RESOURCE PARTITIONING IN THE COMMUNITIES OF TERRESTRIAL TURTLES: A REVIEW OF THE EVIDENCES

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RÉSUMÉ. — *Le partage des ressources dans les communautés de tortues terrestres : une revue des évidences.* — Le présent travail analyse les études de l'organisation des communautés de tortues terrestres afin d'examiner les principaux patterns de partage des ressources et de voir si la compétition interspécifique constitue ou non une force structurante importante pour ces ectothermes. Ces reptiles montrent quatre traits quasi constants dans leur écologie et leur histoire de vie : (i) une faible richesse spécifique, (ii) une forte longévité, (iii) une alimentation de type herbivore/omnivore et (iv) une faible densité de population. Sur la base de ces caractéristiques, on peut prédire que la compétition interspécifique serait moins pertinente pour l'organisation des communautés de tortues que pour celles des autres reptiles (lézards et serpents). L'examen de la littérature internationale amène à conclure que la plupart des communautés de tortues de par le monde ne sont actuellement pas influencées par la compétition interspécifique. Une grande partie de leur diversité spécifique reflète le remplacement géographique d'une espèce par une autre. Dans les régions où deux espèces, ou davantage, sont sympatriques, la compétition interspécifique est relativement faible car ces espèces tendent à se partager très nettement l'espace ou la nourriture. La confrontation de simulations de type Monte Carlo du chevauchement de niche à des chevauchements de niche réels dans une région d'Afrique tropicale où a été bien étudiée la communauté composée de trois espèces de tortues terrestres, trois de lézards scincidés, quatre de caméléons et dix-neuf de serpents, met en évidence que la compétition interspécifique est statistiquement plus faible entre les tortues qu'entre les autres reptiles, la dimension spatiale de la niche étant celle qui sépare le plus clairement les tortues. Les tortues terrestres seraient donc particulières parmi les reptiles pour ce qui concerne la non-influence du processus de compétition dans l'écologie de leurs communautés.

SUMMARY. — In this study I reviewed the studies on the community organization of terrestrial turtles to examine the main patterns of resource partitioning, and to predict whether interspecific competition may be or may not be an important organizing force for these ectotherms. These reptiles exhibit four (nearly) constant ecological/life-history traits that may affect the role and the influence of interspecific competition: (i) low species richness, (ii) high longevity, (iii) herbivorous/omnivorous dietary habits, and (iv) low population density. Based on the expectations derived from these ecological characteristics, I predicted that interspecific competition should be of lesser relevance for these turtle communities than for other reptilian communities (lizards, snakes). After reviewing the international literature, I concluded that most of the turtle communities around the world appear currently uninfluenced by interspecific competition. Much of their species diversity reflects geographic replacement of one species by another. In the regions of the world where two or more species are sympatric, current interspecific competition is also of relatively low importance, because the sympatric species tend to partition very clearly the spatial axis or the food axis. By Monte Carlo simulations of niche overlap data versus current niche overlap data at a geographic region in tropical Africa where the community ecology of three sympatric species of terrestrial turtles, three of scincid lizards, four of chameleons, and nineteen of snakes, was accurately studied, I concluded that the interspecific competition among turtles was statistically lower than that among these other reptiles, with the spatial niche being the niche dimension most clearly partitioned by turtles in comparison with the other ectotherms. Hence, terrestrial turtles would be unusual among reptiles with respect to the un-influence of the competition process for their community ecology.

Competition studies have experienced a "gold age" during the 60's and the 70's, when the Wilson and McArthur's ideas dominated the discipline of community ecology (e.g., see

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MacArthur & Levins, 1967; May & MacArthur, 1972; May, 1974; Saint Girons, 1975; Wilson, 1975; etc.). However, the subsequent years were characterized by a certain "scepticism" as for the importance of these studies is concerned (e.g., see the "competition controversy": Schoener, 1974, 1982, 1983, 1985, 1986; Connell, 1980, 1983; Barbault, 1991; Bronmark *et al.*, 1991; Simberloff & Dayan, 1991). Nonetheless, in recent years there has been a growing renaissance of studies dealing with the mechanisms of species coexistence, resource partitioning, and the role of interspecific competition. These recent studies have especially used an experimental approach on field-based data (e.g., see Griffiths *et al.*, 1993; Capizzi & Luiselli, 1996; Luiselli *et al.*, 1998; Krijger *et al.*, 2001; Petersen & Hunter, 2001; Ray & Sunquist, 2001; Luiselli, 2003a; Mokany & Shine, 2003), or an approach characterized by the use of null models and simulation procedures (Lawlor, 1980; Winemiller & Pianka, 1990; Gotelli & Graves, 1996; Laurent & Kingsbury, 2003; Friggens & Brown, 2005).

