

BIOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF SOFT TICKS (IXODIDA: ARGASIDAE) AND THEIR IMPACT FOR PREDICTING TICK AND ASSOCIATED DISEASE DISTRIBUTION

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Summary:

As evidence of global changes is accumulating, scientists are challenged to detect distribution changes of vectors, reservoirs and pathogens caused by anthropogenic and/or environmental changes. Statistical and mathematical distribution models are emerging for ixodid hard ticks whereas no prediction has ever been developed for argasid ones. These last organisms remain unknown and under-reported; they differ from hard ticks by many structural, biological and ecological properties, which complicate direct adaptation of hard tick models. However, investigations on bibliographic resources concerning these ticks suggest that distribution modelling based on natural niche concept and using environmental factors especially climate is also possible, bearing in mind the scale of prediction and their specificities including their nidicolous lifestyle, an indiscriminate host feeding and a short bloodmeal duration, as well as a flexible development cycle through diapause periods.

KEY WORDS : Argasidae, soft tick, *Ornithodoros*, biology, ecology, geographical distribution, natural niche, predictive modelling

Résumé : CARACTÉRISTIQUES BIOLOGIQUES ET ÉCOLOGIQUES DES TIQUES MOLLES (IXODIDA: ARGASIDAE) ET IMPLICATIONS QUANT À LA PREDICTION DE LEUR DISTRIBUTION ET DES MALADIES ASSOCIÉES

Dès lors que des preuves du changement global s'accumulent, les scientifiques se doivent de détecter les changements de distribution de vecteurs, de réservoirs et de pathogènes causés par des modifications anthropogéniques ou environnementales. Alors que des modèles de distribution statistiques ou mathématiques, commencent à émerger pour les tiques dures (ixodidés), aucune prédiction n'est disponible pour les tiques molles (argasidés). Ces organismes restent inconnus et sous-estimés; ils diffèrent des tiques dures par leurs propriétés structurales, biologiques et écologiques, qui compliquent la simple adaptation de modèles initialement développés pour les tiques dures. Toutefois, l'étude des données bibliographiques concernant ces tiques suggère qu'il est possible de prédire leur distribution basée sur le concept de niche naturelle en fonction de variables environnementales essentiellement climatiques. Il est alors nécessaire de choisir correctement l'échelle d'étude et de considérer leurs spécificités incluant leur statut nidicole, leur opportunisme pour les hôtes et la faible durée de gorgement sur hôte, ainsi que la flexibilité du cycle de développement par l'entrée en diapause.

MOTS CLÉS : Argasidae, tique molle, *Ornithodoros*, biologie, écologie, distribution géographique, niche naturelle, modélisation prédictive.

INTRODUCTION

Argasid (or soft) ticks differ from ixodid (or hard) ticks by many structural, biological and ecological properties. They lack a dorsal scutum in adult and nymphal stages as the most discriminating morphological feature and always exhibit a nidicolous to endophilous lifestyle as their major ecological attribute (Pospelova-Shtrom, 1969). Their specialization to sheltered microhabitats and their characteristic short blood feeding duration usually hides their presence such that their role in human and animal health is generally ignored (Hoogstraal, 1985). However, they can cause toxicosis, paralysis, irritation, allergies and exsanguination, and can play an important role as vec-

tors and reservoirs of pathogens (Jonjegan & Uilenberg, 2004). Illustrations of the diseases transmitted by soft ticks include: 1) human tick-borne relapsing fever (TBRF) transmitted worldwide by *Ornithodoros* ticks and caused by spirochetes of the genus *Borrelia*, 2) viral encephalitis transmitted by ticks infesting seabirds, shore birds and roosting birds, 3) the african swine fever virus (ASFV) transmitted by *O. moubata* and *O. porcinus* in Africa, 4) fowl spirochetosis or anaplasmosis-like infections caused by *B. anserina* and *Aegyptianella pullorum*, respectively, and transmitted by *Argas persicus* worldwide, and 5) epizootic bovine abortion caused by *B. coriacea* and transmitted by *O. coriaceus* in North America. Argasid ticks of recognized medical and veterinary importance typically belong to the genera *Argas*, *Ornithodoros* and *Otobius* (Jonjegan & Uilenberg, 2004). As evidence of global climate change accumulates (Intergovernmental Panel on Climate Change, synthesis report, 2007: <http://www.ipcc.ch/ipccreports/ar4-syr.htm>), so does recognition of its potential consequences for human and animal health. Scientists are challenged to

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detect changes in the distribution of vectors, reservoirs and pathogens, and to attribute these shifts to anthropogenic and/or environmental changes (McMichael *et al.*, 2006). As a consequence, it is essential to reveal any of biological and ecological characteristics of soft ticks, in contrast to those of the ixodid line, to understand their peculiar distribution patterns and habitat preferences and their specific role as parasites, vectors and pathogen reservoirs (Hoogstraal, 1985; Sonenshine, 1993).

The present paper aims *i)* to review such characteristics of soft ticks, with a special emphasis on the genus *Ornithodoros*; *ii)* to present their epidemiological impact in terms of risk for tick and associated disease distribution; and *iii)* to propose new research priorities to improve model predictions on changes in the distribution of soft ticks and tick-borne diseases.

BIOLOGICAL AND ECOLOGICAL CHARACTERISTICS OF SOFT TICKS

NIDICOLOUS LIFESTYLE

The peculiar nature of oilskin and cement components of argasid ticks' cuticle makes it highly resistant and reduces water evaporation, allo-

wing soft ticks to survive at high temperatures and under relatively dry conditions (Lees, 1947). For example, *O. moubata* and *O. savignyi* tolerate air temperature up to 63 °C and 75 °C, respectively (Morel, 1969). This phenomenon results in the common presence of soft ticks in tropical and subtropical zones and their spread into arid areas of Central Asia and Africa (Sahara) (Morel, 1969).

