develop (GIBBONS *et al.*, 1990). Feeding activity apparently decreases when mean temperature is decreasing (CAGLE, 1946, 1950), but feeding and basking become more frequent when ambient temperatures rises to 20 to 30°C (BURY, 1978). Numbers and activity levels are both highest in summer. Courtship and mating occur in spring, egg laying occurs in June (ROVERO & CHELAZZI, 1996; SCHNEEWEISS & STEINHAEUER, 1998).

For these reasons, protecting freshwater turtles depends directly on the quality of both aquatic and surrounding terrestrial habitats. Nowadays, a high proportion of freshwater species is in need of conservation because of the alteration and exploitation of freshwater habitats. These threats are major causes of decline for many species (BUHLMANN *et al.*, 1997). Among vertebrates that inhabit aquatic systems, turtles are a pervasive group whose semi aquatic behaviour makes them especially important for understanding the link between aquatic and terrestrial habitats (BODIE & SEMLITSCH, 2000; BODIE, 2001; JOYAL *et al.*, 2001).

The European pond turtle (*Emys orbicularis*) occurs over an extensive distribution range, from Portugal in the west to the area of the Aral Sea (Kazakhstan) in the east, from northern Germany and Moscow province (Russia) to southern Italy, Sicily and northern Africa and south-eastwards from

Turkey to the eastern Caucasus Republics and the southern shore of the Caspian Sea (FRITZ, 1998; KUZMIN, 2002; FRITZ, 2003). Nonetheless, despite its European distribution, little is known about habitat use in wild populations. This may have especially negative consequences in face of the conservation problems that threaten the species over a great part of its range (HONEGGER, 1981), given the difficulties in designing effective management plans for a species without an adequate knowledge of its biological and ecological requirements. As *E. orbicularis* is listed in the Habitat Directive of the European Commission (Annexes II and IV) and in the Bern Convention (Annexe II), a number of conservation programs have been started already.

We investigated its use of aquatic and terrestrial habitats in a system of ponds. Specifically, we tested whether habitats were used differentially by turtle sexes and life stages over meaningful biological spatial and temporal scales. Analyses of movements provide an understanding of the potential impact of habitats on turtle life histories and provide direct results for application to wetland conservation and management.

MATERIALS AND METHODS

Study area

Data were collected from March to October 2000, 2001 and 2002 over a large study area in the Isère department, France (Fig. 1). Among the 90 sites known for the species, two were chosen and subjected to capture-mark-recapture monitoring programs. The site of Lemps (WGS84 coordinates: 5° 21' 40" E 45° 45' 21" N), comprises a 13 hectares pond located within a protected area. It is isolated from other wetland areas. The site of La Serre (WGS84 coordinates: 5° 25' 25" E 45° 43' 42" N) comprises five ponds

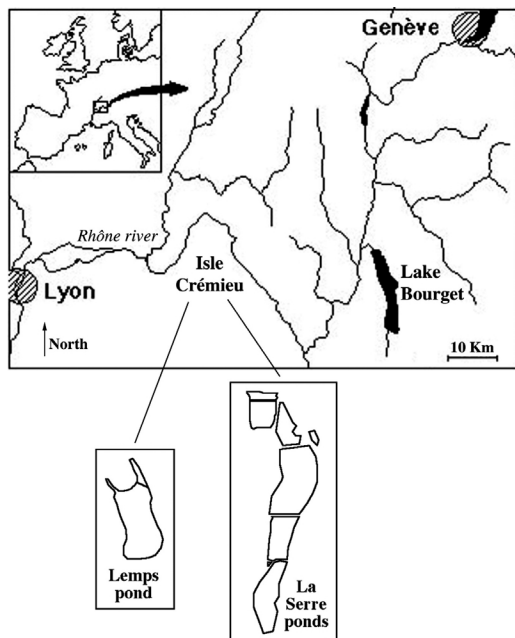


FIGURE 1. Location of the study sites in the Isle Crémieu region, near the Rhône river, southeastern France.

FIGURA 1. Localización de los enclaves de estudio en la región de Isle Crémieu, cerca del río Ródano (sudeste de Francia).

connected to each other by ditches or separated by dykes (45 hectares submerged area); a part of the site is protected. The distance between the two study sites is 10 km.