Terrestrial turtles have never been popular among community ecologists, and indeed they were totally unknown under the aspect of the study of community interactions up to about 20 years ago (Bury, 1979; Toft, 1985). However, terrestrial turtles have become model organisms for several types of studies during the recent years, and because of the rapid increase of knowledge of their ecology and their peculiar life-history characteristics, these animals offer a good opportunity to test hypotheses about community ecology and competition, which is why I decided to write the present article.

Much literature has appreciated the difficulties of determining the prevalence of current competition in nature, and hence it is necessary to define the evidence or criteria required to document that interspecific competition is operating or to demonstrate a lack of interspecific competition. The following criteria are used in this paper:

(1) Competing species often coexist at one spatial scale but have different distributions at a finer scale of resolution. Hence, these patterns should be evident in terrestrial turtle case studies to demonstrate their current competition.

(2) Species are often excluded by interspecific competition from locations at which they could exist perfectly well in the absence of interspecific competition. Otherwise, the relative importance of interspecific competition should be scarce.

(3) The relative intensity of interspecific competition can be tested by comparing different patterns of sympatric phylogenetically divergent organisms, to test whether there is any evident difference among groups under the same environmental conditions.

Other evidences of interspecific competition can be found in the literature. However, given that the terrestrial turtle literature is not so big and totally lacks experimental manipulative studies (see below), I will try to test just these "criteria of competition" with the few appropriate study cases available to us, because for other criteria there are no applicable data coming from terrestrial turtle study cases.

GENERAL PECULIAR ECOLOGICAL ATTRIBUTES OF TERRESTRIAL TURTLE SPECIES THROUGHOUT THE WORLD

Before examining the role of interspecific competition and the patterns of resource use in sympatric terrestrial turtles, it is necessary to introduce (i) the peculiar ecological attributes of these animals, and (ii) the hypotheses that can be derived from the application of these ecological attributes to competition theory.

I determined four main ecological attributes of terrestrial chelonians that may have some relevance in determining resource use and competition patterns:

(1) *Low species richness.* — The number of terrestrial chelonian species across the world (i.e. their species richness) is extremely low if compared to that of other vertebrates of relatively comparable size (Table I). The majority of the species (about 77%) belong to the family Testudinidae, which has a wide distribution in tropical Africa, Madagascar, India, southeast Asia, South America, and with a few species in Mediterranean Europe (3 species), North America (4), and western Asia (1) (Ernst & Barbour, 1989; Ernst *et al.*, 1994). A few other species belong to the families Geoemydidae and Emydidae (e.g., *Cuora galbinifrons, Geoemyda spengleri, Heosemys depressa, H. silvatica, Melanochelys tricarinata, Pyxidea mouhotii, Rhinoclemmys annulata, R. areolata, R. pulcherrima, R. rubida, Clemmys insculpta, Terrapene carolina, T. ornata, T. nelsoni*) (Table I). As a consequence of the low species richness, the number of sympatric terrestrial turtles is found to be very low throughout the world (2 up to 4, see Iverson, 1992a, 1992b, 1992c). Indeed, the highest numbers of sympatric Testudinidae tortoises were 4 in Africa (with most regions having 1-2 species), 2 in Europe (0-1 species in most regions), 3

TABLE I

Number of species of terrestrial chelonians presently known throughout the world compared to data for other vertebrate groups of grossly similar size

Taxon	Number of species	Families (# terrestrial species)	References
Terrestrial turtles	Approximately 65	Testudinidae (about 50), Geoemydidae and Emydidae (about 15 species)	Halliday & Adler, 2002, complemented by Ernst & Barbour, 1989
Freshwater turtles	Approximately 230		Halliday & Adler, 2002, complemented by Ernst & Barbour, 1989
Terrestrial snakes (excluding blindsnakes)	Over 2200		Halliday & Adler, 2002
Terrestrial lizards	Over 4500		Halliday & Adler, 2002
Terrestrial rodents	Over 1700		Clutton-Brock, 2002
Small carnivores	Approximately 170		Clutton-Brock, 2002
Insectivores	Approximately 365		Clutton-Brock, 2002

in Asia (1-2 species in most regions), 0-1 in North and Central America (up to 2 if we consider also *Terrapene* species), and 2 in South America (1 species in most regions) (Iverson, 1992c). No species are present in Australia, and no sympatry between Testudinidae occurs in North and Central America where the four species are always allopatric (Iverson, 1992c). Compared to another group of chelonians, the sea turtles, the terrestrial turtle species richness is higher (sea turtles have a global species richness of just 7 species), but the comparable local species richness is lesser (sea turtles have often 5 species sympatric). So, the patterns of species richness at local and global scales are completely different in terrestrial turtles from those in other chelonians like the sea turtles.