However, the success of their developmental cycle depends on cooler conditions, which are provided by the sheltered microhabitats they colonize. Most argasid ticks are nidicolous living in the nests, burrows, and caves of vertebrate animals or in human and livestock habitations, where they survive in cracks, crevices, under rock ledges, among nest fibres, or in sandy, rocky, or dusty ground surface (Sonenshine, 1993). Some, known as endophilous nidicoles like many *Ornithodoros* tick species (Figs 1A, B, C, D) live inside these microhabitats while geophilous nidicoles prefer harborage nearby host habitations. In addition to intrinsic microclimatic conditions of shelters, body heat and moisture from the respiration and excrement of the host within the microhabitat help establish the atmospheric conditions required for the development of these ticks (Sonenshine, 1993). Soft ticks show strict, narrowly defined temperature and humidity tol-

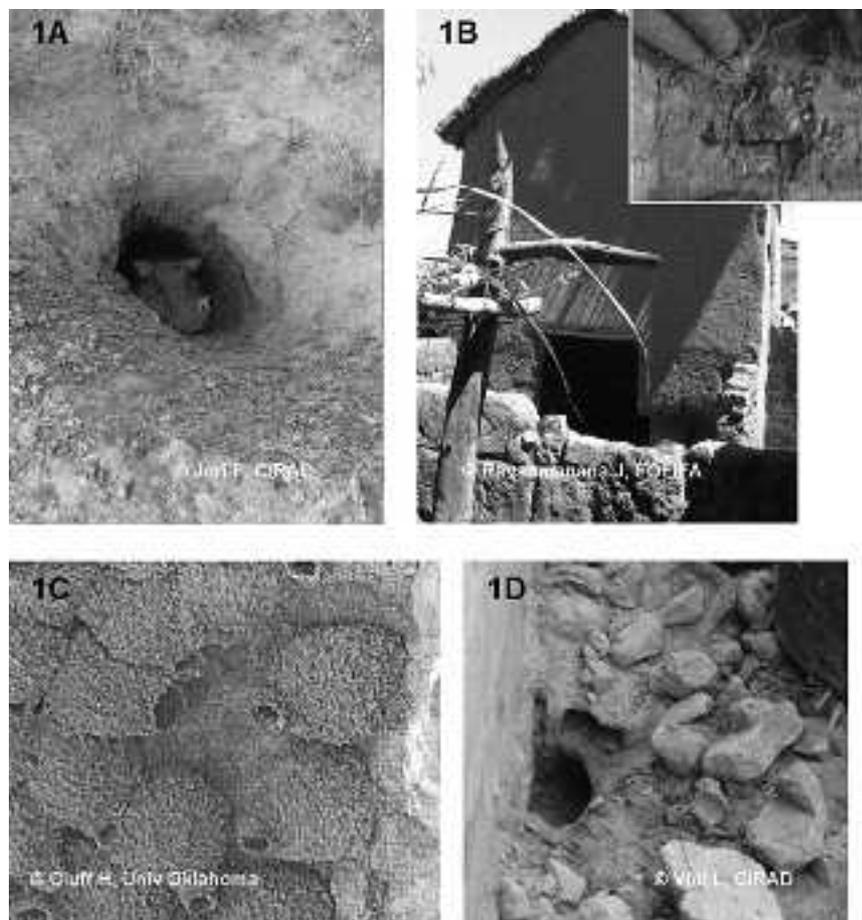


Fig. 1. – Examples of typical microhabitats for endophilous *Ornithodoros* soft ticks, including (1A) warthog burrows infested by *O. moubata* spp. in Mozambique, (1B) crevices colonized by *O. porcinus domesticus* and opening inside human and pig buildings in Madagascar, (1C) mud nests of rocky cliff swallows inhabited by *O. concanensis* in the United-States, or (1D) rodent burrows infested by *O. sonrai* and opening inside human houses in Senegal.

rances for development and activity, reflecting the conditions of their microhabitat. These optima are distinct for closely related species and may be so specific as to be included in the species definition (Morel 1969).

DEVELOPMENTAL CYCLE

In contrast to ixodid ticks, soft ticks present many nymphal instars (2-8) between the larval and adult stages (Fig. 2). Each immature stage requires at least one bloodmeal on a vertebrate host prior to moulting, except larvae of some *Ornithodoros* species like *O. moubata* (Fig. 2). The number of nymphal moults varies from two to nine according to species; the quality and the amount of blood ingested also influence this number (Morel, 1969). When emerging, soft tick adults are long-lived, with a maximum life span as great as 25 years for some species (Sonenshine, 1993), and are able to feed several times when hosts are available (1-10) (Morel, 1969). In argasid females, each bloodmeal is generally followed by egg laying, with or without a previous copulation because females are able to retain sperms within endospermatophores (Fig. 2). Compared to hard ticks, soft tick clutches are small (5-500) but, a given female can produce from two to five clutches over her lifetime. This iteroparous strategy could be seen as an adaptation to host scarcity and/or climatic variability; however, even with multiple clutches, soft ticks never achieve the amount of eggs produced by some ixodid ticks (Morel, 1969).