Capture

The two sites were sampled monthly from May 2000 to September 2001 (Table 1). Drift-type traps made of a 5-m-long net were stretched perpendicularly to the shoreline, with a hoop trap fastened to the end of the net, so that turtles swimming in either direction along the shoreline are driven towards the traps. Traps were placed in the water along the margin of each site (1 trap each 50 meters). Trap were checked and rebaited daily. Each site was trapped continuously for four nights. A minimal interval of 30 days was left between two different sessions in the

TABLE 1. Home range size for both sex and site (ha). Area use size was computed using Kernel area method based on 95% contours (WORTON, 1989; KENWARD & HODDER, 1996).

TABLA 1. Dominios vitales (ha) de acuerdo al sexo y al enclave. El tamaño del área se calculó mediante el método de Kernel de acuerdo a WORTON, 1989 y KENWARD & HODDER, 1996.

	Males	Females
La Serre		
May 2000-May 2001	5.28 (2.69 (2.99 - 10.32)	6.84 (3.87 (1.19 - 12.96)
May 2001-May 2002	7.20 (2.58 (3.92 - 10.8)	7.49 (3.64 (0.27 - 13.01)
Lemps		
May 2001-May 2002	7.20 (2.58 (3.92 - 10.8)	7.49 (3.64 (0.27 - 13.01)

same site (more details available in CADI, 2003).

Turtles were individually marked with notches on the marginal scutes (STUBBS *et al.*, 1984) and examined for establishing sex and life stage (juvenile vs adult, by secondary sexual characters; ERNST *et al.*, 1994). For recaptured individuals, date, individual number, and trap number were recorded for the 3-year sampling period. Turtles were released into the water at the end of the session, on the shore near the trap in which they have been caught. Capture locations are represented on the digitized habitat types with ADE 4 computer program (THIOULOUSE *et al.*, 1997).

Telemetry

Locations of the monitored individuals were obtained by telemetry. Because habitat use is potentially different between sexes in some freshwater turtles (MOLL & LEGLER, 1971; VOGT, 1980), we monitored both males and females. Transmitters were too heavy to be carried by hatchlings, and hence could not be used.

Ten adult female and ten adult male *E. orbicularis* were captured, measured, marked, fitted with transmitters (TW-3, Biotracks, UK, Receiver Mariner 57 148–149 Mhz and Yagi antenna), and released within 1–24 h in

each site (from 17 May 2000 to 31 July 2002 in La Serre site, and from 21 May 2001 to 31 July 2002 in Lemps site). Transmitters were attached to the upper central anterior margin of the carapace of each turtle with aluminium machine screws, and plumber's epoxy was mold into the seams. Transmitter packages weighed less than 5% of each turtle's body mass. All individual's transmitter frequencies were searched each day from the end of March to the beginning of October, then once a week during the rest of the year. As females usually dig their egg chambers in the afternoon or evening (MITRUS & ZEMANEK, 2000; KOTENKO, 2000), all individuals' transmitter frequencies were searched each day during the afternoon then two times in the beginning and the middle of the night. Occasional long-range (> 1 km) movements by some individuals required that searches by foot, all-terrain vehicle or boat with mounted antennae were performed. All turtles were located daily in aquatic or in terrestrial habitats. Two 24 h continuous monitoring sessions were carried out at La Serre on a number of individuals (11 individuals in June 2002 and 13 individuals in July 2002).

Locations were mapped onto a rectified scanned image of a 1998 true-color aerial photograph (scale 1:7000) of the study area using Map Info 6.5 geographic information

system (GIS) software. Comparisons of the under laid image with field observations indicated that telemetry location displacement was generally less than 5 m.

Habitat classification and locations analysis

Wetland habitats within the study area were surveyed during 1999–2000 to determine broad habitat types. Six habitat types were identified: open water, with presence of *Salicion cinerea*, Phragmition, Magnocacion, Nymphaeion, Potamion, and *Alnion glutinosae*. The perimeter of each landscape element belonging to one of the six habitat types was digitized into the GIS using the rectified image of the study-area photograph as a template. The proportion of the study area composed of each habitat was calculated using the Range VI computer program (Anatrack, UK) area function. The boundaries of the study area used for habitat proportions were defined with the shoreline of the ponds (other are “terrestrial habitat”). Each telemetry location was assigned to a habitat type using the Map Info feature-join function. Comparisons of the overlaid locations on the digitized habitat types corresponded to field observations. The distance of each telemetry location from the previous daily point (distance between a daily location and the last one) and the distance of each individual location from each other individual (daily distance between each individual and the other) were calculated. Distances between each location and the last overwintering site were also calculated. Area use size was computed using different methods (CADI, 2003). Because of its best link with the data, we choose to present in this paper kernel area method (WORTON, 1989). Data were analyzed with Ranges VI based on 95% contours (KENWARD & HODDER, 1996).