(2) *High longevity.* — Terrestrial turtles are characterized by extended longevity, with several species which are known to live for more than 30 years up to over 150 years, and in general are among the most long-lived animals (Gibbons, 1987; Hailey, 1990; Hailey & Lambert, 2002). In addition, these reptiles often show high nest or juvenile mortality, and this may be an important factor in the regulation of population density and so also a factor which could limit intraspecific competition by keeping populations on such a low level that food competition does not exist.

(3) *Herbivorous or omnivorous dietary habits.* — A survey of general dietary habits of the world's terrestrial chelonians (based on information provided in Ernst & Barbour, 1989) showed that 65.5% of the species are herbivorous, 32.8% are omnivorous (and many of them also primarily herbivorous), and just a single species (1.7%) is predominantly carnivorous. However, the distribution of herbivory is significantly different between terrestrial Testudinidae and terrestrial Emydidae (observed vs expected $\chi^2 = 119.86$, df = 5, $P < 0.0001$), in that it is by far the prevalent feeding adaptation in Testudinidae, whereas the prevalent feeding adaptation in Emydidae is omnivory (carnivorous habits are an exception). Hence, terrestrial chelonians are the only terrestrial ectotherms (apart from a few lizards, e.g. iguanas, etc.) having generalized herbivorous or omnivorous feeding habits, whereas other groups of terrestrial ectotherms are exclusively or predominantly carnivorous (amphibians, lizards, snakes, see Halliday & Adler, 2002). In addition, all detailed studies on terrestrial turtle diets agree that the various species are generalist foragers which may take a wide range of vegetal matters, and that feed on many plant species as they occur in the environment (e.g., Bruno & Maugeri, 1977; Bruno, 1986; Hailey, 1988, 1995; Mason *et al*., 1999; Loehr, 2002b; Luiselli, 2003b; etc.). On the other hand, carnivorous ectotherms of similar size (for instance, snakes) are well known to be often relatively specialized in their feeding preferences, and certainly much less generalists than most turtles (e.g., Toft 1985; Luiselli, 2006).

(4) *Low population density.* A survey over recent literature on population density of terrestrial turtles across the world indicated that the majority of the populations studied (85%) exhibited a very low population density (< 15 specimens/ha, Table II), and, among the few populations with high density, most occurred in islands without sympatric competitors (e.g., see Hailey *et al*.,

1988; Hailey & Willemsen, 2000). Since these patterns were consistent with species inhabiting extremely divergent environments (for instance, deserts in North America — *Gopherus agassizii*, as well as rainforests in tropical Africa — *Kinixys erosa* and *Kinixys homeana,* and Mediterranean climates — *Testudo hermanni*, etc.) (Table II), it is more than likely that the low density is a general characteristic of population demography of terrestrial turtles. On the other hand, the densities of other terrestrial ectotherms is much higher: snakes, for instance, have several populations exhibiting densities higher than 50 specimens/ha and may exhibit densities as high as 729 or even 1849 specimens/ha (for a review, see Parker & Plummer, 1987; see also Hofer, 2001), and lizards may easily exceed densities of 700-1 000 individuals/ha in particularly productive areas (Turner, 1977; Diego-Rasilla & Pérez Mellado, 2004; etc.). Although terrestrial turtles have often low population density, they are also comparatively large. It has been shown that turtle biomass densities may be high, and herbivorous turtles may have higher biomass than omnivorous or carnivorous species (Iverson, 1982). Hence, the above pattern may appear partially confounded. However, general theory establishes that herbivores should always have much higher biomass than carnivores and that predators should always be relatively rare (Whittaker, 1970; Spencer, 2000; Ahlering & Carrel, 2001). If we then compare the biomass of terrestrial turtles with that of carnivorous snakes (which are also ectotherms and therefore relatively similar in terms of metabolism), we would expect much larger biomasses of the former compared to the latter organisms. This is clearly untrue, as many snake populations reach very high biomasses (over 30 kg/ha, e.g., Godley, 1980; Filippi 1995; etc.), which is much more than the maximum snake biomass (4.6 kg/ha) established by Iverson (1982) and considered by him as one of the parameters used to conclude that turtles may have remarkably high biomasses compared to other reptiles. Thus, I am led to definitely conclude that terrestrial turtles exhibit in general low population density (in terms especially of number of individuals but also in terms of biomass), especially if compared to other organisms of comparable metabolism (i.e. other reptiles) or other vertebrates of their same trophic guild (i.e. herbivorous mammals of comparable size, like many rodents and lagomorphs).

HYPOTHESES AND GENERAL PREDICTIONS

Based on competition theory assumptions (e.g., Schoener, 1983, 1985, 1986, etc.), the main hypotheses on the expected variation of the intensity of interspecific competition in terrestrial turtles in relation to the above-examined ecological and life-history characteristics can be summarized as follows:

(1) Since terrestrial turtle species richness is usually low throughout the world (if compared to other vertebrates), interspecific competition should be comparatively lower in these chelonians than in any other ectotherm groups, which is analogous to what happens with snakes showing a reduced role of interspecific competition in the species-poor assemblages (e.g., at northern latitudes and at higher elevations; Luiselli, 2006).