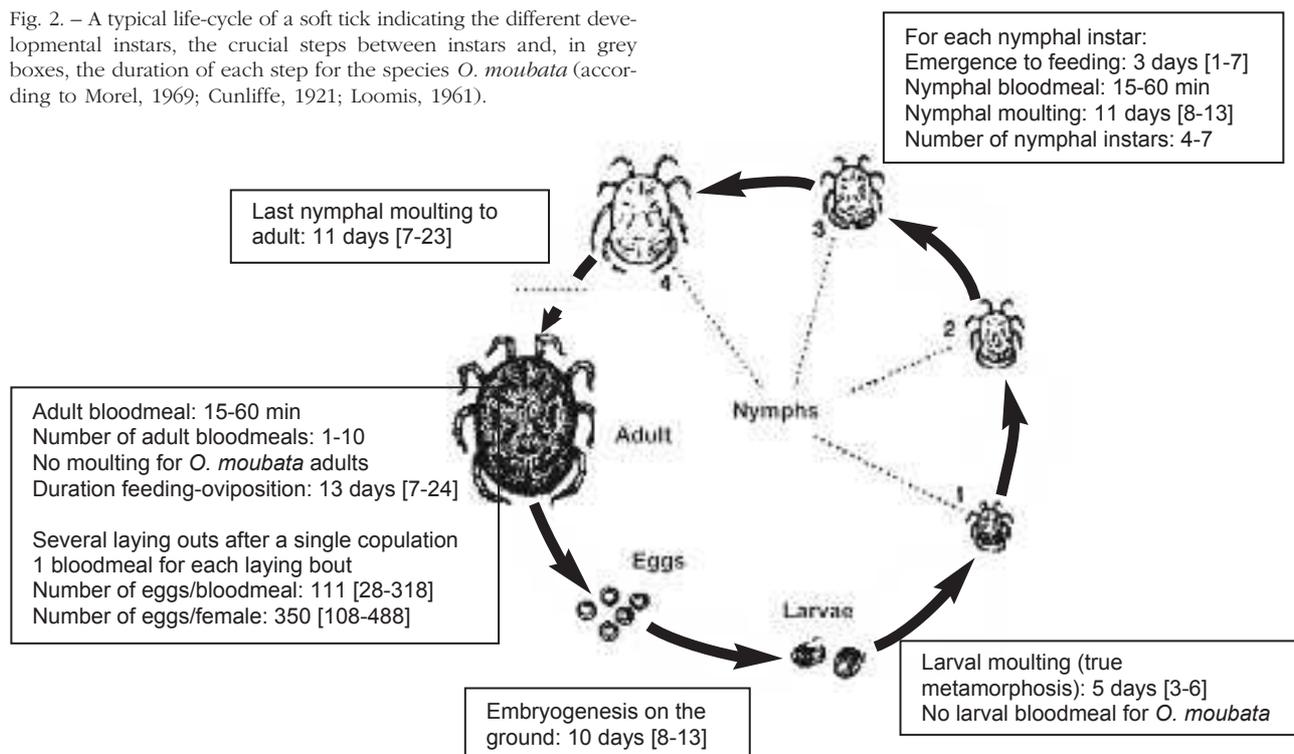
Regarding this aspect, as well as the multiplicity of nymphal instars, the life-cycle of a soft tick could be

considered less efficient than that of a hard tick. However, its total duration may be optimized thanks to short pre- and post-feeding delays, as well as short moulting periods and rapid feeding (see below). Set apart from possible interrupted seasonal development, *Argas persicus* or *Otobius megnini* showing only 2-3 nymphal instars complete their development in 49-118 days, whereas more *O. moubata* and *O. porcinus*, with 4-7 nymphal instars require 76-155 days. Developmental cycles of 80-120 days for one-host hard ticks like *Boophilus microplus* or of 80-300 days for three-host hard ticks like *Dermacentor andersoni* or *Amblyomma americanum* are usually reported (Loomis, 1961; Morel, 1969). Regardless of interspecific variability, the global duration and success of the developmental cycle of soft ticks depend on the efficiency of blood feeding and on climatic conditions. High to significantly high effects of temperature and humidity are noticed on mean egg incubation period and hatching success, larval and nymphal prefeeding/premoulting durations and adult preoviposition/oviposition duration (Cunliffe, 1921; Wheeler, 1943; Loomis, 1961; Hafez *et al.*, 1971; Balashov, 1972; El Shoura, 1987; Endris *et al.*, 1991; Olmedo *et al.*, 1995).

BLOOD FEEDING

A major characteristic of soft ticks is the short duration of bloodmeal, particularly for nymphs and adults (15-60 minutes). The duration is typically longer for larvae (12 hours to several days) (Fig. 2). This feature

Fig. 2. – A typical life-cycle of a soft tick indicating the different developmental instars, the crucial steps between instars and, in grey boxes, the duration of each step for the species *O. moubata* (according to Morel, 1969; Cunliffe, 1921; Loomis, 1961).



may be seen as an adaptation to their nidicolous lifestyle; they reduce possible exposure to unfavourable external conditions by detaching rapidly from their vertebrate hosts before these hosts leave the microhabitat in search of food or a sexual partner (Sonenshine, 1993). Soft ticks have developed physiological strategies to favour such rapid blood feeding, including high tegument distension during blood feeding and excretion of excess water and ions via coxal glands as soon as blood is ingested or just after detachment (Hoogstraal, 1985). Many pathogens maintained in soft tick reservoirs like *Borrelia* or ASFV are excreted in coxal fluid, which increases their transmission capacity through tick-to-tick transfers (Gaber *et al.*, 1984; Kleiboeker *et al.*, 1998).

