

Platzy Jul 01
565.4 '688 RIR JOHN



Technische Universität Darmstadt
AG Tierökologie Prof. Dr. S. Scheu

Wintersemester 2001
Fachbereich 10 Biologie

BIRKHOFFER 2001
P 105



Diplomarbeit

Territorial Behaviour of *Leucorchestris arenicola* (Araneae: Sparassidae)

von

Klaus Birkhofer

Referent: Professor Dr. Stefan Scheu

Koreferent: Professor Dr. Rüdiger Wehner

Die Arbeit wurde angefertigt in dem Gobabeb Training and Research Centre,
Namibia

DRFN

Desert Research
Foundation of Namibia

Gobabeb Library

IV Discussion

IV.1 Territorial Behaviour of *Leucorchestris arenicola*

Territorial behaviour might be common in spiders (RIECHERT 1981, MARSHALL 1995), but, as stipulated by WISE (1993), further proof, especially for wandering spiders, would be necessary to accept this hypothesis. Following the definition of territoriality used in this study, adult individuals of *L. arenicola* should display agonistic behaviour against any conspecific intruder in a fixed area around the burrow. Such behaviour could include drumming, leg waving or direct attacks with the consequence of a retreat by the intruder, or fighting between both individuals.

Territory owners were interested in new neighbours, as shown by the conspecific presentation experiment. Setting a positive reaction minimum of at least forty percent of all tested individuals as the limit for defining an average territory border distance, males reacted to presented individuals up to four metres (43%). Females showed less of a reaction at four metres (13%), but a comparable reaction at a three-metre distance (40%). On average adults were active on the surface every third night during the observation period, but 70 % of the mentioned reactions to presented intruders occurred in the first test night. Adult *L. arenicola* individuals were interested in new neighbours at certain distances and were able to perceive such intruders.

No direct encounter experiments between two spiders were accomplished, mainly because work was conducted in a nature reserve under the condition of strictly non-destructive work. RIECHERT (1978) distinguished 33 different behaviour patterns in 81 experimental encounters between adult *Agelenopsis aperta* (Araneae: Agelenidae) individuals, such a high variation in intraspecific behaviour is also known from Lycosids (NOSSEK 1984). It was proposed in the latter study that such behavioural variation should cause a surprise effect in an intruder leading to a fast retreat. Information about the behaviour between two interacting Sparassid spiders mainly came from monitoring data. Assuming the specific territory borders for females and males, only 23 %, respectively 29 % of these territory owners tolerated neighbours at closer distances in the field.

Avoidance of these neighbours could be a consequence of intense fighting (ROVNER 1968, ROBINSON 1980), as sometimes body remains were found on the meeting point of two spiders. However, it is more likely that display behaviour, as for example drumming, seeks to avoid these direct conflicts, as is known from other ground-living spiders (ASPEY 1977, CLOUDSEY-THOMPSON 1996). Additional information about interaction between two neighboured spiders was recorded by analysing tracks. Seven recorded cases of conflicts between two neighbours had the consequence of disappearance for one of the interacting spiders. All these conflicts occurred between neighbours at distances closer than three metres. EIBL-EIBESFELDT (1970) argued that it would be wrong to regard territorial neighbours as animals in a contiguous state of fighting. The majority of territories should be established within a certain period and all neighbours should recognise the borders from this time on. In conclusion adult individuals of *L. arenicola* repel conspecific neighbours at certain distances.

Social spacing in a generalist predator could have two possible reasons. It could be a consequence of territorial behaviour or it could directly result from cannibalism (MARSHALL 1996). SCHAEFER (1972) described interspecific killing between wolf spiders without the consequence of ingestion for the killed spider. Therefore, to describe territoriality, the behaviour should differ from foraging activity (cannibalism), and as a major assumption, *L. arenicola* should be able to determine the intruder as a competitor rather than as potential prey.

A study on *Agelenopsis aperta* (RIECHERT 1978) showed that this territorial spider distinguishes between potential prey and conspecifics. According to RIECHERT territorial behaviour has to be described carefully for all generalist predators. Agonistic behaviour against conspecifics could not coercively be explained by territorial behaviour. A number of publications on spiders have shown that there is recognition of conspecifics as competitors rather than as potential prey (HERGENRÖDER 1983, BLECKMANN 1985, FERNANDEZ-MONTRAVETA 1994, PUNZO 2000, MOYA LARANO 2002). The latter study described a cannibalistic territoriality system for a Mediterranean lycosid species. Individuals excluded conspecifics from defended areas, with the frequent consequence of cannibalism during territorial defence. Cannibalism could act as a density-dependant mortality factor, as shown for young instars of a wolf spider species (WAGNER 1996).

