Atti Accademia Nazionale dei Lincei

Classe Scienze Fisiche Matematiche Naturali

Rendiconti

Guido Chelazzi

Improvements in the field study of animal spatial habits (particularly of litoral molluscs)

Atti della Accademia Nazionale dei Lincei. Classe di Scienze Fisiche, Matematiche e Naturali. Rendiconti, Serie 8, Vol. **74** (1983), n.6, p. 437–446.

Accademia Nazionale dei Lincei

<http://www.bdim.eu/item?id=RLINA_1983_8_74_6_437_0>

Atti della Accademia Nazionale dei Lincei. Classe di Scienze Fisiche, Matematiche e Naturali. Rendiconti, Accademia Nazionale dei Lincei, 1983.

Guido Chelazzi

IMPROVEMENTS IN THE FIELD STUDY OF ANIMAL SPATIAL HABITS (PARTICULARLY OF LITTORAL MOLLUSCS) (*)

Introduction

The study of animal movements in their natural environment is one of the main topics of behavioural ecology. Through the controlled variation of their position in space mobile organisms can withdraw from stress sources and accede to resources, performing a dynamic habitat selection (Jander, 1975). Moreover, differing activity patterns can be an important factor in the coevolution of species exploiting separate niches of the same ecological system (Vandermeer, 1972; Partridge, 1978).

Traditionally, most studies on vertebrate spatial habits have been made by intercepting previously marked animals by means of traps or nets in the study area (Jewell, 1966; Sanderson, 1966). These discontinuous and often temporally random position data led to such important concepts as " home range " (Seton, 1909; Burt, 1943; Jewell, 1966; Mohr, 1966). Though a useful and widely accepted term it is analytically ambiguous as it implies a geometrically simple use of space which in many cases does not fit the complexity of the observed phenomena.

In fact, it is now known that most animals do not use geometrically simple areas but rather a portion of the biosphere divided into complex subunits (Hediger, 1942; Adam and Davis, 1967; Leuthold, 1977) each of which often serves a different purpose. Moreover, it was soon recognized that the home area also needs a temporal definition (Martinsen, 1968; Maza *et al.*, 1973; Randolph, 1977) since animals modify their spatial habits in time, following short- (diurnal, tidal) and long-term (seasonal) rhythms and may change their activity pattern during ontogenesis.

Shortcomings of traditional methods

An analysis based on a traditional sampling of positions has some important shortcomings. First, behaviourally heterogeneous samples are usually collected as normally no information is available on the activity of animals upon interception and second, all the widely used analytical methods imply hypothetical short-term movement patterns seldom quantitatively verified.

(*) Conferenza tenuta nella seduta dell'8 maggio 1982.

One of the most commonly used methods is that based on a "centre of activity" (Scott, 1947; Hayne, 1949; Harrison, 1958). It admits a circular symmetry of the home range and presence of a centripetal tendency which increases as long as the animal moves away from the geometric centre of its familiar area, but home ranges often lack any definite centre (Jenrich and Turner, 1969; Dixon and Chapman, 1980). Other methods require the presence of sharp boundaries which permit drawing the perimeter of the familiar area by hand or with computerized algorithms (Blair, 1940; Dalke, 1942; Mohr, 1947; Voigt and Tinline, 1980). Instead, with some exceptions the boundaries of familiar areas are very dynamic and positions outside the main cloud of fixes are frequently recorded (Burt, 1943; Harvey and Barbour, 1965) making the use of these methods incorrect.

The complex methods implying either a circular normal or bivariate distribution of fixes (Calhoun and Casby, 1958; Jenrich and Turner, 1969; Mazurkiewicz, 1969; Koeppel *et al.*, 1977)—though being more flexible than the previous analytical methods in fitting the actual shape of the field fixes—implies preconstituted hypotheses on movement patterns. Such is the case of the "Ornstein-Uhlenbeck" model (Dunn, 1977) which assumes that animal movements are affected by a centripetal tendency, and follow a basically Markovian process in moving around their home range. However, in many applications of the method (Dunn and Gipson, 1977) this remains to be demonstrated.

These difficulties partly justify the criticism expressed by some authors concerning the use of complex analytical methods in the automatic study of the spatial distribution of fixes (MacDonald *et al.*, 1980). Nevertheless, recent improvements in sampling procedures through radio-tracking and other long-range monitoring techniques have removed some of the shortcomings (Brown, 1966; Amlaner, 1977).