Soft ticks are commonly polyphagous, that is changing host for each bloodmeal, except for some species like *Ot. megnini* where larvae and nymphs engorge and moult on the same ungulate (Morel, 1969). Argasid ticks seem to exhibit varying degrees of host preference, ranging from strict specificity, as for certain bat-parasitizing tick species of the genera *Ornithodoros*, *Antricola*, *Nothoaspis*, *Carios*, *Chiropterargas* or *Secretargas*, to little or no described specificity for burrow-inhabiting endophilous *Ornithodoros* species (Sonenshine, 1993). Indeed, it has been suggested that most soft ticks actually show indiscriminate host feeding and that apparent variation in host preference likely reflects microhabitat preference and host availability within the microhabitat (Morel, 1969). As a consequence of their nidicolous lifestyle, soft ticks may simply choose hosts that are directly available in their favourable microhabitat, resulting in an apparent selection of small vertebrate hosts, domestic livestock and humans. However, host preferences are difficult to investigate in soft ticks because they feed rapidly and are thus difficult to find on the host; only PCR amplification of host genes within tick midgut may allow us to detect such relationships (Kent, 2009).

Indiscriminate host feeding was clearly demonstrated for some *Ornithodoros* tick species, including: *i*) *O. tartakovskyi* transmitting TBRF in Central Asia and able to feed on terrapin, skink, agama, gecko, sand snake, toad, hedgehog, dog, mouse, bee-eater, roller and sparrow (Vasil'eva, 1971); *ii*) *O. verrucosus* and *O. alactagalis* in Soviet Georgia that feed on tortoise, snake, toad, burrow-inhabiting bird, fox and bird, rodent, fox, respectively (Gughusvili 1980); *iii*) *O. sonrai* in Senegal, which is able to feed on many rodent and insectivore species that are naturally infected by TBRF (Trape *et al.*, 1996) and which occasionally feeds on pigs living close to small mammal burrows and is thus contaminated by ASFV (Vial *et al.*, 2007), *iv*) *O. moubata* spp. transmitting TBRF in Tanzania that is able to feed on pigs and chickens, and which has been

recently found infected by *B. duttonii* in a region where no animal reservoir is known (McCall *et al.*, 2007).

SEASONAL POPULATION DYNAMICS

As a possible adaptation to a nidicolous lifestyle and host scarcity, argasid ticks, especially adults, are very resistant to starvation for several years and are able to enter a quiescent phase for two to eight months (Morel, 1969). Seasonal morphogenetic diapause is usually correlated to host availability and delays developmental activity such that the expansion of the tick population is optimized during the seasonal period when hosts are present (Sonenshine, 1993). However, host seeking activity is not directly affected by this diapause. For example, *O. kelleyi* feeds seasonally during the spring on bats returning from winter caves to abandoned buildings or cracks infested by ticks; these ticks, collected in winter when bats are absent, feed readily when offered these hosts in laboratory (Sonenshine & Anastos, 1960). In Egypt, *A. arboreus* infesting the nests of herons and other roosting birds delays oviposition until the following spring when it feeds during the fall, but oviposits without delay when it feeds in July (Khalil, 1974; Khalil & Shanbaky, 1976). Conversely, soft ticks infesting nest or burrows of non-migratory hosts are not considered to exhibit seasonal activity, especially when they are indiscriminate feeders (Sonenshine, 1993). In many cases, this may be due to the fact that these ticks inhabit microhabitats where climatic conditions are buffered all along the year (Sonenshine, 1993). However, diapause remains an inherent attribute of the biology of many nidicolous ticks and seasonal climate changes can impact feeding activity and the consequent reproductive and developmental cycle (Morel, 1969). Nevertheless, such patterns are most often observed at the geographic limits of the species' distribution, in temperate or sub-Saharan areas where ticks carry out feeding or ovipositional diapause during winter or dry season, and not at the center of the distribution in tropical or subtropical areas. For example, *O. tholozani* from Central Asia does not feed on cattle during winter and shows a diapause of six months, while the same species is active during the whole year in Israel (Moskvin, 1927; Avivi, 1967). Similar observations have been reported in Spain for *O. erraticus* that does not feed on its common pig host until pigpens reach a temperature of 13-15 °C (Oleaga-Perez *et al.*, 1990). In Egypt, the same species (actually its small variant *O. sonrai*) inhabiting rodent burrows shows the highest densities of adults during the summer and early fall and the lowest during the winter months, suggesting a seasonal decline in successful feeding and moulting. The rodent hosts in this area have been found in burrows throughout the year (Khalil *et al.*, 1984).

PREDICTIONS ON SOFT TICK AND DISEASE DISTRIBUTION

THE CONCEPT OF THE NATURAL NICHE

Predictions of vector and vector-borne disease occurrence are based on two major concepts: 1) the natural nidity of transmissible diseases meaning that, independent of humans, infectious diseases exist in nature under a combination of local conditions and in the presence of vertebrates and arthropods that act as vectors and/or reservoirs of the pathogenic agent (Pavlovsky, 1966), and 2) the fundamental ecological niche of a species, defined as a set of environmental conditions within which a species can survive and persist. This niche consists of an “n-dimensional hypervolume” that determines suitable habitat for the species but is distinct from the distribution of the species plotted in the geographical space (Hutchinson, 1957). Under the first concept, and provided strict assumptions on disease transmission dynamics, it is possible to approximate disease distribution using some indices, such as those based on vector presence and/or abundance. According to the second concept, such potential vector presence and/or abundance should be predicted instead of being described, in order to extend predictions into non sampled areas or future periods. This method uses habitat suitability based on favourable or tolerable environmental conditions for a species survival, development and dynamics.