Therefore, cannibalism could not only be a consequence of high densities, but could also have further consequences for territorial behaviour in spiders. Experimental studies on adult agelenids (RIECHERT 1981) and Lycosids (NOSSEK 1984) showed no correlation between the state of satiation and the cannibalism rate.

In a territorial system cannibalism should be an exception during encounters. In the present study conspecifics were recognized and visited at larger distances than normal foraging activity. The mean attack distance on prey (0,8 metre) was significantly smaller than the distance at which at least 80% of all tested adults still reacted to conspecifics (3,0 metre). Both results showed that reaction to conspecifics occurred in high frequencies at much greater distances than prey was captured regularly.

Further proof for a relatively low rate of cannibalism came from HENSCHER (1994), who observed the diet composition of *L. arenicola* in a two-year study. He found 2,7 % of the spider's diet consisting of conspecifics. Low rates of cannibalism are also known in wolf spiders. In a study on a *Lycosa* species (Araneae: Lycosidae), less than one percent of all tested spiders preyed on conspecifics (NOSSEK 1984). The authors explained higher occurrences of cannibalism in other experiments as caused by a narrow diet offered to the tested individuals in the laboratory. A field study on *Aphonopelma hentzi* (Araneae: Theraphosidae) in the Chihuahuan desert showed a high degree of intersexual cannibalism (PUNZO 1999).

The discussed results and similarities in related spider families described the avoidance of neighbours as competitors through overt behaviour. Following the applied definition, it is legitimate to describe *L. arenicola* as a territorial spider species.

IV.2 Use of Space

Home range calculation with Home Ranger resulted in a significantly larger area for adults than for subadults (Mann-Whitney U test, $P < 0,01$). Due to the fact that this home range was mainly the foraging area of a spider, such a result could be interpreted under energetic aspects. Adult individuals are larger than all subadult stages and their energy needs should, therefore, be higher. Use of a larger home range for foraging could increase the prey availability, and therefore, support individuals with higher energy needs (RIECHERT 1981). The high standard deviation for subadults could be explained with similar argumentation. Different subadult sizes should need a different amount of prey, therefore, high variation of home range size between different development stages created this deviation. Focusing on food as one important resource, one has to consider that prey is usually very scarce and unpredictable in desert ecosystems. It is highly probable that home range size and shape shows a huge variation over the season and for different development stages; only the last difference was shown in this study. Analogous to the territory size, the home range size could be correlated to densities, as GRIMM (2001) showed it for arionid slugs.

Circular territory size was calculated with the radius as half of the average mean nearest neighbour distance. The calculated area was smaller for adults than the area resulting from territorial trials. Adults would defend a **core territory** of an average $9,1 \text{ m}^2$ around the burrow entrance against any intruder inside an average home range area of $23,7 \text{ m}^2$. Such territorial behaviour is described for ants in habitats with patchily distributed but stable resources (JMHASLY 1999). These animals established trunk routes away from this core to resources at further distances.

The results taken from territorial trials allowed further conclusions about the sensory limit of adult territory owners. Adult males were more sensitive to intruders than females, but both areas calculated using of the territorial trial data were much larger than the area calculated assuming a circular territory (Core Territory) following MARSHALL (1996). The average mean nearest neighbour distance of 3,4 metres was slightly above the proposed border limit for female spiders (3 m) and between the proposed limits for male individuals (3-4 m).

Because of the spacing pattern and behavioural features of *L. arenicola* the territory size calculated for the core territory could not explain the reaction to burrow-constructing spiders. A mean nearest neighbour distance of 3,4 metres showed an avoidance of all burrow-constructing new neighbours inside such a radius (**Neighbour Avoidance Territory**), resulting in an average area of 36,3 m², a size that would be in limits set by the territorial trials (28,3 m-50,3 m; Table 15). Any conspecific crossing this area would be difficult to perceive until intruders reached a certain distance to the burrow (Core Territory). The measured home range of 23,7 m² was smaller than this neighbour avoidance territory, but could be increased during times with lower prey availability levels. Arguments related to such a super territory hypothesis are discussed in chapter IV.3.1.

Table 15 Summary of all observed adults and subadults with on SD and showing the proposed shape of these areas. TT=Calculation with values taken from territorial trials; MNND=Calculation with values taken from mean nearest neighbour distance.

Area	Development Stage	Size [m ²]	Shape	Definition
Home Range	adult	14,8+/-11,7	Circular	-
Home Range	subadult	10,5+/-9,3	Polygon	Home range subadults
Home Range	adult	23,7+/-8,8	Polygon	Home range adults
Territory	subadult	6,2	Circular (MNND/2)	Core territory
Territory	adult	9,1	Circular (MNND/2)	Core territory
Territory	subadult	24,6	Circular (MNND)	?
Territory	adult	36,3	Circular (MNND)	Neighbour Avoidance Territory
Territory	male	28,3-50,3	Circular (TT)	-
Territory	female	28,3	Circular (TT)	-

According to an activity rate of 39 % per adult spider and night, a spider left its burrow only approximately one third of all nights. A nocturnal American burrow-living Theraphosid species spent a similar period outside the burrow during activity peaks (41%) (PUNZO 1999). Foraging walks should not take too long, because time and distance to one's own burrow would increase the risk of predation. As a result *L. arenicola* individuals should not spend a lot of time outside the burrow, with the exception of mature males.