The point is how to use radio- and sonar-tracking. If simply used to substitute other methods of irregular position sampling, about the only benefits derived are to increase the range of monitoring and eliminate continuous handling of the animals under investigation. Instead, the importance of these techniques is that they permit sampling in time on a more regular basis, and almost continuous monitoring of the animals (Adams and Davis, 1967). Despite the widespread use of radio-tracking in the study of animal spatial habits (Amlaner and MacDonald, 1980), examples of regular or continuous tracking are relatively scanty. Only careful frequent monitoring (Siniff and Jessen, 1969), particularly feasible when automatic recording systems are used (Deat *et al.*, 1980), gives information on "microscopic" movements and permits building a realistic model of the animal spatial habits.

Unfortunately, with few exceptions (Wolcott, 1980), radio-tracking is not suited to the study of the invertebrates. This is the case of littoral molluscs whose ecology is based largely on short- and long-term movements—ranging from homing behaviour to zonal migrations (Newell, 1979; Underwood, 1979; Chelazzi, 1980)—in phase with diurnal or tidal rhythms. Molluscs are generally too small to be equipped with radio-transmitters, but the presence in many species of an external shell, and the graduality of their movements, make them an excellent subject for the study of spatial habits. A number of alternative techniques can be designed to provide continuous or regular-discontinuous tracking which, together with the relatively simple geometry of many coastal systems, guarantee the coupling of ethological and environmental data, constituting the basis for an ecological approach to the study of the behaviour of intertidal species.

NEW METHODS FOR THE FIELD STUDY OF LITTORAL MOLLUSCS AND OTHER ANIMALS

Most of the quantitative studies on spatial habits of littoral molluscs have been conducted at a " macroscopic " level, through a scattered sampling of positions (Underwood, 1977). Instead, a microscopic analysis of their movements is possible only through almost continuous tracking. This can be obtained by positioning marked animals relative to a grid placed on the shore (Vannini and Chelazzi, 1978) or photographing them at set intervals (which reduces the imprecision of the subjective monitoring) as was done with the prosobranch gastropod *Nerita polita* (Chelazzi, 1982); however, the latter method probably disturbs nocturnal animals and does not permit the analysis of such important aspects of spatial behaviour as trail-following, typically present in many littoral chitons and gastropods (Funke, 1968; Thorne, 1968; Cook and Cook, 1975). The trail-following involved in the homing behaviour and clustering of rocky shore molluscs (Cook, 1969; Lowe and Turner, 1976) can be properly analyzed by using special tracking techniques such as the reconstruction of individual paths from the fecal pellets left by the animals during their movements (McFarlane, 1980). A more precise technique with wider application was introduced by Chelazzi *et al.* (in press) on the intertidal tropical gastropod *Nerita textilis*. A red LED lighter powered by a small battery was fixed to the shell and photographs were made nightly of the study area. Long-time exposures provided a full reconstruction of the animals' activity and revealed important details of their feeding excursions, and the occurrence of intra- and interindividual trail-following. The resolution of this optical tracking is sensibly higher than that obtained by other methods and the technique can be applied to many nocturnal species, included those moving in splash zones which are inaccessible for direct sampling of positions.

When long-term massive position recording is needed, continuous tracking can be substituted by the discrete positioning of several individually marked animals. In this case previous information on the temporal activity pattern of the animals is crucial in order to plan the temporal schedule of the intermittent recording, and distinguish positions relative to different behavioural phases of the animals. If properly scheduled, intermittent positioning over long periods gives full information on the spatial strategy of a species, as demonstrated by the study conducted on two sympatric chitons of the genus *Acanthopleura* (Chelazzi *et al.*, 1983). Once distinct clouds of fixes—relative to the different activities—have been obtained for each animal, these can then be analyzed separately or by combining different samples of co-ordinates. A specific model of spatial strategy can then be obtained through computerized algorithms.