RELEVANT CHARACTERISTICS OF SOFT TICKS TO PREDICT THEIR NICHE

Considering the peculiar biology and ecology of argasid ticks, it seems difficult to adapt predictions of suitable habitats for hard ticks to soft ticks. The major feature that often discriminates these groups of organisms in relation to their environment is the nidicolous life-style of argasid ticks. These ticks, especially endophilous ones, are limited to specialized niches and have developed well-adapted life history traits that insure their persistence in their microhabitat. For example, the short blood feeding period for nymphs and adults may result in low dispersal capacity, or at least “step by step” dispersion, and thus in a more limited distribution of soft tick species and their associated pathogens (Sonenshine, 1993). Such patterns have been illustrated by different field and experimental studies: *i*) in Madagascar, *O. p. domesticus* was present over an eight year period (2000-2008) at the same pig barn, but was absent in neighbouring farms at both sampling occasions (Ravaomanana, personal communication). Natural infection by ASFV was still detectable in ticks in 2008 whereas no potentially infected pig had been

introduced to the barns since 2004 (Vial, personal communication); *ii*) in Senegal, *O. sonrai* was present in 1991 and 2002 in same human buildings of Dielmo village, and corresponded to two permanently positive clusters of disease transmission (significantly more TBRF cases detected in humans throughout the study period) (Vial, 2005; Vial *et al.*, 2006a); *iii*) for *O. tartakovskyi* ranging from Turkmenia to Kazakhstan and *O. erraticus* with its large variant in North Africa and its small one in West Africa (renamed *O. sonrai*), a positive correlation has been obtained between decreased fertility or complete sterility and the geographical distance between cross-bred tick populations (Chabaud, 1954; Balashov, 1971), suggesting low or insignificant gene flow between natural populations within a described species range.

Being nidicolous, especially endophilous, consists of adding an intermediate environmental layer between the external conditions outside the microhabitat, readily measurable and commonly used for species distribution models (*e.g.* air temperature, air humidity and evaporation, sunshine, wind, altitude, hydrography, landscape and land use), and the internal conditions of the microhabitat that directly influence soft tick survival, development and dynamics (*e.g.* temperature, moisture, darkness, host presence). Internal conditions depend on external ones, but the specific organization of the microhabitat and the structure of the intermediate layer (*e.g.* depth and width of the opening, nature and size grading of soil, etc.) buffer outside conditions. This buffering effect should be taken into account for soft tick distribution models. For instance, a few studies have investigated the relationships between the internal and external conditions of different microhabitats inhabited by endophilous ticks or closely-related arthropods, but it is already possible to extract some general patterns (Table D). Niche temperature and relative humidity usually show lower amplitude than outside air conditions, determining the lower and upper limits of optimal conditions for tick survival and development. According to the spatial scale considered, the influence of landscape, hydrography and anthropogenic activities on the organisation of the microhabitat and the structure of the intermediate layer will be more or less important for predictions. At regional scale, as for hard ticks, it is possible to consider that most distribution patterns can be extracted from climatic conditions (Cumming, 2002), except at range margins where the presence of rivers or mountains may change the microclimate and allow the presence of soft ticks in seemingly unsuitable habitats. Conversely, at local scale, differences in the distributional patterns may depend mainly on pedology, hydrography, landscape composition or organization, and vegetation. For example, *Ornithodoros* species belonging to the now obsolete group *Theriodoros* Pospelova-Shtrom 1953, are located in dif-

Authors	Climatic zone	Microhabitat	Arthropod species	Temperature and humidity relationships
Pospelova-Shtrom, 1953	Temperate continental climate (Turkmenistan)	Gerbil burrow	<i>O. tartakovskyi</i>	In summer: $T_{int} \approx \text{Mean or Max}T_{ext} < 26\text{ }^{\circ}\text{C}$ $\text{MaxRH}_{int} \approx \text{MaxRH}_{ext}$ $\text{MinRH}_{int} > 70\%$
		Cave (fox den)	<i>O. verrucosus</i>	Similar moisture deficit but with lower amplitude inside microhabitat
Avivi, 1967	Temperate mediterranean climate (Israël)	Sand-stone caves	<i>O. tholozani</i>	In summer: $T_{int} \approx \text{Max}T_{ext} - [19-20] < 26\text{ }^{\circ}\text{C}$ $\text{MaxRH}_{int} \approx \text{MaxRH}_{ext}$ $\text{MinRH}_{int} > 60\%$ In winter: $T_{int} \approx \text{Min}T_{ext} + [3-4]$ $\text{MaxRH}_{int} \approx \text{MaxRH}_{ext}$ $\text{MinRH}_{int} \approx \text{MinRH}_{ext}$
Butler <i>et al.</i> , 1984	Temperate to subtropical oceanic climate (Florida)	Gopher-tortoise burrow	<i>O. turicata</i>	$T_{int} \approx T_{ext} - [4-7] < 25\text{ }^{\circ}\text{C}$ $\text{RH}_{int} \approx \text{MeanRH}_{ext} + [40-55] > 8\%$
Yunker & Guirgis, 1970	Sub-saharan desert or semi-desert (Egypt)	Gerbil burrow	<i>Hyalomma</i> spp.	In summer: $T_{int} \approx \text{Max}T_{ext} < 30\text{ }^{\circ}\text{C}$ $\text{RH}_{int} \approx \text{MeanRH}_{ext} + [30-60] > 80\%$ In winter: $T_{int} \approx \text{Min}T_{ext} < 15\text{ }^{\circ}\text{C}$ $\text{RH}_{int} \approx \text{MeanRH}_{ext} + [30-60] > 80\%$
Heger <i>et al.</i> , 2006	Sub-tropical to tropical climate (Venezuela)	Wall crack of human houses	<i>Rodnius prolixus</i>	$T_{int} \approx \text{Mean}T_{ext}$ $\text{Ampl } T_{int} \ll \text{Ampl } T_{ext}$ Similar moisture deficit but with lower amplitude inside microhabitat

Table I. – Mathematical relationships (extracted from various studies) linking internal and external temperature and humidity of varied microhabitats inhabited by different endophilous tick species, or closely-related arthropods, in distinct climatic zones.