Spatiotemporal avoidance of neighbours in overlapping territories should be a main strategy, especially assuming acceptable, non-fatal consequences in case of an encounter.

Relatively low fighting costs (RIECHERT 1988) and a low risk of intraspecific killing due to of the high repertoire in behavioural display, e.g. leg drumming, Opisthosoma drumming and jumping, support this argument. Spatiotemporal avoidance in overlapping territories is described for ants in habitats with patchily distributed and unstable resources (JMHASLY 1999).

A core territory should be defended against any intruder on the surface including potential prey animals, with a maximum size not larger than the average prey capture distance (Fig. 26). Burrow-constructing conspecifics were repelled at distances much larger, mainly because an already established territory owner sensed them more easily. From an economical point of view an active spider crossing a territory for a short time and only on a few occasions should not cause the same loss of energy than a new neighbour that settled somewhere inside the average mean nearest neighbour distance. Sharing a foraging territory decreased energy income significantly in *Agelenopsis aperta* (RIECHERT 1981).

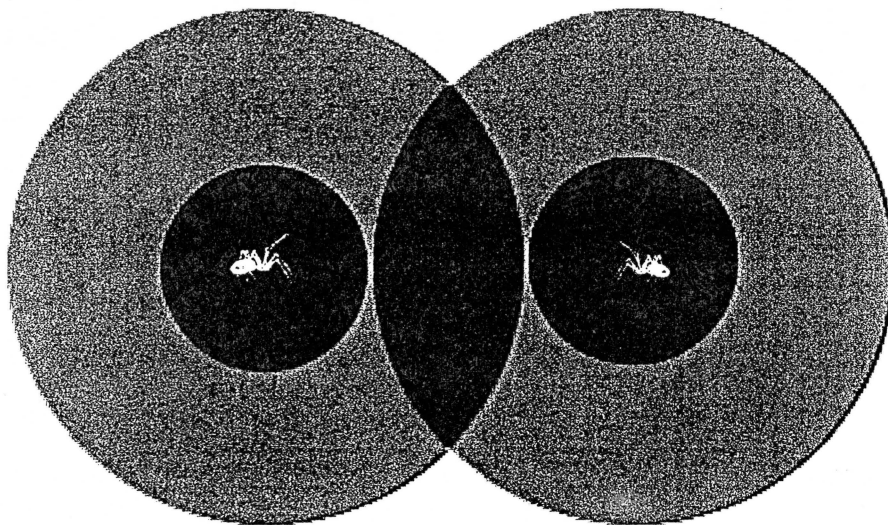


Fig. 26 Proposed spatial relationship between two neighbored territory owners (Spiders). Black circle=core area (defended against any intruder); Grey circle=Neighbour Avoidance Territory (defended against conspecifics constructing a burrow) including the flexible home range (foraging area) with a dark grey zone overlapping (characterised through temporal avoidance).

If subadults showed territorial behaviour at all or to a similar degree than adults could not be shown by this study. Their spacing could be the consequence of adult spiders' behaviour or a direct consequence of their own territorial behaviour. At least for small juveniles territorial behaviour was not assumed, because of the high risk of losing a dispute against a bigger intruder. A size bias in territorial conflicts is well known from other studies (RIECHERT 1981, MARSHALL 1999), so subadults should be careful in defending a fixed area.

Using the density peak on the 20th of December (95 subadults, 30 adults) and the average territory size resulting from dividing the mean nearest neighbour distance (core territory), subadults would cover an area of 585 m² and adults an additional area of 272 m² with their exclusively used territories. The combined area covered by circular-shaped territories of *L. arenicola* inside the 3500 m² large area would only be 857 m². In contrast, the home range area of all spiders would cover 1709 m², nearly double that of the area defended against surface activity through territorial behaviour. Using the average mean nearest neighbour distance of adults and subadults (Neighbour Avoidance Territory) as a neighbour tolerance limit, 3429 m² of the observed 3500 m² would be defended by spiders against any burrow constructing intruder. According to the little knowledge of territorial behaviour of subadults, this calculation should overestimate the covered area. Nevertheless, such a high value showed that the carrying capacity of the habitat could be reached during single abundance peaks and that space should be a valuable resource during density peaks.