Telemetric data, differences in habitat use for each sex were determined using a log-likelihood contingency G-test (ZAR, 1974) with the null hypothesis that use was randomly distributed among all identified habitats. The expected distribution of locations was determined from the habitat availability.

RESULTS

Population distributions from capture data

From 2000 to 2001, 790 captures were performed in the course of eight sessions. We identified a total of 194 individuals at La Serre (immatures $n = 81$, males $n = 63$, females $n = 50$) and 52 in Lemps (immatures $n = 10$, males $n = 32$, females $n = 10$). Immatures make up 41.75 % of all captures in La Serre, but only 19.23% at Lemps, where only a single juvenile was found.

Figures 2A, B show the spatial distributions of captured individuals in both sites, sorted by age and sex. In La Serre, all the population can be found in the main pond and in a smaller, annex pond. A few individuals were captured, very occasionally, in other wetlands. Male and female capture distributions were not significantly different ($\chi^2 = 47.31$, $p = 0.052$); however, adults and immatures did show different distributions of their capture site ($\chi^2 = 124.02$, $p < 0.001$). In Lemps, captures are distributed all along the banks, and there are no significant differences either between males and females ($\chi^2 = 40.06$, $p = 0.281$), or between adults and immatures ($\chi^2 = 70.93$, $p = 0.534$).

We located individual turtles at the outset of hibernation during the April 2001 session (Fig. 3). In La Serre, hibernation sites are concentrated on the northern dyke of the main pond. In Lemps, they are found at the northeastern and southeastern ends of the site.

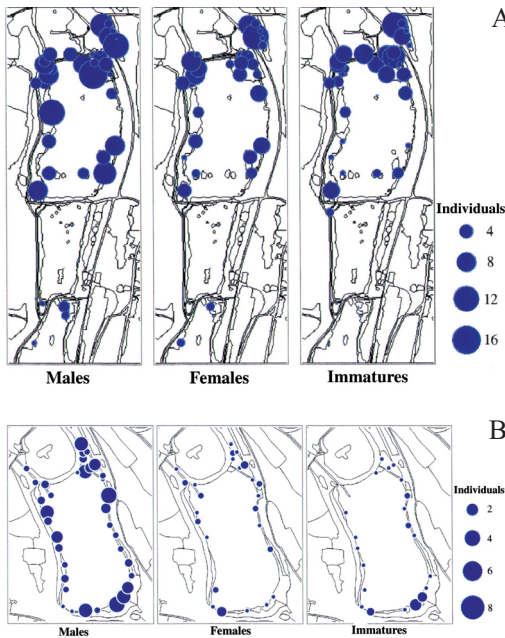


FIGURE 2. Capture locations in both sites for each age and sex class. The circle size shows the cumulated effective capture on the same trap. (A) La Serre (scale 1:2500). (B) Lemp (scale 1:5000).

FIGURA 2. Puntos de captura en ambos enclaves para cada clase de edad y sexo. El tamaño del círculo muestra la captura acumulada en la misma trampa. (A) La Serre (escala 1:2500). (B) Lemp (escala 1:5000).

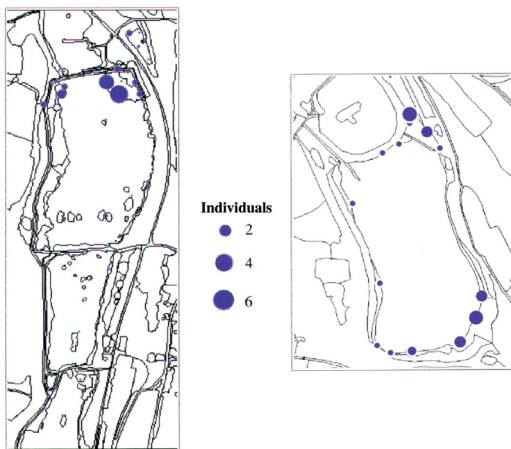


FIGURE 3. Capture locations at the beginning of the activity period in La Serre and Lemp (April 2001).