ferent continents but within the same eco-climatic region showing continental or Mediterranean temperate to sub-tropical climates and vegetation characterized by low grasslands, steppes and semi-deserts (Morel, 1969). All of these species likely colonize rodent or reptile burrows and are directly in contact with soil, which highly depends on the external climate. However, one of these species *O. sonrai* (formerly *O. erraticus* small variant) is present in Egypt, despite the fact that global temperature and humidity in most areas of the country seem unsuitable for its survival and development; its presence is mainly due to an equilibrium of sufficiently dry areas and proximity to a water source (the Nile Valley or local oases) that maintains a minimum relative soil humidity inside microhabitats (Hoogstraal *et al.*, 1954). At local scale, pedology is responsible of local heterogeneity, with a high infestation of burrows composed by silt, silt-sand or sand-clay soil and a complete absence of *O. sonrai* from pure sand situations, even when open to humid sea or river breezes, as well as wet ground of extremely saline areas (Hoogstraal *et al.*, 1954).

Finally, regarding the common indiscriminate host preference lifestyle of many soft ticks, host availability seems to be less important to predict their geographical

distribution than for hard tick species. However, at local scale, the nature of the host community may act as an evolutionary driver of tick populations. For example, three genetically distinct tick populations have been detected within the distribution range of *O. sonrai* in Senegal, Mali and Mauritania, using PCR amplifications of the 16S rDNA gene (Vial *et al.*, 2006b). Although no cause has been clearly identified, the geographical distribution of these three clusters apparently corresponded to rodent community zoning, with a predominance of Gerbillinae species associated with group 3 in northern Saharan to Sahelo-Sudanan regions, a predominance of Murinae species associated with group 1 in south-western Senegal, and the presence of *Mus musculus* in Richard-Toll associated with group 2 (Duplantier *et al.*, 1997).

CURRENT ADVANCES FOR PREDICTING SOFT TICK DISTRIBUTION

For now, no distributional model has been developed for any argasid tick. The only reference for soft ticks is from Cumming & Van Vuuren (2006) who modelled continental changes of geographical range for 73 African tick species, dealing with *O. moubata* and *Ot. megnini* in the same way as for hard ticks. While results seemed

conclusive for *Ot. megnini* that shows life history traits close to exophilous hard ticks, the model could not explain the high variability of *O. moubata* presence data, suggesting an influence of other, still unidentified, environmental factors acting on its distribution. Presence data are available for many species from past field studies and could be used for modelling or as preliminary assessments of soft tick distributions. For example, Morel (1969) devoted part of his career to recording the results of hard and soft tick sampling conducted by various scientists in Africa and Mediterranean Basin starting at the beginning of the twentieth century. For each record, he specified the location, date, host or habitat, stages and verified the identification by observing original specimens if available. These data are available on a CDrom published by CIRAD in 2003 and an example application of this data is given in Figure 3. More recently, the Integrated Consortium on Ticks and Tick-borne Diseases (ICTTD) (<http://www.icttd.nl/>) proposed to produce and update a worldwide tick presence database associating each record with GPS coordinates and Cumming has already published some

data for African ticks (<http://www.wec.ufl.edu/faculty/cummingg/TickDiP.htm>). However, such data may show some biases: *i*) they essentially correspond to historical data from the 1930s to the 1960s when many field collection campaigns were organized. Since this time distribution patterns may have changed; *ii*) they may show a bias in sampling because information comes from distinct collectors using different protocols and techniques and samplings may have been done in accessible areas only, for example along the main roads, which is not representative of realized distribution; *iii*) they only correspond to presence data because some scientists did not document absences or because records come from museum collections where only specimens that were found are stored; *iv*) they are subjected to misidentification according to the expertise and the sense of responsibility of the collector and because of complexity and ambiguity of the morphological keys used at this period for tick identification. Other available resources on soft tick biology and ecology can be obtained through: *i*) field observations of habitat/microhabitat preferences or the seasonal dyna-