IV.3 Function of Territorial Behaviour

IV.3.1 Energy Acquisition

According to RIECHERT (1981) territorial behaviour could have a variety of advantages for a territory owner and is widespread in spiders. Provision of sufficient resources is an important reason for territorial behaviour and was impressively documented by studies on *Agelenopsis aperta* in northern America (RIECHERT 1978, RIECHERT 1981). The sheet web-spinning agelenid defends an area in excess of its web against conspecific intruders. Living in a relatively harsh environment, food is quite unpredictable.

An energy-based territoriality was described for this species, in contrast to most territories in invertebrates serving reproductive functions (RIECHERT 1978).

L. arenicola defended significantly larger areas against conspecific individuals constructing a burrow than normally used for prey capture activity during the observation period. Under the assumption of an energy-based territoriality this would violate cost-benefit criteria. One possible explanation for maintenance of such a large area could be the so-called super territory (VERNER 1977). The observation period was at a time with relative high prey availability, in contrast to winter months with lower prey levels. It is possible that *L. arenicola* keeps its neighbour avoidance territory at the same size through the whole year, to guarantee sufficient energy supply during times with low energy support.

Defence of a super territory was discussed under cost-benefit aspects, and was rejected with the argument that it would be uneconomical to defend a territory that is larger than necessary at any given time (DAVIES 1997). RIECHERT (1978) outlined two possible arguments against this point of view. First, the cost of defending such an area may not be as expensive as assumed, and second, a precise assessment of the prey availability by the predator should be difficult under quick fluctuations as they could occur in desert ecosystems. RIECHERT (1988) observed energetic costs of fighting for the territorial spider *Agelenopsis aperta* in terms of decrements to milligrams wet-weight of future egg production resulting from single contests. This study showed insignificant costs for such territorial disputes, in contrast to injury, potential predation or the loss in food during time spent with these interactions.

A mechanism to reduce costs was proposed by EASON (1999). Under cost-benefit criteria a quick reaction to an intruder should result in reduced defensive costs. According to EASON intruders are easier to repel by a territory owner if they are in the new location for a short time. From all 32 positively reacting adult spiders at different distances, 22 reacted to the newly presented neighbour in the first presentation night.

For *L. arenicola* approximately 71 % of all spiders under the cone established a complete burrow with lid in the first night. Thus it should be easier to fight off an intruder on the surface than one that has already constructed its burrow. In addition costs to avoid a new neighbour should be relatively low, because floating was not a common behaviour and construction of a new burrow by an intruder should be relatively rare for all adult territory owners. No patrolling of the neighbour-free area happened during the study period, so only subadults or burrow site-searching adults should cause a reaction at these distances. Surface-walking neighbours crossing the territory without entering the core area were only encroached randomly.

Besides feeding territory size adjustment through different development stages was shown for agelenids (RIECHERT 1981) and for wolf spiders by MOYA LARANO (2002). Differences between populations in different habitat types were (RIECHERT 1978) described in spiders. Observation of prey availability in these habitats showed a strong correlation between territory size and prey availability inside each population. RIECHERT (1978) conducted experiments studying the ability of *Agelenopsis aperta* to adjust their territory size to different levels of prey, as demonstrated by the so-called rubber disc model. As shown experimentally, *Agelenopsis aperta* appeared to be highly inflexible in adjusting its territory size, leading to the conclusion that this behaviour is under strong genetic influence and that the median territory size is an evolved characteristic of a population. Adjustment to different prey levels is only made through a regulation of web size inside the defended territory. This would be comparable in *L. arenicola* to an adjustment of the home range size inside the neighbour avoidance territory. Due to the short observation span no seasonal fluctuations in prey availability and consequences on home range or territory size were observed. The home range size of these two groups was significantly larger for adults, therefore, home range size could be directly related to energy needs of different development stages.

L. arenicola perceived surface activity by conspecifics and prey only up to certain distances and a guaranteed distance to the nearest neighbour should stabilize energy income. MARSHALL (1999) described a negative correlation between nearest neighbour distance and mass gain for *Geolycosa xera archboldi* (Araneae: Lycosidae), leading to the conclusion that a higher number of neighbours should have a negative effect on mass gain. For *L. arenicola* defence of a large territory against conspecifics, with a flexible home range inside, could minimize costs and guarantee survival in seasons with low prey levels.

A major question assuming the flexibility of home range area was the ability to perceive potential prey at different distances. Surface waves in sand and the perception via slit sense organs were intensively examined by BROWNELL (BROWNELL 1977; 1984) who worked with *Paruroctonus mesaensis* (Scorpionida). This nocturnal scorpion has a sensory range between 30 and 50 cm on the sand surface (BROWNELL 1979). So-called Rayleigh waves travel with a speed of 40 to 50 metres per second in sand, a medium with a relatively low velocity compared to other substrates. Brownell described sand as a reasonably good conductor of mechanical vibrations, even if sand filters certain frequencies. Insects at distances up to several decimetres fall into the sensory range of the scorpion. Burrow construction should cause stronger signals than a walking insect or spider on the surface. For this reason it should be easier for *L. arenicola* to sense a new neighbour during burrow construction.