(2) Because a variety of plant matter is usually a more readily available food source, and because most terrestrial turtles are food generalists (Bruno & Maugeri, 1977; Bruno, 1986; Hailey, 1988, 1995; Mason *et al*., 1999; Loehr, 2002b; Luiselli, 2003b; etc.), interspecific competition should be comparatively lower among sympatric terrestrial turtles (which are mostly herbivorous) than among other groups of carnivorous ectotherms (e.g., snakes or lizards). However, it should be considered that in some particular habitats and climates the terrestrial turtles may face seasons of low food availability (for instance, the dry season in semiarid tropical climates), hence there are some periods in some regions in which interspecific competition for food may also occur.

(3) Terrestrial turtles typically exhibit modest population densities, therefore interspecific competition should be relatively lower than in other ectotherms, which are known to reach very high population densities (e.g., snakes or lizards).

Because of the interference of the three points stated above, I predict that:

(i) Interspecific competition is today a minor force in structuring natural assemblages of terrestrial turtles (it is not known whether as a result of niche separation it evolved to reduce competition in the past).

(ii) Interspecific competition is certainly of lesser relevance for terrestrial turtle communities than for other reptilian communities (lizards, snakes).

TABLE II

Survey of the average population density for different populations of terrestrial species of turtles throughout the world. Note that the great majority of the populations had low density (< 15 specimens/ha). Populations exceeding that density value are highlighted in bold

| Species	Density (specimens/ha)	Geographical area	References
Fam. Emydidae			
Clemmys insculpta	0.66	USA	Ernst (2001)
Clemmys insculpta	2.60	USA	Tuttle & Carroll (1997)
Clemmys insculpta	**19.10**	**USA**	**Niederberge & Seidel (1999)**
Terrapene carolina	14.77	USA	Langtimm *et al.* (1996)
Fam. Testudinidae			
Kinixys homeana	0.91	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys homeana	1.65	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys homeana	2.85	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys homeana	1.98	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys homeana	0.15	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys homeana	0.79	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	0.43	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	1.06	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	1.35	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	1.28	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	0.09	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys erosa	0.38	Nigeria	Luiselli (2003c); Luiselli *et al.* (2006)
Kinixys belliana	0.08 to 2.7	Nigeria	Akani *et al.* (unpublished report)
Kinixys spekii	0.16	Zimbabwe	Coulson & Hailey (2001)
Testudo (Agrionemys) horsfieldi	0.2	Kazakhstan	Kuzmin (2002)
Testudo (Agrionemys) horsfieldi	3.9 to 10.3	Kazakhstan	Kuzmin (2002)
Testudo graeca	1.67	Greece	Hailey (1988)
Testudo graeca	**7 to 21**	**Greece**	**Hailey *et al.* (1988)**
Testudo graeca	3,73	Algeria	Rouag *et al.* (2006)
Testudo hermanni	10.0	France	Stubbs & Swingland (1985)
Testudo hermanni	**14.4 to 76.9**	**Greece**	**Hailey & Willemsen (2000)**
Testudo hermanni	**10 to 19**	**Greece**	**Hailey *et al.* (1988)**
Testudo hermanni	4.88	Sardinia	Corti & Zuffi (2003)
Testudo hermanni	0.94	Italy	Mazzotti (2004)
Testudo hermanni	0.88	Italy	Filippi *et al.* (unpublished report)
Testudo marginata	0.12	Sardinia	Filippi *et al.* (unpublished report)
Gopherus agassizii	0.08	USA	Krzysik (2002)
Gopherus agassizii	0.11	USA	Krzysik (2002)
Gopherus agassizii	1.25	USA	Bury & Luckenbach (2002)
Gopherus agassizii	0.32	USA	Bury & Luckenbach (2002)
Gopherus polyphemus	2.59 (1.46 to 3.73)	USA	McCoy *et al.* (2002)
Gopherus polyphemus	0.7 to 2.7	USA	Breininger *et al.* (1994)
Gopherus berlandieri	0.26	USA	Kazmaier *et al.* (2001)
Chersina angulata	**21.3 to 38.3**	**South Africa**	**Van Heezik *et al.* (1994)**
Chersina angulata	0.12	South Africa	Mason *et al.* (2000)
Homopus signatus	**17.0**	**South Africa**	**Loher (2002)**
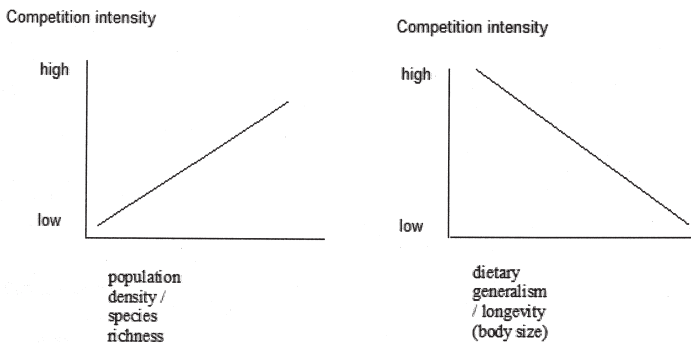
Figure 1.– Hypotheses on the expected variation of the intensity of interspecific competition in relation to the main life-history characteristics of terrestrial tortoises. In the graphics, the intensity of interspecific competition is on axis y, and the various life-history attributes are on axis x. Values increase from left to right (axis x), and from bottom to top (axis y).