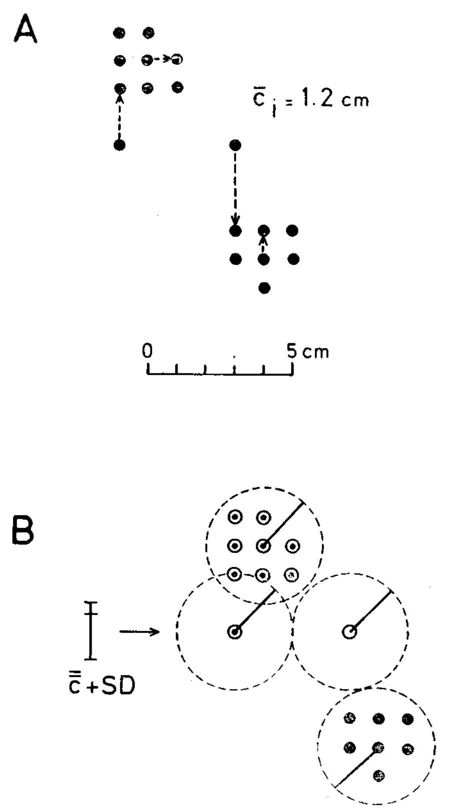

Fig. 1. – Graphic representation of the method employed to analyze spatial distribution of *Acanthopleura* fixes. In A. computation of the individual compactness index ($\bar{c}_i$) on the basis of the distance between nearest fixes (dashed lines). In B. automatic searching for subunits (black and dotted circles) and free points (white circle), on the basis of $\bar{\bar{c}} + \mathrm{SD}$.

For example, if the positions where the animals retreat during resting phase can be extracted from the global sample of fixes a study can be made of the structure of their resting distribution rather than simply giving information on the amplitude of the home area. This was done with *Acanthopleura* spp. as follows. First an index of compactness was obtained for each animal by simpl., computing the mean distance between each fix and the nearest one ($\bar{c}$) (fig. 1, A). It must be noted that the index is sensible only to this mean distance (fig. 2, A, D) and not to either the shape of the cloud (fig. 2, A, B) or division of the system in two or more subunits (fig. 2, A, C). Then the number of subunits in each system of resting points was obtained by assigning different fixes to the

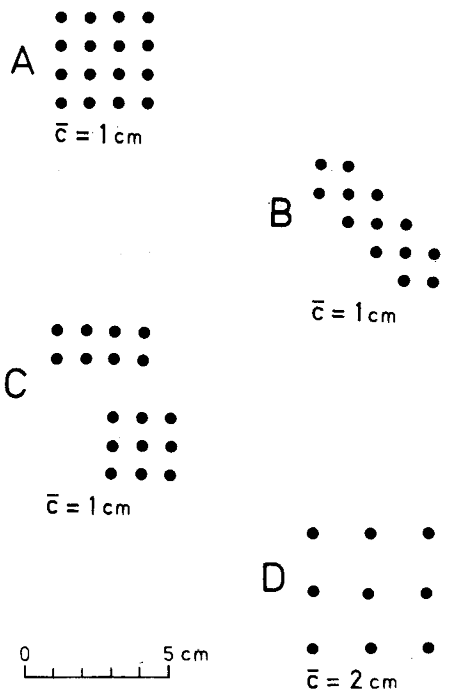

Fig. 2. – Values of the compactness index relative to four different configurations of clouds of fixes.

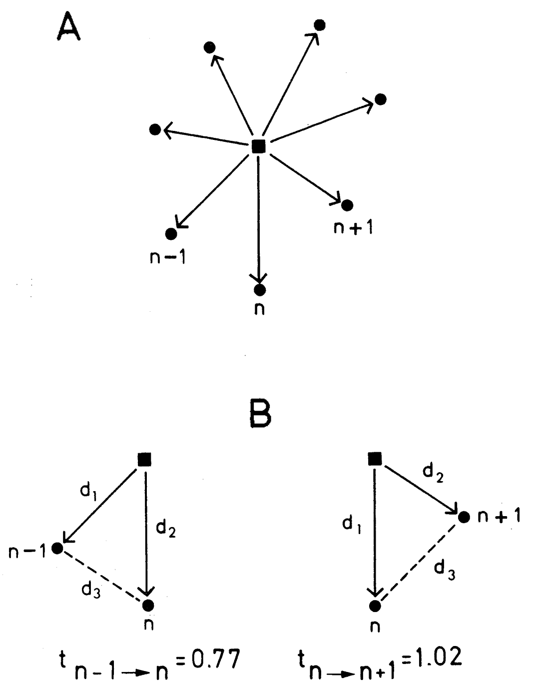

Fig. 3. – Schematic representation of the method employed to analyze the feeding excursions of *Acanthopleura* spp. An individual system of resting (square) and feeding (circles) fixes (A) is resolved in two trios of successive positions (B) to show the computation of the rapport $t = 2\, d_3/(d_1 + d_2)$.