FIGURA 3. Puntos de captura al inicio del periodo de actividad en La Serre y Lemp (abril de 2001).

A Habitat use from telemetry data

We successfully located turtles with transmitters 12480 times out of 13579 (i.e. 1099 times [8%] during searches, transmitters either were not heard or were impossible to locate precisely). All of 40 individuals were followed until the end of the study (with one change of transmitter for each individual).

Distances

Distances between two consecutive locations changed simultaneously in the two sexes (Spearman rank correlation test: La Serre, ($\rho = 0.491$, $p < 0.0001$ and Lemp, ($\rho = 0.626$, $p < 0.0001$). Fig. 4 shows the annual and cyclical changes in distances moved daily. Movements started in May and end in November; they strongly increased from May, and decreased in August. This cycle was repeated throughout the three activity periods we monitored.

During hibernation, 75% of the turtles were located in the same area in La Serre. In Lemp, there were two groups of individuals, north of the pond (35% of the followed individuals, five males and two females) and south of the pond (55% of the followed individuals, five males and six females). Distances between each location and the previous hibernation spot increased simultaneously with the values of everyday distances (Figs. 4A, B), showing a significant post-hibernation dispersal (Spearman rank correlation test: La Serre, ($\rho = 0.820$, $p < 0.0001$ and Lemp, ($\rho = 0.664$, $p < 0.0001$).

Daily cycles

During its activity period, the European Pond turtle seemed to be active early at night and in the middle of the day (Figs. 5A, B). Activity was evidenced by the distance between two locations. Male and female everyday distance variations were not

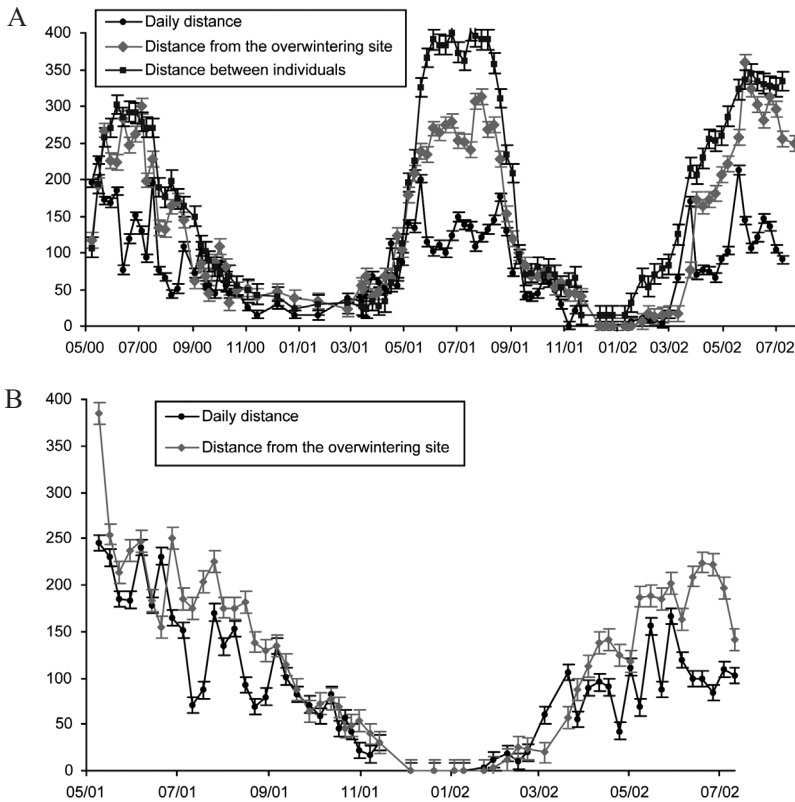


FIGURE 4. Daily distance and distance from the overwintering site during the monitoring (May 2000 – July 2002) for both sexes. (A) La Serre. (B) Lempis.

FIGURA 4. Distancia diaria y distancia desde el lugar de hibernación durante el periodo de monitorización (mayo de 2000 a julio de 2002) para ambos sexos. (A) La Serre. (B) Lempis.

different (Spearman rank correlation test: June, ($\rho = 0.594$, $p < 0.05$, and July, ($\rho = 0.643$, $p < 0.05$). Activity peaks occurred at the same hours in June and July (12.00 and 20.00 h) and were not different between the two months (Mann-Whitney U test: $U = 46$, $p = 0.35$).