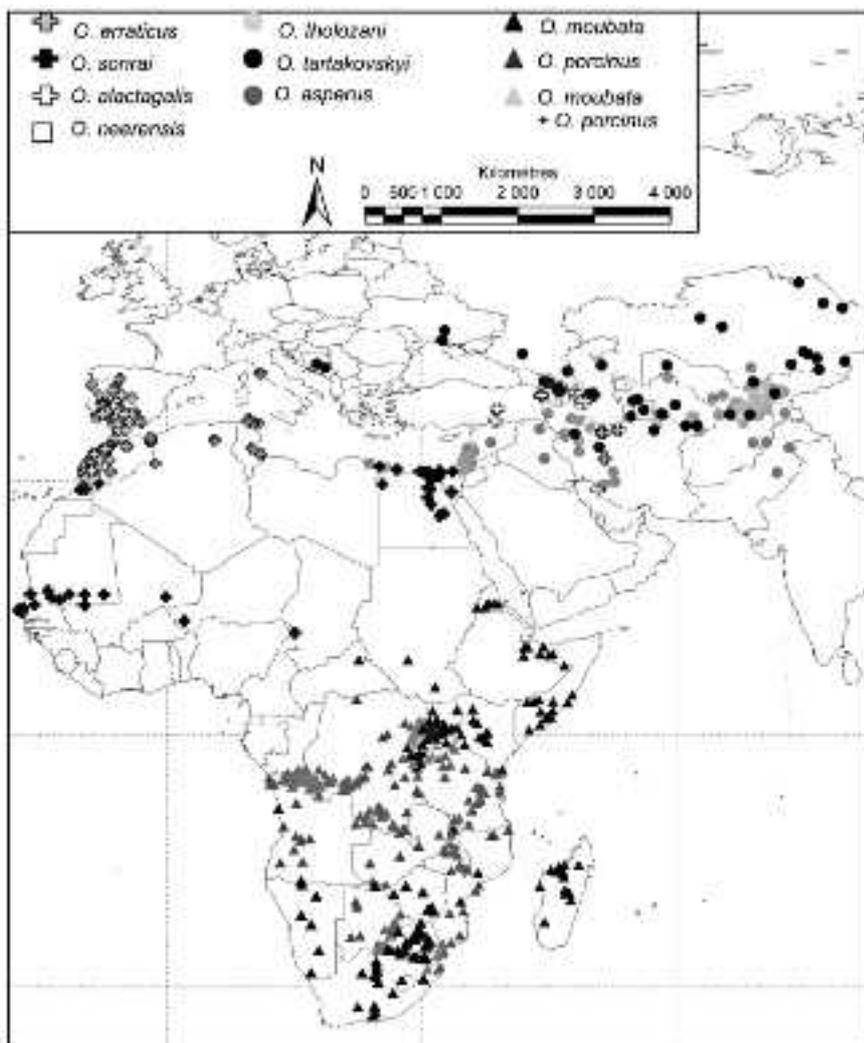


Fig. 3. – Geographical location of Morel's presence data for several species of *Ornithodoros* ticks transmitting TBRF and/or ASFV in Eurasia and Africa. 1052 records were reported and 865 were geographically localized using the US Army Gazeeter (<http://tomcat-dmaweb1.jrc.it/fuzzyg/query/>).

mics of tick populations; and *ii*) laboratory experiments investigating the influence of climatic conditions (*e.g.* temperature, humidity and sunshine) on survival, life cycle and feeding success. Such data may be useful, as a preliminary approach, to predict the possible relationship between geographical range of soft ticks and some environmental factor. For example, the African subgenus *Ornithodoros sensu stricto* Koch 1944 was highly documented in the 1960s by Walton who clearly demonstrated that *O. moubata* consisted of a complex of species and subspecies, each showing distinct morphological, biological and ecological features (Walton, 1979). His 20 years of intensive research on TBRF in East Africa provided new insights on *O. p. domesticus*, suggesting the existence of at least four different ecological “races” locally adapted to different regions and presenting distinct temperature and humidity optima (Walton, 1962, 1964, 1979). During the same period, Pierce (1974) investigated *O. p. porcinus* distributional patterns according to climate, soil, vegetation, host and season. Within the same subgenus, the biology of *O. moubata sensu stricto* from Southern Africa was investigated in the laboratory by Cunliffe (1921), Jobling (1925) and Loomis (1961) according to temperature and humidity conditions. The subgenus *Theriodoros* Pospelova-Shtrom 1950 was studied both in Central Asia and Middle East, for the group *Pavlovskyella* Pospelova-Shtrom 1953, and in Africa and the Mediterranean Basin for the group *Theriodoros sensu stricto* Pospelova-Shtrom 1953. Within the first group, the biology of *O. tholozani* was well-documented (Desportes & Campana, 1946; Balashov, 1972), with a special emphasis on favourable microclimatic conditions for its settlement in Israel and Russian regions, and anthropogenic effects in domestic areas (Avivi, 1967; Vasil'eva *et al.*, 1991; Abidov *et al.*, 1993). Within the second group, Baltazard *et al.* (1950), Blanc *et al.* (1951) and Chabaud (1954) have investigated differences in morphology, biology, ecology and vectorial competence between *O. erraticus* and *O. sonrai*. Boiron (1949) in Senegal, Hoogstraal (1954) and Khalil *et al.* (1984) in Egypt and more recently Oleaga-Perez *et al.* (1990) in Spain studied the effect of climate, soil and host on the settlement patterns in these species in both domestic and wild areas. Recent advances have also been provided by El Shoura (1987) under laboratory conditions. Table II gives an example of optimal and critical climatic conditions defined for several *Ornithodoros* tick species using these bibliographic resources. As for presence data, information is mainly lacking for American species, with the exception of studies published by Butler (1984), Beck *et al.* (1986), Adeyeye & Butler (1989), Adeyeye & Phillips (1996) and Phillips & Adeyeye (1996) for *O. turicata*.

PERSPECTIVES FOR SOFT TICK AND DISEASE MODELLING

As a first approach for soft ticks, it would be possible to use available presence data in pattern-matching (or

statistical or associative) models. These models match observed distributions to various current environment variables in a statistical framework and apply spatial or temporal projected changes in environmental variables, especially climate, to the distribution by interpolation or extrapolation (Kitron & Mannelli, 1994). Bearing in mind the potential biases of presence datasets, such models enable one to predict a species' range without knowing how each biological parameter is affected by the environment and are easily adapted to risk mapping (Rogers & Randolph, 2006). However, bibliographic resources on soft ticks remain essential to assess the ecological significance of such models. Another preliminary approach would be to directly use resources on soft tick biology and ecology under specific environmental constraints to implement distribution models. Because available data on soft ticks are heterogeneous according to tick species and the environmental impact of conditions on soft tick survival, development and dynamics are only partially documented, an alternative would be the use of intermediate approaches like fuzzy knowledge-based models (Zadeh, 1965). This approach has been developed for artificial intelligence techniques and is emerging in ecology for predicting species distributional ranges and population dynamics (Bock & Salski, 1998; Kampichler *et al.*, 2000; Mackinson, 2000; Adriaenssens *et al.*, 2006). It is based on expert or bibliographic knowledge that is represented by a set of logic linguistic rules in the form: IF <premise> THEN <conclusion>, which can be interpreted as a linguistic description of the relationship between environmental conditions and species survival, development or dynamics. The selection of definitive reliable linguistic terms to input into the model is obtained by their combination, according to common optima and/or limits, obvious interactions between terms and the choice of the most important variables by experts. Available soft tick presence data is then only useful to validate the predictive results of the model. Such a method presents many advantages: *i*) it does not suffer from the same biases as presence data; *ii*) it is based on biological and ecological assertions insuring meaningful predictions; *iii*) it seems less restrictive than pattern-matching models and enables one to predict potential invasions and adaptations; *iv*) it is very malleable with any possible logic rules and any mathematical combinations of rules; *v*) it seems optimal to rapidly produce preliminary risk maps for decision makers. However, it may suffer from expert subjectivity and the reliability of bibliographic data. For instance, both methods are currently being tested on *Ornithodoros* datasets extracted from Morel's publications and the ICTTD database (Vial, personal communication).