same unit when their distance did not exceed the second-order mean distance between nearest fixes, relative to the whole sample of animals, plus its standard deviation ($\bar{\bar{c}}$ + SD) (fig. 1, B). This resulted in the analysis of subunits relative to the overall mean compactness of rest systems, independent from arbitrary geometrical criteria. In this way resting habits can be analyzed not only in terms of homing performance, but also of spatial pattern of rest systems. This permits a comparison between species or different populations of the same species, and a better grasp of the ecological determinism of their behaviour patterns.

The simple two-phases (resting-feeding) pattern of algal-grazing intertidal molluscs also permits the study of a spatial pattern of resource exploitation. This was done in *Acanthopleura* spp. by combining samples of resting and feeding fixes using a method (fig. 3) based on trios of successive feeding-resting-feeding fixes. Instead of a traditional analysis of the amplitude of the utilized area, it was possible to distinguish between random, conservative and dispersive use of the feeding area (fig. 4) and take into account the temporal evolution of the feed ng strategy (fig. 5).

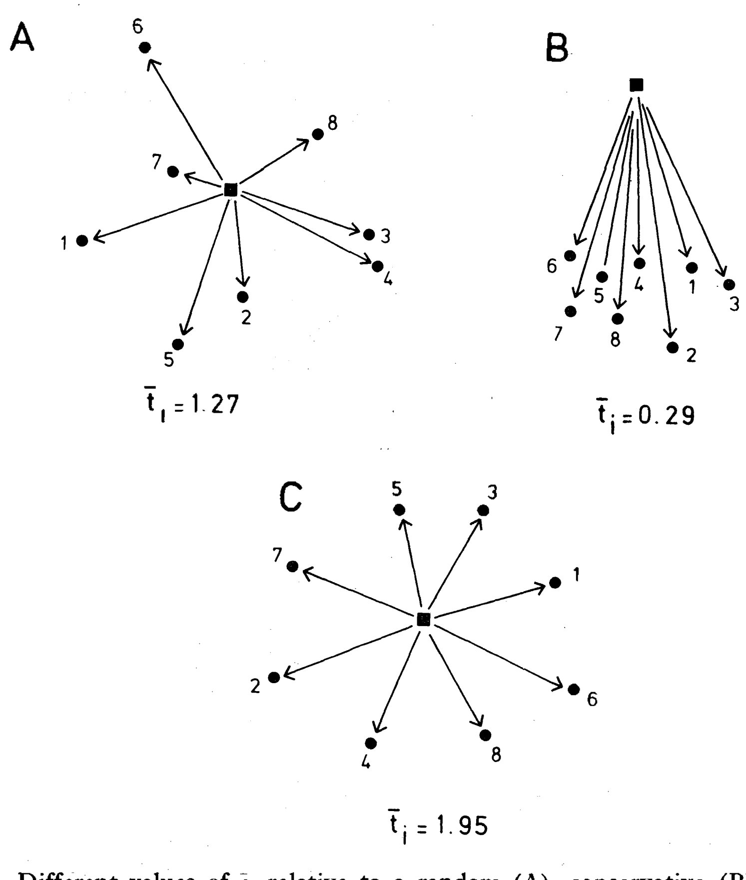

Fig. 4. – Different values of $\bar{t}_i$ relative to a random (A), conservative (B) and dispersive (C) pattern of exploitation of the feeding ground.

Both the methods applied to *Acanthopleura* spp. can be used in space utilization studies of species taxonomically very distant from chitons, included vertebrates. The only condition is to work from spatial data obtained by temporally-assessed position recordings.