A REVIEW OF THE LITERATURE

IS TODAY COMPETITION IMPORTANT FOR THE ORGANIZATION OF TERRESTRIAL TURTLE COMMUNITIES?

While numerous studies have examined the potential role of interspecific competition within other reptilian communities (e.g. lizards and snakes, see Toft, 1985; Luiselli, 2006, and references therein), very few studies have examined the same issues concerning terrestrial turtle communities. The lack of available information on terrestrial turtle communities may reflect the low number of turtle species or is possibly due to implicit perception and/or views of ecologists that these chelonians are not suitable species for community studies, because they do not compete as much as other reptiles (lizards and snakes). However it is also possible that they were simply forgotten by community ecologists as it has happened with snakes up to approximately 30 years ago (see review in Toft, 1985; Luiselli, 2006), before these latter organisms becoming popular models in evolutionary ecological research (Shine & Bonnet, 2000). Nonetheless, there are some terrestrial turtle study systems that have been investigated in detail, which may give some interesting insights into the general issue examined in this article. Fortunately, these few study systems cover a wide array of ecological and bioclimatic contexts (from the open dry woodlands to the rainforests in Africa, including the Mediterranean vegetation zone in Europe), and hence may allow some generalizations.

Hailey & Coulson (1995) studied the habitat niche of two broadly sympatric testudinid tortoises (*Geochelone pardalis* and *Kinixys spekii*) in dry open woodlands of Zimbabwe throughout a period of 10 years. They analysed the habitat niche of both species and found a considerable overlap between them (Pianka's O = 0.761). The two species were defined as habitat generalists, the only major difference being the greater use of riverine grassland by *G. pardalis* and the much larger home ranges of *G. pardalis* (Hailey & Coulson, 1995). However, in the same study system there was an obvious niche separation in the feeding dimension, as these two tortoises were clearly divergent in food preferences (*G. pardalis* being strictly herbivorous and *K. spekii* being omnivorous, with many fungi and invertebrates taken; see Rall & Fairall, 1993; Hailey, 1995, 1997; Hailey *et al.*, 1997, 2001; Kabigumila, 2001). Hence, Hailey and colleagues concluded that there should be no competition between these two species, because of the above-explained niche differences and because populations are limited by some other factor such as predation (Hailey & Coulson, 1995), which is very high in the study habitats in Zimbabwe (Coulson & Hailey, 2001).

Over an 8-year period, a study of three closely-related tortoise species (*Kinixys erosa, Kinixys homeana,* and *Kinixys belliana nogueyi*) was conducted by myself and associates in southern Nigeria's rainforest. We examined disparate aspects of their niche as habitat, food habits, seasonal and daily rhythms, population density, and thermal ecology. At a regional scale, we ran a logistic regression model of the three species local distribution to identify various environmental and habitat factors favouring the presence/absence of each species (Luiselli *et al.,* 2000). It was concluded that *K. belliana* was clearly different in terms of habitat requirements, i.e. it was clearly separated from the other two species along the spatial niche axis. Indeed, *K. belliana* used only dry bushlands, and was hence very sporadic in the wet forested study region. On the other hand, the local distribution of *K. erosa* and *K. homeana* overlapped greatly, and the majority of capture sites for *K. erosa* were also capture sites for *K. homeana* (Luiselli *et al.,* 2000). The same pattern of habitat associations was also seen on the same *Kinixys* species in western Cameroon (Lawson, 1993, 2000). Lawson, however, based his conclusions on empirical evidence and not on robust predictive statistics. In both Cameroon and Nigeria, however, there were subtle differences in microhabitats use, with *K. erosa* being more hygrophilous than *K. homeana.* In addition, in both *K. homeana* and *K. erosa* the thermal ecology attributes were similar, and their main thermal need was the avoidance of overheating in tropical environments (Luiselli, 2005). Hence, it appears more than likely that the similar habitat preferences of *K. erosa* and *K. homeana* reflect the need for taking advantage of shady forested environments, with unshaded and open wooded areas being a limiting factor for both species (Luiselli, 2005). Luiselli (2003b) studied the temporal and feeding dimensions of the niche of these two species (*K. homeana* and *K. erosa*), and observed a very high similarity in terms of temporal niche (month-by-month activity intensity, which peaked in both species during the wet season). On the other hand, the two species diverged considerably in terms of feeding habits both in dry and in wet months, although both species were basically omnivorous, taking earthworms, gastropods, arthropods and fungi as usual food types. Indeed, *K. homeana* was much more prey generalist