According to HENSCHL (1997) *L. arenicola* detects moving prey up to a distance of 3 metres away from the burrow. BARTH (2001) studied the wandering spider *Cupiennus salei* (Araneae: Ctenidae) intensively. The slit sense organs are the main receptors for vibration, especially one slit sense area, the metatarsal organ (Lyraförmiges Organ). Electrophysiological experiments led to the conclusion that spiders, compared to other vertebrate and invertebrate animals, have a highly sensitive vibration perception. *Cupiennus salei* is a South American spider, mainly living on plant substrate. Similar to *L. arenicola* these spiders showed drumming and palp signalling during courtship. A theoretically calculated range of these signals on a plant was approximately two metres. Information from the field showed females reacting to male drumming at distances even greater than three metres.

Besides this result for male-female communication, females and prey produced significantly weaker signals and BARTH (2001) described perception of vibration as a close-distance sense. Another factor favouring the high range of vibration signals in this species was the low average absorption of such signals on plants.

Spiders need a high sensitivity for vibration, mainly because of the high importance for intra- and interspecific communication. NOSSEK (1984) described courtship behaviour and avoidance of fighting situations through various behavioural patterns as very important mechanisms in wolf spider behaviour.

Summarizing these results from other Arachnids and interpreting the average prey capture distance of 80 centimetres for adult *L. arenicola* it seems highly improbable that perception of surface signals in distances up to the proposed Neighbour Avoidance Territory border was possible. Perception of surface signals seemed to be a major motivation for spiders to forage in a given night and should limit the activity radius somehow. Conspecifics were visited at larger distances, with two possible explanations. First, construction of a burrow should cause stronger signals than surface-walking by an insect, and second, perception of silk-attached pheromones is known in a number of spider species. So perception of conspecifics could be mediated by chemical reception rather than by mechanical signals (PAPKE 2001).

Assuming a circular shape of a spider's territory, the observed grids would carry the maximum number of adult *L. arenicola* individuals under the calculated development stage ratio (3426 m² neighbour avoidance territory of 3500m²). This would lead to the complete coverage of the entire surface in respect to burrow site-searching conspecifics through territory owners, as mentioned by HENSCHER (1997). Defence of a super territory would be useful in such a harsh habitat like the Namib desert, showing high fluctuations in prey availability, especially under conditions making it difficult to assess these fluctuations, e.g. living in a burrow without long-range senses to control the surface. According to cost-benefit criteria, defence of a super territory should not result in a large waste of energy during periods with high prey availability. Actually, in summer it should be possible to keep energy levels similar foraging at closer distances than in winter months without too many costs for fighting off conspecifics.

IV.3.2 Population Effects

A system with higher flexibility in individual territory size (rubber disc) should have less limiting effects on population size in contrast to a more inflexible territory (RIECHERT 1981). The relative constant mean nearest neighbour distance of 3,4 metres for *L. arenicola* and a low frequency of neighbours at closer distances could be interpreted as a population size-limiting consequence of territorial behaviour. Space and especially high quality sites are rare in these desert habitats, and therefore, a defendable resource reaching a certain density limit should exclude further new settlers. As shown with the average territory size of *L. arenicola* and an abundance peak, in relation to a given development stage, nearly the whole observed area should be covered by the sensory range of already established territory owners. Even without knowledge on seasonal fluctuations, such a situation would create an upper density limit to abundance during a season with relative high prey availability. It should be mentioned that this population-limiting effect could not be interpreted as a function of territorial behaviour, rather as a side effect.

RIECHERT (1981) and DAVIES (1978) described another criterion supporting the hypothesis of a population-limiting effect in territorial behaviour of *L. arenicola*. Floaters have serious disadvantages in terms of energy acquirement and reproductive success compared to territory owners. It is logical that a non-territorial individual of *L. arenicola* would have such disadvantages. The risk of intraspecific encounters and attacks during burrow construction would be increased in such an aggressive species. Non-feeding related surface activity would increase the risk of predation and decrease the energy income as shown for other spider species (LUBIN 1993, MORSE 1997). In addition survival rates are very low for such individuals failing to construct a shelter during a given night because of the hostile surface conditions during the daytime. Therefore, floating would not be an alternative strategy.

A conservative strategy of tolerating competition rather than taking the risk of relocation was proposed for a wolf spider in northern America (MARSHALL 1999). This tolerance would fit the proposed overlapping of territories, with spatiotemporal avoidance as the main conflict-limiting mechanism.