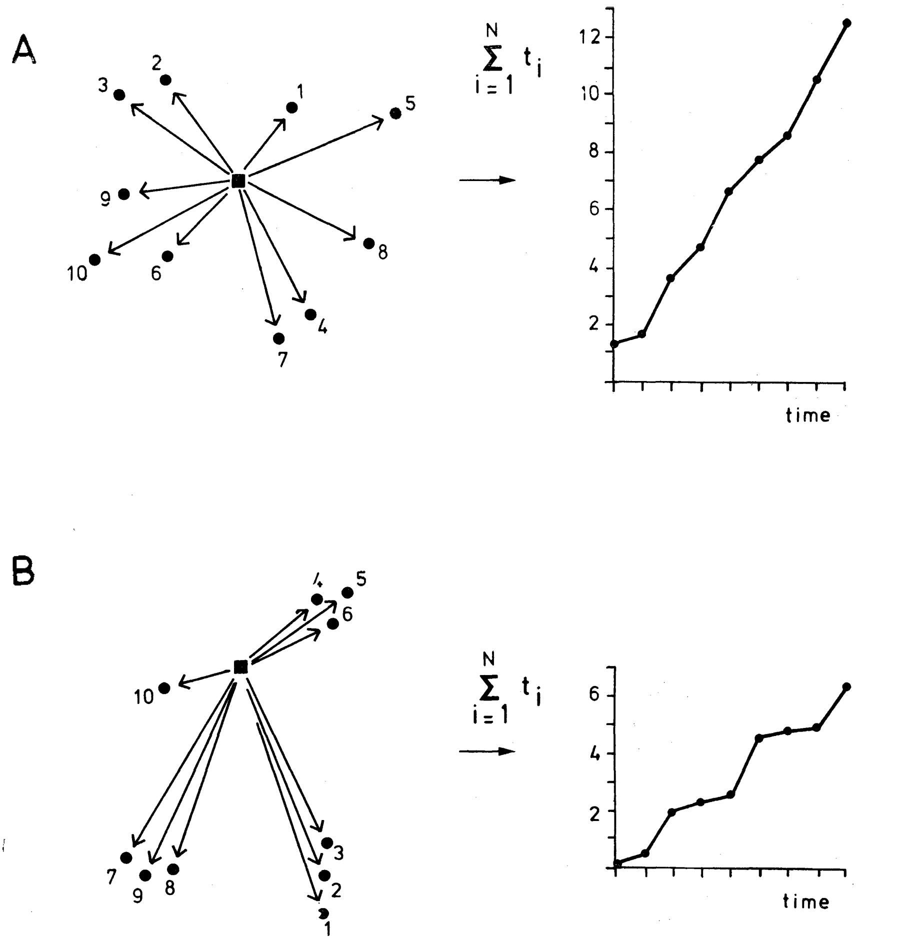

Fig. 5. – Temporal evolution of the *t* rapport relative to a random (A) and conservative-shifting (B) exploitation of the feeding ground.

In conclusion, the isolation of single aspects of orientation in space, followed by analysis under simplified and controlled conditions, is a common and useful strategy in studying the mechanisms and cues utilized by the animals (Schmidt-Koenig, 1975; Pardi, 1979). Still this approach hardly contributes to an understand'ng of the true ecological significance of spatial orientation. Knowledge of individual or specific strategies of space exploitation basically requires a field analysis of the phenomena, which need has brought about the creation of techniques for recording and analyzing positions. Moreover, the field study is a necessary complement to laboratory research on the physiological aspects of orientation, since it gives the proper experimental models and suggests new specific problems to the reductive study.

More important than assessing new complex analytical methods based on unverified behavioural assumptions in order to elaborate traditionally gathered data, is the need to improve field sampling methods so that integral information on movement patterns and/or relevant activities can be obtained. These methods must assign physiological or behavioural connotations to the positions recorded, so that the complex anatomy of utilized areas (i.e. the space exploitation strategy used by the animals) will be revealed and not simply general geometric information on " home range ". Moreover, when such macrophenomena as diffusion or competition between species are investigated, mass-investigation should be supported by microscopical studies which may significantly improve the euristic value and interpretative capacity of the models obtained by analyses conducted only at a macroscopic level.

Acknowledgements

I wish to thank Prof. L. Pardi for his criticism and advice during the preparation of this paper.

References

Adams L. and Davis S. D. (1967) – *The internal anatomy of home range*, « J. Mammal. », *48*, 529-536.

Amlaner C. J. (1977) – *Biotelemetry from free-ranging animals*. In: Animal marking, Proc. RSPCA Symp., Stonehouse Edit., London, 205-228.