Short range movement

Home range was computed for each sex and site over two activity cycles (from one hibernation event to the next, including all terrestrial and aquatic locations) in La Serre, and only one cycle in Lempis. In La Serre, male and female home range sizes were not

different (Mann-Whitney U test: $U = 48$, $p = 0.87$); in Lempis, female home ranges were larger than male home ranges (Mann-Whitney U test: $U = 9$, $p < 0.05$). Lempis female home ranges were also larger than La Serre female home ranges (Mann-Whitney U test: $U = 7$, $p < 0.05$). Male home ranges showed no differences between sites (Mann-Whitney U test: $U = 41$, $p = 0.49$).

Individual home ranges computed over the whole year overlapped much more in Lempis ($70.47\% \pm 28.61$) than in La Serre ($43.48\% \pm 31.41$). In La Serre, home ranges computed in the 2001/2002 period overlapped those of 2000/2001 at $71.98\% \pm 15.39$.

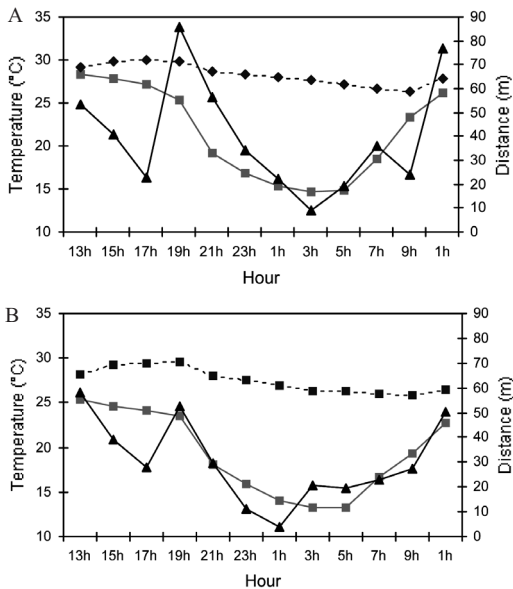


FIGURE 5. Mean distance measured between two locations every two hours (dark line), air temperature (spotted line) and water temperature (grey line). (A) in June. (B) in July.

FIGURA 5. Distancia media recorrida según registros efectuados cada dos horas (línea oscura), con indicación de la temperatura del aire (línea discontinua) y del agua (línea gris). (A) en junio. (B) en julio.

Long range movement

When aquatic connections were absent, long distance movements (for egg laying or changing ponds) imposed crossing terrestrial habitats. In Lemps, no terrestrial movement was observed outside the egg-laying period. In La Serre, eight turtles (three males and five females) over 20 have changed ponds during foraging periods (average distance moved on land: 143 ± 217 m, min-max: 5-520 m; May and June). All turtles came back, between mid-August and mid-September, before hibernation.

We observed egg-laying movements of 124 ± 90 m (min-max: 10-300) in La Serre ($n = 16$), and of 257 ± 171 m (min-max: 30-490) in Lemps. During the nesting season (June), most females were reported to nest at night (La Serre, $n = 21$. 76 %; Lemps, $n = 8$,

100%). The longer the distance between pond and egg-laying site, the earlier in the afternoon turtles came out of the water.

Aquatic habitat selection

Over the whole annual cycle, habitat use shows a strong selection for aquatic vegetation (Fig. 6). Turtle distribution over available habitat is not random (La Serre, $G = 32.82$, $df = 5$, $p < 0.0001$; Lemps, $G = 93.73$, $df = 5$, $p < 0.0001$). Open waters make up 82.58% of habitats available in La Serre and 83.37% in Lemps. Despite this high availability, open waters are little used, compared to aquatic habitats with a strong plant density. In Lemps, the habitat "rooted floating vegetation" (Nymphaeaeion and Potamion) is strongly selected, with 33.27% of locations. The habitat "marshy Alnus woods" (*Alnion glutinosae*), being the most terrestrial, is not used. Less than 2% of the locations were made on dry land. During overwintering, 90% of locations are found in Salicion cinerea in La Serre, but only 35% in Lemps. Other winter locations in Lemps were found in Phragmition (35%) and Magno-caricion (30%).

Spatial interaction between individuals

The average distances between individuals fluctuate parallel to distances with hibernation sites (Spearman rank correlation: La Serre, $\rho = 0.912$, $p < 0.0001$; Lemps group 1, $\rho = 0.768$, $p < 0.0001$ and group 2, $\rho = 0.388$, $p < 0.0001$). This shows that the population scatters in every direction during the activity period, turtles distancing themselves from one another and from their hibernation sites, to occupy the whole wetland.