It was also proposed that interference competition for burrow sites in a *Lycosa* species could play a role in population regulation. However more studies are needed to make further conclusions (MOYA LARANO 1996).

Many spider populations may not reach the potential density maximum, mainly because the carrying capacity fluctuates during the season (RIECHERT 1978), a situation which could occur in deserts with strong fluctuations of prey availability, water sources and climatic extremes over the season. A genetically fixed territory size would lead to population densities fitting the carrying capacity of a habitat during periods with minimum resource support, as shown for *Agelenopsis aperta* (RIECHERT 1981).

IV.3.3 Reproduction

RIECHERT (1978) proposed that territoriality in invertebrates normally serves reproductive functions, especially for males obtaining territories. Particularly for reptiles' home range size, regulation is focused on courtship, increasing mating success with a maximum overlapping of home ranges between males and females. In lizards and turtles male individuals possessed significantly larger home ranges than females (SMITH 1995, MORROW 2001). For males and females of *L. arenicola* no significant difference was found between the reactions to conspecific intruders at similar distances. Male individuals, however, reacted at four metres with the same strength as females to new neighbours at three metres. In addition, males did not tolerate any other male within four metres around their burrow. At the same distances 29 % of all male territory owners had a female neighbour. This last result could be biased by the fact that females were more common.

MARSHALL (1996) proposed that territories for *Geolycosa xera* (Araneae: Lycosidae) not containing resident prey populations and only including priority of access to ephemeral resources should have more in common with lek mating systems than with feeding territories. Such systems were characterised through males defending an area waiting for potential mating partners. No such strategy is known for *L. arenicola*; the male individuals were active in mating partner search.

In general, there are few studies on territory or home range size adjustment related to mating success in spiders. MOYA-LARANO (2002) proposed that territoriality might have evolved in a wolf spider species to increase the availability of prey and to improve access to males. A few results and behavioural features in *L. arenicola* could have an impact on related conclusions.

Females are able to mate more than once a season and can even produce more than one egg sack per year (HENSCHEL 1990). Males wander around in search for females, due to a very limited life span as mature males. Thus maximizing mating in a short time should be a major intention. Large territories for males could increase the amount of female neighbours and would complicate access to this female for other males. A higher number of known potential mating partners would also reduce the risk of predation, because searching for females increases the amount of time spent outside the burrow.

According to SHOOK (1978) this increased mortality risk for males could be a reason for the observed sex ratio of 2,6 females to one male in *L. arenicola*. For females the main advantage of a large territory would be an increased probability of males crossing this specific territory. In addition other females would be excluded from this area and potential mating inside of it.

DAVIES (1997) pointed out that it is very common that territories are only maintained during the breeding season, mainly for the acquisition of mates. Males maintaining territories in patches with optimal combination of factors should have a larger number of female neighbours than males in less favourable microhabitats. In addition territories with the same number of potential mating partners as neighbours should be smaller and thus easier to defend than areas where the density of adult animals is less. Mate location implicated through aerial or contact pheromones is known in spiders and could function as a site quality sign for wandering males (ROBINSON 1982, PAPKE 2001). This may be possible for wandering *L. arenicola* males, but these individuals usually returned to their original burrow rather than relocate to a new site.

IV.3.4 Further Influences on Territory Size & Shape

SHOOK (1978) proposed that part of the home range of the desert-living *Lycosa carolinensis* (Araneae: Lycosidae) is limited by changes in topographical relief. In the Sonoran desert of northern America washes or mounts surrounding bushes influenced the boundaries of home ranges.

HENSCHEL (1998) found a positive correlation between burrow site choice and distance to plants. But this mainly arises from a higher prey density associated with plants, as proposed for *Agelenopsis aperta* (RIECHERT 1981).

Territory size-limiting structures for *L. arenicola* were areas with a flint-covered surface, causing difficulties in burrow construction. Plant-covered areas or sites with dead wood were also not suitable for burrow construction needs of *L. arenicola*, but formed only approximately 6 % of the observed area.

Important predators of *L. arenicola* are all quite mobile, as for example Gerbils or Lizards. Both groups use burrows mainly located close to larger grass hummocks or *Acanthosicyos* plants. Due to the low number of such plants in the observed grids no effect could be investigated. An interesting subject would be to determine if the advantages through higher insect support through settling close to plants would outweigh the disadvantages through a higher predation risk.