Amlaner C. J. and MacDonald D. W. (1980) – *A handbook on biotelemetry and radio tracking*. Pergamon Press, Oxford.

Blair W. P. (1940) – *Home ranges and populations of the meadow vole in southern Michigan*, « J. Wildl. Mgmt », *4*, 149-161.

Brown L. E. (1966) – *Home range and movements of small mammals*, « Symp. zool. Soc. Lond. », *18*, 111-142.

Burt W. H. (1943) – *Territoriality and home range concepts as applied to mammals*, « J. Mammal. », *24*, 346-352.

Calhoun J. B. and Casby J. U. (1958) – *Calculation of home range and density of smal mammals*. U. S. Public Health Serv. Public Health Monograph, *55*.

Chelazzi G. (1980) – *Zonazione dinamica e meccanismi di orientamento nei molluschi litorali*, « Atti Accad. Fisiocr. Siena », *1980*, 275-293.

Chelazzi G. (1982) – *Behavioural adaptation of the gastropod* Nerita polita *L. on different shores at Aldabra Atoll*, « Proc. R. Soc. London », *B 215*, 451-467.

Chelazzi G., Focardi S. and Deneubourg J. L. (1983) – *A comparative study on the movement patterns of two sympatric tropical chitons (Mollusca: Poliplacofora)*, « Mar. Biol. », *74*, 115-125.

Chelazzi G., Innocenti R. and Della Santina P. (in press) – *Zonal migration and trail-following of an intertidal gastropod analyzed by LED tracking in the field*, « Mar. Behav. Physiol. ».

COOK S. B. (1969) – *Experiments on homing in the limpet* Siphonaria normalis, « Anim. Behav. », *17*, 679-682.

COOK S. B. and COOK C. B. (1975) – *Directionality in the trail-following response of the pulmonate limpet* Siphonaria alternata, « Mar. Behav. Physiol. », *3*, 147-155.

DALKE P. D. (1942) – *The cottontail rabbits in Connecticut*, « State Geol. and Nat. Hist. Survey Bull. », *65*, 1-97.

DEAT A., MAUGET C., MAUGET R., MAUREL D. and SEMPERE A. (1980) – *The automatic, continuous and fixed radio tracking system of the Chizé Forest: theoretical and practical analysis.* In: A handbook on biotelemetry and radio tracking, Amlaner, C. J. and MacDonald, D. W. Edits, Pergamon Press, Oxford, 439-451.

DIXON K. and CHAPMAN J. A. (1980) – *Harmonic mean measure of animal activity areas*, « Ecology », *61*, 1040-1044.

DUNN J. E. (1977) – *The multivariate Ornstein-Uhlenbeck process in studies of home range*, « Univ. of Arkansas, Stats. Lab. Tech. Rept », *2*, 1-12.

DUNN J. E. and GIPSON P. (1977) – *Analysis of radio telemetry data in studies of home range*, « Biometrics », *33*, 85-101.

FUNKE W. (1968) – *Heimfindevermögen und Ortstreue bei* Patella L. (*Gastropoda: Prosobranchia*), « Oecologia », *2*, 19-142.

HARRISON J. L. (1958) – *Range of movement of some Malayan rats*, « J. Mammal. », *39*, 190-206.

HARVEY M. J. and BARBOUR R. W. (1965) – *Home range of* Microtus ochrogaster *as determined by a modified minimum area method*, « J. Mammal. », *46*, 398-402.

HAYNE D. W. (1949) – *Calculation of size of home range*, « J. Mammal. », *30*, 1-18.

HEDIGER H. (1942) – *Wild Tiere in Gesangeshaft*, Schwabe, Basel.

JANDER R. (1975) – *Ecological aspects of spatial orientation*, « Ann. Rev. Ecol. Syst. », *6*, 171-188.

JENRICH R. I. and TURNER F. B. (1969) – *Measurement of non circular home range*, « J. Theor. Biol. », *22*, 227-237.

JEWELL P. A. (1966) – *The concept of home range in mammals*, « Symp. zool. Soc. London », *18*, 85-109.

KOEPPEL J. W., SLADE N. A., HARRIS, K. S. and HOFFMANN R. S. (1977) – *A three-dimensional home range model*, « J. Mammal. », *58*, 213-220.

LEUTHOLD W. (1977) – *African ungulates. A comparative review of their ethology and behavioural ecology*, Springer-Verlag, Berlin.