The overlay of home ranges at the outset of hibernation and in the middle of the activity period clearly shows the spacing of individuals in the course of the season (for example in La Serre 2001: April, 65.75 ± 25.23 % and July, 11.32 ± 43.29 %).

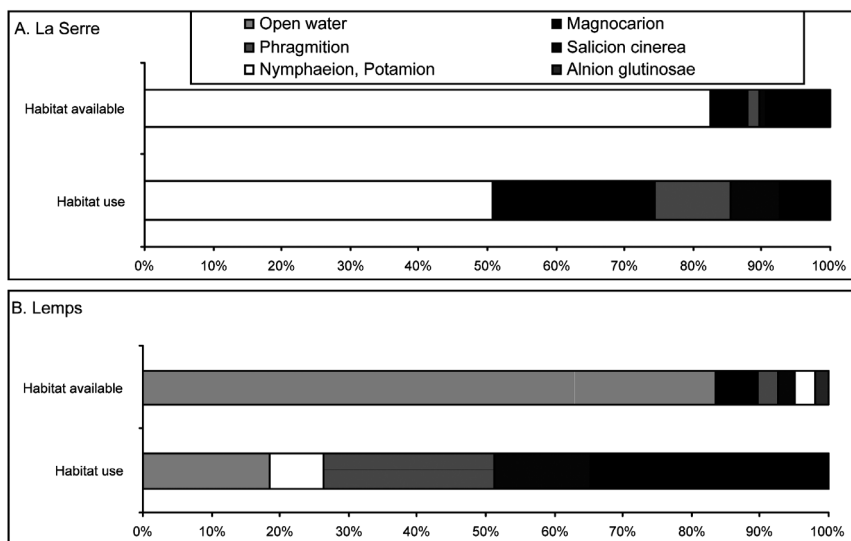


FIGURE 6. Habitat selection for both sites. (A) La Serre. (B) Lemps.

FIGURA 6. Selección del hábitat en ambos enclaves. (A) La Serre. (B) Lemps.

Site fidelity

When selecting an egg-laying site, many females return exactly to the same site selected the previous year (75% for La Serre; 40% for Lemps).

During the foraging period, some individuals go back to precise sites, with high fidelity from one year to the next. This is particularly true of the turtles that move over dry land to smaller, satellite ponds ($n = 4$, hence 20% in La Serre, homing 100%).

Finally, 81.25% of individuals followed used approximately the same hibernation sites (± 25 m) in 2000/2001 and in 2001/2002, with a mean total distance from the hibernation site to the summer site of 211 ± 245 m (min-max: 40-908).

Home range size estimation from capture and telemetric data

Home ranges are computed from all the 2001 sessions and the locations between 1 April and 30 September 2001 (activity period

2001) (Table 2). Estimates of home ranges from capture data are not significantly different from home ranges obtained by telemetry ($\chi^2 = 0.001$, $p = 0.999$ for La Serre, and $\chi^2 = 0.023$, $p = 0.999$ for Lemps).

TABLE 2. Home range size comparison for both sex with capture (5 sessions from 2001) and telemetry (from January to December 2001) in each site. Area use size was computed using kernel area method based on 95% contours (WORTON, 1989; KENWARD & HODDER, 1996).

TABLA 2. Comparación entre los tamaños de espacio vital en cada sexo obtenidos por telemetría (de enero a diciembre de 2001) y captura directa (cinco sesiones en 2001). El tamaño del área se calculó mediante el método de Kernel de acuerdo a WORTON, 1989 y KENWARD & HODDER, 1996.

	Males	Females
La Serre		
Telemetry	20.11 (n = 1221)	24.69 (n = 1044)
Capture	14.53 (n = 105)	19.45 (n = 68)
Lemps		
Telemetry	13.28 (n = 1024)	12.94 (n = 539)
Capture	11.1 (n = 129)	11.53 (n = 37)

DISCUSSION

Turtle locations in our two sites show that the annual cycle of pond turtles can be divided into two parts: an activity period from April to October and a lethargic, hibernation period from November to March. Similar observations have been made in other parts of pond turtle range (Italy, ROVERO & CHELAZZI, 1996; Hungary, FARKAS, 2000; Ukraine, KOTENKO, 2000). Period duration can be influenced by weather conditions.