IV.4 Dispersion

IV.4.1 Habitat Choice

Patches supporting the needs of a certain species are often distributed unevenly, resulting in a clumped distribution of individuals. In contrast, the distribution in favourable patches may differ from being crowded to accommodate unexpectedly few individuals (ANDREWARTHA 1967). Clumped distribution was shown by POLIS (1986) for juveniles of the scorpion species *Pauroctonus mesaensis*. This was a result of an association between these scorpions and distribution of vegetation, with subadults settling close to vegetation patches. Adults did not show a significant preference for vegetation and were distributed more regularly. KRONK and RIECHERT (1979) analysed distribution of *Lycosa santrita* (Araneae: Lycosidae) in a desert riparian system. Juvenile spiders were highly associated with grass hummocks, even if no increase in prey availability was observed in these areas. Adults moved away from these patches to bare ground substrate, where prey availability was highest. SHOOK (1978) found a random distribution of *Lycosa carolinensis* in relation to each other, but a regular distribution in relation to shrubs inside the habitat. All these species created a relatively stable and predictable environment within their burrows and were characterised through a more sit-and-wait-like foraging strategy. In contrast to the burrow microclimate the biological environment on the surface was quiet unpredictable. Leaving a burrow increases the risk of predation (SAMU 1999) and the energy needs due to searching of a new burrow site and construction of the new burrow. A main motivation in juvenile *L. arenicola* individuals to change the burrow is molting, and as a consequence, a bigger burrow is needed. Adults changed burrows after breeding (females) and during long distance walks (males). MORSE (1980) described a direct correlation between the spacing and the kind of resource defended. Territories including all sufficient resources should cause a relatively even spatial distribution, at least in homogenous habitats. Aggregated or clumped distributions were found if animals were only defending a territory for a specific resource (for example nesting sites).

As mentioned earlier a high proportion of spiders settled at distances closer than ten metres to vegetation in a study by HENSCHER (1990). But such an association to plants should not be a significant burrow site choice criterion, due to the very sparse vegetation in *L. arenicola* habitats. In addition no significant increase of prey availability in correlation with plant coverage was described for other desert habitats (KRONK 1979). For the life history of *L. arenicola* a lack of structure should have no influence, as described for many web-building spiders (SAMU 1999). Climatic extremes and fluctuations were avoided through burrow construction, so these abiotic factors should not influence distribution. A relatively homogenous habitat like a sand desert, even on a micro-scale level, should not influence dispersal patterns.

IV.4.2 Individual Age

SHACHAK (1983) described dispersion patterns in the desert scorpion *Scorpio maurus palmatus* (Scorpionidae) as a function of age, changing from clumped to random. Juveniles showed a clumped distribution with Morasita indices (comparable to the calculated d-values) of $2,0 \pm 0,9$. In contrast to this, adults had a value of $1,0 \pm 0,1$ and thus were randomly distributed. MARSHALL (1995) described territorial aggregation in hatchlings of *Geolycosa xera archboldi* as a consequence of limited dispersal from the maternal burrow. The ecology of these arachnids was similar to the ecology of *L. arenicola*. Cursorial dispersal, as known in *L. arenicola*, should limit the dispersal range, especially in habitats where surface activity is only possible during the nights. The observed clumped distribution for subadults could thus be a consequence of the limited dispersal from the maternal burrow, an assumption also supported by the fact that females leave their burrow after the hatchlings reached a certain instar. Such behaviour would create free room for a territory owner in a formerly inhabited territory. At least a few hatchlings could construct burrows in this area with a relatively low predation risk.

IV.4.3 Mating Partners

In *Pardosa pullata* and *Trochosa terricola* (Araneae: Lycosidae) a random distribution during the mating season was shown by SYREK and JANUSZ (1977). Outside this season the individuals were evenly distributed, considered by the authors as a symptom of their territorial behaviour.

Such a description of a periodical territoriality was very uncommon in invertebrates and much more widespread in birds and lizards. In addition, the authors mentioned the possibility that these territories were not only feeding areas, but also areas defended to hatch spiderlings. No experimental or census data from this study supported a mating- or courtship-related territory size or site choice. Logical conclusions, such as an increased number of potential mating partners as neighbours, could be a side effect or an intended consequence of territorial behaviour. Burrow patch choice should not be influenced by the neighbour composition in subadults and adults. To be so, burrow site-searching individuals should be able to assess the sex of their neighbours before burrow construction, a relatively improbable sensory performance assuming a high number of neighbours from different development stages.

IV.4.4 Social Spacing

According to PAPKE (2001) agonistic behaviour would serve to maintain a widely dispersed population. MARSHALL (1996) observed regular spacing patterns for the territorial Lycosid *Geolycosa xera*. This species showed a relatively constant mean nearest neighbour distance of 30 centimetres. Two possible causes of this constant mean were experimentally tested: spacing as a consequence of sensory limitation and cannibalism and spacing as a result of territorial behaviour. Mean nearest neighbour distance was mainly obtained through agonistic behaviour of larger territory owners against smaller neighbours, therefore fitting the definition of territoriality. RIECHERT (1978) found a regular distribution of eight *Agelenopsis aperta* populations in northern America and interprets this as a sign for social spacing. Both authors only used the constancy of the mean nearest neighbour distance to achieve further conclusions about the dispersion. In juveniles clustering or aggregation of individuals is known from studies by RIECHERT (1978) and MARSHALL (1999) and is mainly interpreted as a consequence of low aggression levels between these development stages.