than *K. erosa,* and appeared to feed more in leaf litter and rotting wood than its potential competitor. In addition, the smaller size of *K. homeana* allowed for an easier coexistence between the two species by a selection of differently sized food (see also Pianka, 1986 for similar cases of desert lizards). Overall, there is a clear niche separation among the three *Kinixys* species, especially along the habitat niche dimension (*K. belliana* versus the other two species), and along the food type and foraging habitat niche dimensions (differences between *K. erosa* and *K. homeana*). In Nigeria as well as in Zimbabwe, the intense predation rates are certainly crucial in regulating tortoise population size. An indirect evidence of the potential existence of some kinds of interspecific competition is also given by the relative density of the two species in syntopic conditions: Luiselli (2003c) observed that *K. homeana* was consistently more abundant than *K. erosa* in six study areas of the Niger Delta where capture-mark-recapture studies were conducted (on average 1.23 specimens/ha versus 0.76 specimens/ha) as well as in general field surveys across the whole southern Nigerian forests, whereas Lawson (1993, 2000) observed exactly the opposite abundance trend for the same species when sympatric in several areas of western Cameroon. Hence, it may be hypothesized that interspecific competition at the local scale may alternatively produce dominance of one species over the other, albeit without extirpation of the locally disfavoured species.

Another well studied study system concerns the sympatric *Testudo* species in Mediterranean Europe (Greece and Turkey) (e.g. see Wright *et al.*, 1988; Willemsen, 1991). In this Mediterranean region there are three species of tortoises (*T. graeca, T. hermanni, T. marginata*) with a broadly parapatric distribution which overlaps at certain areas (Watson, 1962). All these species are herbivorous generalists, which are unlikely to partition the food resources available in the environment. Wright *et al.* (1988) demonstrated that the potential for competition between *T. graeca* and *T. hermanni* is also very low in the sympatric zones because competition is avoided along a space axis. The two species clearly utilized different habitats, with *T. graeca* occupying more open habitats. Indeed, studying the habitat associations of these two species in 12 distinct sites in northeastern Greece and European Turkey, and after selecting 9 types of different habitats (i.e. creating a 12 x 9 data matrix), Wright *et al.* (1988) concluded that *T. graeca* was the only species found in 15 "cells", *T. hermanni* was the only species in 14 "cells", whereas both species occurred together in just 6 "cells" (17% of the total "cells"). Hence, the spatial overlap was certainly very low in this study system. *Testudo hermanni* and *T. marginata* also occupied clearly different habitats in the zones of southern and western Greece where they are sympatric (Watson, 1962; Wright *et al.*, 1988), whereas *T. graeca* and *T. marginata* do not overlap their respective ranges (Wright *et al.*, 1988). Another area where these three species are found to be sympatric is in Sardinia, one of the two larger Italian islands (Puddu *et al.*, 1988). The analysis of the coexistence dynamics of these three tortoises in Sardinia is complicated by the fact that only *T. hermanni* is autochtonous, whereas the other two species have been introduced by humans in the 18th and 19th centuries (Bruno, 1986). Also in Sardinia these species are found in different habitats, but *T. hermanni* is generally much more common than the other two species (Bruno, 1986).

A few species of terrestrial turtles are equally at home on land or in water (e.g., species of the genera *Clemmys* and *Terrapene coahuila,* see Ernst & Barbour, 1989). In these cases, the different frequency in the use of the aquatic habitat seems to be a main spatial niche difference between sympatric species: in a marshy pasture of Pennsylvania (USA) the three species of *Clemmys* clearly subdivided the space based on their "aquatic tendency", with *C. guttata* being the most aquatic, followed by *C. muhlenbergii* and then the almost exclusively terrestrial *C. insculpta* (Ernst & Barbour, 1989).

Overall, my review of the available data indicated that:

(i) As expected from the predictions, most of the terrestrial turtle communities around the world are certainly uninfluenced by interspecific competition dynamics because much of the species diversity of terrestrial turtles reflects geographic replacement of one species by another (Iverson, 1992a, 1992b, 1992c; Hailey & Coulson, 1995): for example, the four species of North American tortoises of the family Testudinidae are strictly allopatric (Lamb *et al.*, 1989).