In the future, investigations on soft ticks should focus on dynamic approaches instead of static ones, using process-based (or mechanistic or biological) models,

Species/subsp.	Optima inside microhabitat		Critical inside microhabitat		Possible diapause	Life-cycle (days) for optimum conditions		Field data distribution	Field data microhabitat
	T (°C)	RH (%)	T (°C)	RH (%)		Min	Max		
<i>O. moubata</i>	(25 [22-32])	50 [50-60]	Min: 5-8 Max: 37	Max: 80	?	36 (3-4NN)	113	Rain < 500 mm No altitude	Warthog burrows/dry cracks in houses
<i>O. p. porcinus</i>	(25 [24-25])	83 [77-83]	?	Min?	Supposed in dry season june-sept			Rain < 900-1,000 mm Rain < 1,250-1,500 mm No altitude	Warthog burrows
<i>O. p. domesticus</i> (race 1)	22 [17-26]	92 [72-96]		Min?				Alt > 1,500 m Alt < 2,100-3,000 m Highlands	Houses
<i>Opd</i> (race 2)	24 [20-27]	62 [50-96]	?					1,200 < Alt < 1,500 m Moderate altitude	Houses and fowl buildings
<i>Opd</i> (race 3)	23 [22-24]	52 [50-55]		Max?				Alt > 1,000 m Moderate altitude	
<i>Opd</i> (race 4)	26 [20-31]	77 [67-96]		Min?				Sea level	Fowl buildings
<i>O. erraticus</i>	30 [25-35]	90 [75-95]	Min: 10 Max: 43	Min: 15 Max?	If T _{ext} too low (13-15 °C) 4-5 months	51	158	50 < Rain < 750 mm No altitude	Rodent burrows/humid cracks or burrows in houses
<i>O. tholozani</i>	25 [16-29]	75 [70-80]	Min: 5	Min: 34 Max: 90	If T _{ext} too low (5-8 °C) 6 months	157	184	250 < Rain < 500 mm	Caves and lairs/human and herd shelters
<i>O. tartakowskyi</i>	25 [16-29]	75 [70-80]	Min: 0	Max: 90	?	80	95	100 < Rain < 300 mm Higher T amplitude T _{annual} > 17 °C	Reptile and small mammal burrows
<i>O. asperus</i>	16 [15-18]	90 [80-100]	Min: 10	Min?	If T _{ext} too low (oct-june) 8 months	153	260	Rain mean: 350 mm rain max > 500 mm low T amplitude altitude	Caves or reptile small mammal burrows

Table II. – Optimal and critical conditions for the survival and development of species from the subgenus *Ornithodoros* sensu stricto Koch 1944 and *Theiridodoros* Pospelova-Shtrom 1950 in Africa, the Mediterranean Basin, Central Asia and Middle East. These data were extracted from historical scientific published papers and unpublished reports.

which seek to describe each biological parameter and mechanism underlying a phenomenon and how these aspects can be affected by the environment (Kitron & Mannelli, 1994). Such approaches are more accurate for modelling complex, weak or temporary processes like seasonal reproduction or blood feeding according to host dynamics (Randolph *et al.*, 2002; Ogden *et al.*, 2005, 2006) and are able to deal with environmental factors other than climate or vegetation, such as anthropogenic effects, landscape uses or species competition/exclusion (Sumilo *et al.*, 2007). By using equations that describe the growth patterns of a tick population, the infectious status of individuals, their contact with susceptible hosts and host immunity can be easily integrated to obtain disease transmission models (Kitron & Mannelli, 1994). However, the application of such models to soft ticks will require the collection of detailed biological and ecological data via field and experimental investigations (*e.g.* life history traits, vectorial competence under variable climates, host preferences and shifts according to abundance or host community composition, human impacts on habitat suitability, etc.) and overcoming the current difficulty of creating risk maps using mathematical models.

CONCLUSION

This paper reviewed the peculiar biological and ecological characteristics of argasid ticks to be taken into account to enhance predictions concerning soft tick and associated disease distribution, with a special emphasis on *Ornithodoros* ticks. These characteristics included: *i*) nidicolous lifestyle, *ii*) indiscriminate host feeding and short bloodmeal duration, and *iii*) flexible developmental cycles via diapause periods. Contrary to the common belief that it may be difficult to predict soft tick distributional patterns according to external measurable environmental data, especially climate, this paper shows that it may be possible, bearing in mind the spatial scale of predictions and the existence of an additional intermediate layer partially buffering external conditions. Host presence seems less important for indiscriminate host feeding soft ticks than for hard ticks. For now, no distributional models have yet been published but investigations are in progress, using pattern-matched models and knowledge-based approaches as promising preliminary studies that can be extended to dynamic process-based models integrating tick-host-pathogen interactions.

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