We show that turtles migrate significant distances in response to seasonal changes. In temperate zones, all turtles hibernate (ROLLINAT, 1934; GIBBONS, *et al.* 1990; PARDE *et al.*, 1999) mostly under water (our results).

Movements are restricted during hibernation; they increase as soon as weather conditions allow (increase in temperature and insulation durations). The long immobile period of the 2000/2001 winter is explained by the presence of a thick layer of ice that forbid any movement for more than a month. Overwintering is essential for turtles living in regions where winter temperatures approach or fall below freezing.

Freshwater turtles that live in larger bodies of water are buffered from thermal extremes by water itself, and many simply retreat under branches and vegetables to wait out the colder periods. Some individuals that remain in aquatic areas become active on sunny days if their body temperatures can be raised sufficiently by aquatic or aerial basking. In spring, probably strongly influenced by the need of food, turtles go back to their shallow and vegetated area. It is conceivable that some turtles travel beyond the limits of the normal population habitat to acquire a predictable resource in another area.

The progressive scattering of locations over the whole wetland area in the course of the activity period corresponds to the colonization

of all the surrounding aquatic biotopes. This scattering is found in adults turtles of both sites, and is probably linked to the optimization of resource acquisition. As no territorial behavior has ever been observed in freshwater turtles, this phenomenon could be due to avoidance of competition for food and basking sites (BURY, 1978). In La Serre, habitat structure is highly heterogeneous: stands of reeds and *Carex* sp., as well as water lilies, which are favorable to mollusks and larvae comprising the majority of turtle diet, are distributed in small patches. The unequal distribution of these small patches, and hence food resources, could explain the wide scattering of turtles observed in both sites (DI TRANI & ZUFFI, 1997; MORALES-VERDEJA & VOGT, 1997). In Lemps, turtles are spread regularly along the bank of the pond. As changing wetlands is not possible, the whole site is used. The cumulated home range surfaces of males and females represent near the surface of the whole pond. This suggests in part that home range size is limited by physical barriers (dykes, canals, BURY, 1978) and also that each individual utilizes the near totality of the wetland. Habitat selection seems to be tied more to abiotic than biotic (vegetation) criteria: minimal water levels, access to sunlight and vegetation density are common to all the habitats used (DI TRANI & ZUFFI, 1997).

During egg-laying in June, females can travel several hundred meters (SERVAN, 1988; ROVERO & CHELAZZI, 1996; PAUL & ANDREAS, 1998; SCHNEEWEISS & STEINHAEUER, 1998; ANDREAS, 2000; KOTENKO, 2000). Movements over dry land to change ponds are swift and direct (NAULLEAU, 1991; LEBBORONI & CHELAZZI, 2000).

Juveniles, contrary to adults, limit their movements to a small area. When exiting their nest, young turtles move across dry land until they reach the nearest body of water and stay there for a number of years (*Emys*,

LEBBORONI & CHELAZZI, 1998; RÖSSLER, 1999; *Trachemys*, GIBBONS *et al.*, 1990). These habitats are characterized by a low water level (10-30 cm) and dense vegetation (with woody plants like willow).

We show a strong homing behaviour for most individuals particularly for overwintering period. We can suppose that the risks to survival from inaction during winter are obviously much smaller than the risks encountered in overland or aquatic travel to hibernation site. Several studies have shown that emydid turtles are able to home after experimental displacement (*Chrysemys picta*, CAGLE, 1944; ERNST, 1970; *Clemmys guttata*, ERNST, 1968; *Emys orbicularis*, LEBBORONI & CHELAZZI, 2000). Moreover, a water-finding ability (orientation towards aquatic habitats outside the home range and beyond the field of view) has been demonstrated for *Trachemys scripta* (YEOMANS, 1995). This strong pattern of habitat use increases the importance of short-term landscape modifications on individual survivorship. At the scale of the annual cycle, the whole aquatic habitat (integrating wetlands of over a few hundred square meters) is used (LEBBORONI & CHELAZZI, 1998). A band of dry land a few hundred meters long (often equal or less than 200m) is traveled when changing ponds and for egg-laying. As homing behaviour was observed for hibernation and egg-laying, we suggest that this pattern of habitat use is repeated at each cycle.