(ii) In the regions of the world where two or more terrestrial turtles are sympatric, interspecific competition is also of relatively low importance, because the sympatric species tend to partition very clearly the spatial niche (for instance, case of Mediterranean *Testudo;* case of *Kinixys belliana* versus the other two sympatric Nigerian *Kinixys*) or the food axis (cases of Zimbabwean tortoises and of the sympatric Nigerian *Kinixys erosa* and *Kinixys homeana*). These latter patterns may be caused by interspecific competition, but the scarcity of the coexistence areas of terrestrial turtles make hard to state that this phenomenon has been of great relevance for the evolutionary history of these reptiles.

Therefore, I conclude that terrestrial turtles are unusual among reptiles with respect to the un-influence of the competition process for their community ecology. Indeed, in contrast with terrestrial turtles, interspecific competition has been demonstrated to be a very important structuring force for the communities of other ectotherms, including amphibians (Toft, 1985; Barbault, 1987, 1991), lizards (Toft, 1985; Barbault, 1987; Pianka, 1996), and snakes (Luiselli 2003a, 2006). Hence, another important argument to be tested is if the interspecific competition is really less intense among sympatric terrestrial turtles than among sympatric lizards, snakes, or amphibians. This is a testable prediction, which needs a quantitative comparative analysis rather than the simple inferences from the literature review.

IS COMPETITION LESS IMPORTANT IN TERRESTRIAL TURTLE COMMUNITIES THAN IN THE COMMUNITIES OF OTHER ECTOTHERMS (E.G., LIZARDS AND SNAKES)?

Efficient tests of the above question require the study of a given system where there are independent communities of terrestrial turtles, snakes, and lizards, all being characterized by relatively rich assemblages of species. In addition, the comparison of the coexistence patterns of these animals in a same habitat and in a same geographic area may be particularly useful because it can highlights the different responses of the communities of these organisms to similar environmental conditions. Of course, given the very low species diversity of terrestrial turtles (see above), and the potential biases caused by the study of the competitive interactions in two-species systems (e.g., Connell, 1980, 1983, and later literature), it is necessary to use as study cases only communities of terrestrial turtles consisting of at least three sympatric species, and to compare the results of these systems with data from other ectotherm communities (snakes, lizards) from the same study regions. To my knowledge, the only study system that fulfils all these requirements is that of the ectotherm communities in the rainforest-plantation mosaic of southern Nigeria, where detailed community ecology datasets have been published not only on the three sympatric terrestrial turtles of the genus *Kinixys* (see review above), but also on 19 species of snakes (e.g., Luiselli *et al*., 1998, 2005; Luiselli & Akani, 1999), on 3 species of terrestrial lizards (family Scincidae) (Akani *et al*., 2002), and on 4 species of semi-arboreal lizards (family Chamaeleonidae) (Akani *et al*., 2001), all of them being sympatric with the terrestrial turtle species (i.e. living under exactly the same ecological and environmental conditions). All the raw datasets from these studies are fully available in the original papers, but a comparative re-analysis of the data is provided in this paper. For the snake data, the semiaquatic species were removed prior to any analysis because their habitat did not overlap at all with that of the terrestrial turtles.

I used as operative measure of the intensity of interspecific competition for each niche axis (spatial, food, temporal, see Pianka, 1986) the niche overlap formulas, assuming that higher values correspond to higher levels of actual competition (e.g., Schoener, 1974, 1982, 1983). For each community (i.e. of terrestrial turtles, snakes, scincid lizards, and chameleons), matrices of species counts by niche classification category were constructed by using datasets presented in the original papers. Niche overlap was quantified using Pianka's (1973) symmetric equation with values ranging from 0 (no overlap) to 1 (total overlap) (Gotelli & Graves, 1996; Friggens & Brown, 2005). To assess whether the overlap values of the various communities would likely have occurred by chance, the original species utilization matrices were randomised by retaining the original values and then shuffling the placement of those values among resource states (randomisation algorithm 3 of Lawlor, 1980), and for each pair 500 random permutations were generated by the software "Ecosim 700". Niche overlap values were calculated from each of these randomly generated matrices, and species-pair and community-summary statistics were computed (Friggens & Brown, 2005). Actual overlap values were then compared to the distributions of the expected values. At the end of these simulations and actual vs simulated data procedures, if indeed competition is lower in terrestrial turtles, the overlap values for at least one of the three niche axis should be significantly lower than those observed in the other communities of ectotherms (i.e. snakes, lizards, and chameleons).