LOWE E. F. and TURNER R. L. (1976) – *Aggregation and trail-following in juvenile* Bursatella leachii pleii, « Veliger », *19*, 153-155.

MACDONALD D. W., BALL F. G. and HOUGH N. G. (1980) – *The evaluation of home range size and configuration using radio tracking data.* In: A handbook on biotelemetry and radio tracking, Amlaner C. J. and MacDonald D. W. Edits, Pergamon Press, Oxford, 405-424.

MCFARLANE I. D. (1980) – *Trail following and trail searching behaviour in the homing of the intertidal gastropod mollusc*, Onchidium verruculatum, « Mar. Behav. Physiol. », 7, 95-108.

MARTINSEN D. L. (1968) – *Temporal patterns in the home ranges of chipmunks* (Eutamias), « J. Mammal. », *49*, 83-91.

MAZA B. G., FRENCH N. R. and ASCHWANDEN A. P. (1973) – *Home range dynamics in a population of heteromyid rodents*, « J. Mammal. », *54*, 405-425.

MAZURKIEWICZ M. (1969) – *Elliptical modification of the home-range pattern*, « Bull. Acad. Pol. Sci. », Ch II, *17*, 427-431.

MOHR C. O. (1947) – *Table of equivalent populations of North American small mammals*, « Am. Midl. Nat. », *37*, 223-249.

MOHR C. O. (1966) – *Comparison of methods for calculating areas of animal activity*, « J. Wildl. Mngmt. », *30*, 293-304.

NEWELL R. C. (1979) – *Biology of intertidal animals*, Marine Ecological Surveys, Faversham, Kent.

PARDI L. (1979) – *Orientamento degli animali*. In: Enciclopedia del '900, Istituto dell'Enciclopedia Italiana, Roma, *4*, 965-988.

PARTRIDGE L. (1978) – *Habitat selection*. In: Behavioural Ecology. An evolutionary approach, Krebs J. R. and Davies N. B. Edits, Blackwell, Oxford, 351-376.

RANDOLPH S. E. (1977) – *Changing spatial relationships in a population of* Apodemus sylvaticus *with the onset of breeding*, « J. Anim. Ecol. », *46*, 653-676.

SANDERSON G. C. (1966) – *The study of mammal movements. A review*, « J. Wildl. Mngmt », *50*, 215-235.

SCHMIDT-KOENIG K. (1975) – *Migration and homing in animals*, Springer-Verlag, Berlin.

SCOTT T. G. (1947) – *Comparative analysis of red fox feeding trends on two central Iowa areas*. « Agric. exp. Sta. Iowa State Coll. Res. Bull. », *353*, 425-487.

SETON E. T. (1909) – *Life histories of northern animals*, Charles Scriber's Sons, New York.

SINIFF D. B. and JESSEN C. R. (1969) – *A simulation model of animal movement patterns*, « Adv. Ecol. Res. », *6*, 185-219.

THORNE M. J. (1968) – *Studies on homing in the chiton* Acanthozostera gemmata, « Aust. J. mar. freshwat. Res. », *19*, 151-160.

UNDERWOOD A. J. (1977) – *Movements of intertidal gastropods*, « J. exp. mar. Biol. Ecol. », *26*, 191-201.

UNDERWOOD A. J. (1979) – *The ecology of intertidal gastropods*, « Adv. mar Biol. », *16*, 111-210.

VANDERMEER J. H. (1972) – *Niche theory*, « Ann. Rev. Ecol. Syst. », *3*, 107-132.

VANNINI M. and CHELAZZI G. (1978) – *Field observations on the rhythmic behaviour of* Nerita textilis (*Gastropoda: Prosobranchia*), « Mar. Biol. », *45*, 113-121.

VOIGT D. R. and TINLINE R. R. (1980) – *Strategies for analyzing radio tracking data*. In: A handbook on biotelemetry and radio tracking, Amlaner C. J. and MacDonald D. W. Edits, Pergamon Press, Oxford, 387-404.

WOLCOTT T. G. (1980) – *Optical and radio optical techniques for tracking nocturnal animals*. In: A handbook on biotelemetry and radio tracking, Amlaner C. J. and MacDonald, D. W. Edits, Pergamon Press, Oxford, 333-338.