HOFFMASTER (1985) observed the distribution and the community composition of eight web-building spider species. He showed a correlation between the aggressiveness of a species and its dispersion. Less aggressive species were distributed randomly or clumped.

Aggressive species, in contrast should be overdispersed due to a high degree of interference competition. HOFFMASTER (1985) also concluded that larger species were more aggressive than small spiders. The results could not show any clumped distribution, but the author mentioned the small sample area as a bias for his results. PUNZO (2000) described a relatively high level of aggression for desert spiders, eventually caused by the low prey density and the harsh environmental conditions. According to HENSCHEL (1998) Sparassids from the Namib and the Negev were the largest and most aggressive hunting spiders in both regions. Adults and their behaviour affect dispersal patterns, as shown by defending and using certain areas without tolerating conspecifics. A strong influence on distribution through social spacing is proposed for adult *L. arenicola*. Assuming such behaviour as the main reason for spacing, a regular distribution would be expected. Only a tendency in d-values with no significant difference to randomness was observed. However, during long periods the d-value was below one and results could be biased by too small sample sizes or a limited seasonal observation span.

IV.4.5 Dispersion of *Leucorchestris arenicola*

Adults were distributed randomly ($d=0,9\pm 0,1$, $plotless=0,52$) during the observation period, with a tendency towards more regular distribution (not significant, $\chi^2=29,34 < \chi^2_{5\%,52}=69,83$). Association to vegetation was not analysed, due to the small sample size. HENSCHEL (1990) stated that a large proportion (96%) of all marked burrows during a nearly two-year study was found within one to ten metres of plants.

Besides this possible effect of association to habitat characteristics, social spacing should have a strong influence on dispersion, with territory owners limiting the number and distance of possible neighbours. WISE (1993) pointed out that a regular distribution is no valid criteria to describe territoriality in a species, mainly because site choice could reflect distribution of favourable habitat conditions more than being a consequence of intraspecific interaction. A similar argumentation may explain deviation from regularity in dispersal of a territorial species. Even under such assumptions a regular dispersion pattern is mentioned as major criterion for territoriality in a more recent study on competition in wolf spiders (MOYA LARANO 1996).

Subadults were distributed patchily, mainly because of the range-limiting cursorial dispersal and less aggressive behaviour. Leaving the maternal burrow and starting with surface activity should be a certain mortality risk, even more so the longer a burrow site search and burrow construction would take. Therefore, these individuals should hurry to at least construct a shelter to avoid predators and climatic extremes. Spiderlings from a maternal burrow should, therefore, stay within close distances, especially after the female has left the burrow site.

V Summary

Adult individuals of *Leucorchestris arenicola* (Araneae: Sparassidae), a burrow living spider from the Namib desert, show agonistic behaviour against conspecifics. The observed behavioural repertoire includes direct attacks, as well as advertisement techniques such as *Opisthosoma* drumming. Intruders were repelled as competitors rather than as potential prey, leading to a description of territorial behaviour for this species.

Different areas around the burrow are defended against walking and burrow constructing intruders. The core territory is used for foraging activity and its size depends on the sensory range of a burrow inhabitant. The territory owner because of the created surface vibration senses most core territory-crossing animals. Burrow-constructing conspecifics were repelled at greater distances. This neighbour avoidance territory optimised energy income for a territory owner. A certain overlap of two such larger territories should not increase the rate of interference competition, due to the very limited temporal surface activity of adult *L. arenicola* individuals. Spatiotemporal avoidance is an important strategy, an overlap of core territories would increase competition significantly. Intruders in the core territory tend to be perceived as potential prey. In contrast, burrow constructing intruders in the neighbour avoidance territory are repelled to minimize exploitative competition. Territorial systems such as this are characterised by a trade-off between resource sharing and the risk of intraspecific fighting. A territory owner could adjust its foraging home range inside the neighbour avoidance territory without a large risk of boundary disputes or interference competition.

The behaviour of *L. arenicola*, an energy-based territoriality, has consequences on spacing and population size. Adult individuals should cause a regular spacing through overt behaviour against conspecifics. Such social spacing was not directly observed during the observation period, but differences between adult and subadult spacing patterns showed an influence of adult behaviour on dispersion. Space should be limited at abundance peaks and during times with low prey availability. Therefore, it should be a valuable resource and defence of minimum areas would provide a territory owner with sufficient energy levels even during prey shortage. Subadults were aggregated at certain patches, mainly as a result of limited cursorial dispersal from the maternal burrow and less aggressive behaviour.