In this study, telemetry provided no significantly larger estimates of home range area than did mark-recapture. Nevertheless, others studies have shown the opposite for other species (*Chelydra serpentina*, OBBARD & BROOKS, 1981; SHUBAUER *et al.*, 1990). They calculated that telemetric estimates of home range were more than twice as large as the mark-recapture estimates. Their results

are not surprising, considering the biases and sampling problems associated with common capture methods. Trap density (too many or too few) or placement could distort or misrepresent home ranges and most likely miss long, unexpected movements out of the study areas. At last, bait traps may distort movements and home ranges by revealing mostly movements of hungry turtles. In our design, the high capture probabilities estimated show a more efficient and less biased sampling (CADI, 2003). Even if telemetry provides a less biased estimate of the movements and home ranges of aquatic turtles (but the monitoring of a large group in which each sex or age are well represented, is costly in time and resources), capture-recapture can provide very interesting spatial information. Usually used for demographic study, this method could also be optimized for spatial data.

The two methods we used provide important information, some complementary, and other redundant. It is however not necessary to consider using such intensive monitoring programs for every site chosen for conservation. We showed that trapping could be employed to detect species presence and, with a modest effort, provide precise enough ideas about population structure (CADI, 2003). From this structure, the basic elements of population demography can be inferred, such as age and sex ratio, as well as population size. Nonetheless, we insist that this protocol is optimized for the main activity peak of the active period of the annual cycle (mid May to late August), which limits the acquisition of information on habitat use by turtles. For this reason, adding a session at the start and at the end of the hibernation periods makes it possible to collect spatial data over the whole annual cycle, even though capture probabilities are reduced at these times. Radio tracking can

then be limited to locating egg-laying sites (followed by sampling the females over the egg-laying period). In the case of fragmented or ramified wetlands, of various perturbation (leisure fishing, sailing, sand or gravel extraction...), further, custom-designed, studies should be performed. Finally, it should be noted that only trapping could provide data on young individuals, radio tracking equipment being too heavy for them.

Life cycles of freshwater turtles span years and involve multiple habitats (CONGDON *et al.*, 1993, 1994; BURKE & GIBBONS, 1995). Because freshwater turtles are long lived, disruption of the life cycle may not be immediately obvious.

We conclude that every component of the annual cycle of freshwater turtles is at risk in human-dominated landscapes (KAUFMAN, 1992; BODIE & SEMLITSCH, 2000). The reliance of freshwater turtles on heterogeneous landscapes necessitates integrated conservation efforts. Failing to protect a single annual or life cycle stage will ultimately doom the entire population to extinction. Conservation of freshwater turtles does not mean that complete understanding of the life cycle is needed before any conservation action can be taken, but it is absolutely necessary to choose the efficiency scale in the landscape. The most critical factor in the maintenance of self-sustaining, free-living populations is the preservation of habitat and conditions required for completion of the life cycle (BURKE & GIBBONS, 1995; LOVICH & GIBBONS, 1997; BODIE & SEMLITSCH, 2000). Turtles cannot exist in the wild without suitable habitat. Hence habitat protection, acquisition, and maintenance should be basic priorities in conservation programs (CADI & FAVEROT, 2004). An ideal sanctuary must include a large breeding nucleus of the species of concern along with optimal nesting and

feeding habitats. In the European pond turtle case, this terrestrial buffer zone must be at least 200 meters all around the wetland (more if possible). The object is to protect the breeding nucleus so that it can continually supply recruitment to the population both inside and outside the sanctuary (Tortoises and Freshwater Turtles Specialist Group, IUCN, 1989). Ideally the protected populations grows to a level at which population pressures force excess individuals out of the sanctuary.

A particular attention must be brought to the small wetlands. As GIBBS (1993) showed, our study suggested that many turtle species have established populations in particularly small wetlands (only few hundred square meters) which are usually forgotten by the legal status.

Last, it is necessary to increase awareness about the importance of wetlands to biodiversity conservation. Wherever and whenever marshes, sloughs, swamps, and similar habitats are threatened, conservationists must take a strong stand against unbridled development and misuse. Biologists must make conservationists, educators, community leaders, and politicians aware of and sympathetic to the habitat needs of freshwater turtles and their aquatic associates. Even fish and game departments, which would seem to be the logical allies, may need to be educated regarding the effects of fisheries practices on turtles. With regard to the public, arguments based on aesthetics and awareness that the turtles are part of the biodiversity, should be made prevalent.

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