Monte Carlo simulations versus actual data on spatial niche overlap for terrestrial turtles (Luiselli *et al*., 2000), snakes (Luiselli & Akani, 1999), scincid lizards (Akani *et al*., 2002), and chameleons (Akani *et al*., 2001) showed that the actual overlap values were not generated by chance (at least $P < 0.001$ at Mantel's permutation test for independent distribution of species pairs), and were then comparable directly. As expected, the mean niche overlap values among terrestrial turtles (mean O = 0.169, $n = 3$ comparisons) were significantly lower than those of all other ectotherm categories (scincids, O = 0.909, $n = 3$; chameleons, O = 0.377, $n = 6$; snakes, O = 0.823, $n = 36$) (one-way ANOVA: $F_{3.42} = 11.313$, $P < 0.0001$), and a Tukey's HSD post-hoc

test confirmed that the differences were statistically significant between turtles and scincids ($P = 0.007$), turtles and chameleons ($P = 0.043$), and turtles and snakes ($P < 0.001$), and were also significant between chameleons and scincids ($P = 0.037$) and between chameleons and snakes ($P < 0.01$). The same type of procedure was repeated also along the trophic niche dimension and along the temporal niche dimension. The null hypothesis of overlap values obtained by chance was rejected for all the groups and for both these niche dimensions (at least $P < 0.001$ at Mantel's permutation test). The mean overlap values for both the trophic and the temporal niche dimensions (turtle trophic dimension: mean O = 0.825, $n = 3$, temporal dimension, O = 0.728, $n = 3$; see raw data in Luiselli, 2003b) were not significantly different at one-way ANOVA among terrestrial turtles, scincids (data in Akani *et al*., 2002), chameleons (data in Akani *et al*., 2001), and snakes (data in Luiselli *et al*., 1998) (for both niche axes, at least $P > 0.223$).

These analyses revealed that, inside a well defined and homogenous (hence well comparable) environmental scenario (the tropical forest of Nigeria), the interspecific competition between terrestrial turtles is significantly less intense than that currently occurring among sympatric lizards of two distinct evolutionary clades (scincids and chameleons), and among sympatric snakes, along one of the three niche dimensions (i.e. the spatial niche dimension). These data also confirm trends observed in other regions of the world (e.g., Mediterranean Europe), where the terrestrial turtles clearly subdivided the spatial niche (e.g., Wright *et al*., 1988). Hence, I conclude that the intensity of the interspecific competition is really lower among terrestrial turtles than among the other ectotherm groups, which showed high overlap values along all the niche dimensions.

It will be certainly productive in the next future to perform similar comparisons between competition intensity in terrestrial turtles versus other groups of reptiles in other environmental scenarios other than African tropical forest to verify the robustness of my observations; however, at the current time, we do not have these data available, and we must content ourselves with the indications coming from the Nigerian study system.

REJECTING ALTERNATIVE HYPOTHESES

The results presented in my paper could also be explained by two other alternative hypotheses, one exactly opposite to that presented:

Hypothesis 1. Competition is very important in terrestrial turtle communities, which explains why so few species can occur together (the opposite hypothesis).

Hypothesis 2. Competition has been important in the evolution of terrestrial turtle communities, leading to niche separation so that minimal ecological competition occurs today.

Hypotheses 1 and 2 are hence based on "historical" considerations and hence are potentially difficult to test (and reject). However, I think that hypothesis (1) can be rejected by examining the fossil materials available on extinct terrestrial turtles. Indeed, these reptiles are easily preserved as fossils and sub-fossils compared to other similarly sized vertebrates because of their shell, and then their history is fairly well documented (e.g., Black, 1984; Lane, 1986). However, there is no evidence that in the past their species diversity was higher than nowadays (e.g., Milstead, 1967; Hervet, 2000; Delfino, 2002), especially during the Quaternary when the herpetofauna in general, and the chelonians in particular, experienced an extraordinary evolutionary stasis (e.g., Holman, 1998; Delfino, 2004). Hence, I am led to reject this "historical" hypothesis as explaining the current "low competition" patterns of terrestrial turtles communities. Hypothesis (2), on the other hand, cannot be falsified, as there may be that the low number of sympatric species (also historically) may depend on a past strength of the interspecific competition process.

FUTURE STUDIES

I think that the comparative evidences presented in this study have sufficiently highlighted the main patterns of terrestrial turtle resource partitioning, and the (low) potential for current interspecific competition among members of this group of terrestrial reptiles. However, it is also obvious from the review data presented here that the species/study systems examined up to now are just few, and perhaps they don't provide adequate information out there to generalize as to whether interspecific competition is or is not an important force in communities of terrestrial turtles in general. Also the simulation vs current data studies presented in this paper seems to bring us towards the same general idea of a low importance of interspecific competition in terrestrial turtles, however, also in this case, the study systems are too few to be sure.

My main suggestion for future studies is hence to document interspecific coexistence patterns in more study systems of terrestrial turtles, especially in tropical Asia, where more than three sympatric species can be found at a same site. In addition, there is a strong need of manipulative studies that may allow experimentally testing of the interspecific competition attributes for these animals. These experimental studies, in addition to the descriptive studies of the type already available for terrestrial turtles, will provide very useful data to definitely accept or eventually reject the main views presented in this paper.

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