

## OPEN DISCUSSION ON TERRITORIALITY

The discussion was opened by *Professor R.C. Bigalke* who called for a definition of territoriality which would fit the peculiar circumstances under which it is exhibited by various species, discussed in the papers presented.

DR. F.R. WALTHER: I would like to make the following suggestions which have emanated from my work on horned ungulates.

The use which an animal makes of space enables one to recognise three categories:

(1) *Action area* includes both of the other two, i.e. home range and territory. It includes migration routes and every place on which the animals set foot, either as individuals or as groups.

(2) The *home range* of an animal or a group is that space where they stay for some time and become familiar with it. The structure of the home range is given by the use made of it in the animals' round the clock activities, i.e. their space/time system. There is no boundary since the home ranges of neighbours may overlap in part. Provided that the society is an open one, individuals are free to leave one herd and join another in a neighbouring home range.

(3) *Territory* is a space in which the animal lives for some time and which has a boundary established by that animal. This definition is restricted to a *place* so that it doesn't include the moving territory which the animal carries around and in which the animal is the centre of the territory. The latter is not territory but individual distance. There is, however, some correlation between them, for in certain species enlargement of the individual distance may precede taking up a territory. The critical point is that in the case of a territory, the animal can move independently of the centre. The boundary becomes evident by certain behavioural symptoms.

(1) *Defence*: This is only one of the behavioural characteristics of territoriality and I would prefer intolerance of, or even dominance over, conspecifics of the same sex within the boundaries to be regarded as the crux of the definition.

(2) *Loss of dominance* or even the assumption of submissive behaviour outside the territorial boundary.

(3) *The threshold for flight* is higher for an animal inside its territorial boundary, even for predators and this can be established by measuring the flight distance.

(4) *Herding response*: In many species only the males are territorial. There are no boundaries for the females, which would tend to wander indiscriminately were it not for the efforts of territorial males to herd them back from his boundary. In so doing, he indicates clearly that, for him, the boundary exists.

(5) *Sudden stop at the boundary*: When a territorial animal approaches its boundary, for instance when chasing an intruder, the territorial animal will stop at the boundary, though the intruder runs out.

(6) *Conflict behaviour*, as was mentioned yesterday, may be shown by the territorial animal as he leaves his territory, even temporarily.

(7) *Marking of the territory*: In those species in which this occurs, the nature of the marking system relates to the structure of the territory. Either the centre, or the boundaries, or both may be marked.

*In summary*, the behaviour of the animal inside his territory is altogether different from that outside his territory. In the definition of territoriality, I feel that the occurrence of a *boundary* is a

major point and defence only *one* possible symptom for the existence of a boundary. Whether the boundary is a line or a zone, does not seem so important.

In regard to the phenomenon of territoriality in ungulates I wish to emphasize the following:

(1) There are some species which are not territorial at all, e.g. the majority of the Bovinae and Caprinae.

(2) In territorial species there may be 3 different types of territory:

(a) One of them seems to exist in the bushbuck, from Verheyen's work, and also in the steenbok from a few – admittedly incomplete – observations which I have made. These species are basically solitary and it seems that male and female may have separate territories. The sexes may join in a no-man's land between the territories, or the male may leave his territory and come into that of the female for mating.

(b) Another type we know for sure to occur in the Dik-dik, but we also have reason to assume that it is found in some species of Neotraginae and Cephalophinae. Here a pair, plus the offspring until it reaches maturity, live in a territory for a *long* time. If ecological conditions do not change, and if the animals are not disturbed, they may stay in the territory all their lives.

(c) The third type is more usual. Here only the males become territorial and this type is combined with harem behaviour. This means that a relatively constant group of females, with their offspring, may stay together with a male more or less throughout his territorial period. This I found in Grant's gazelle in clearings in bush areas where territories of this species have an average diameter of roughly 800 metres.

In Thomson's gazelle, even in precisely the same areas in which Grant's gazelle, described above, occur, the territorial males have no constant harems with them. The territories average about 200 metres in diameter and are located within the home ranges of the female herds. The single territorial males are visited by the roaming females on their daily circuit. As a result, the females are together with a given male in his territory for only a few hours per day. Apparently this seems to be the most common kind of territoriality in the so-called antelopes.

Estes observed a very similar situation in the wildebeest and he recalled that single territorial bulls kept their territory in the Ngorongoro crater for months and even years. However, in the neighbouring Serengeti Plains, the wildebeest moved permanently. As this has been discussed already, it will not be repeated here; the territories exist only during the rut, and are only kept for a few hours or, at most, for a few days. In Uganda Kob, Buechner found the so-called "arenas" to be very small territories, of diameter between 30 and 50 metres, which are clustered together. Only the females in oestrus come into these arenas. But in the same species, besides these small territories in the arenas, Leuthold found very large territories outside the arenas.

In Grant's gazelle, the occurrence of single territorial males, together with relatively small, but approximately constant, harem groups in the *bush* area has already been mentioned. The situation is different on open range. Here too, certain males become territorial; however their territories are within the home-ranges of large mixed herds, composed of females, young animals and fully adult but non-territorial males. In the same way as the female herds in the Thomson's gazelle, these mixed herds come into the territories in the course of their daily circuit. The territorial Grant's buck in the *bush* area, like the territorial Tommy buck, drives away every other adult male which happens to enter his territory. However, the territorial Grant's males in the open plains areas do not do so. They show a moderate dominance over the known territorial males as long as these are in

their territory but they do not fight them and usually do not chase them away. They perform dominance displays in which the territorial male is always clearly superior, and they interfere as soon as one of the known territorial males tries to approach a female. As long as the herd is inside the territory, only the territorial buck has the right to copulate. When the mixed herd leaves his territory he may remain solitary or may even leave together with the herd. Outside his territory, he behaves no differently from any other adult bachelor, until the herd comes back to his territory where he regains dominance over the other adult males and the exclusive right to copulate.

I have tried to show you that even in the same species we have different types of territoriality and may only add that it makes a great difference whether we observe an animal at the beginning, height or end of his territorial period.

When we are talking about territory, we must therefore bear in mind that there are species – specific types, different types within the species and differences according to the age of the territory.

DR. JEWELL: It is very useful to start, as Dr. Walther did, by considering the whole spectrum of behaviour that comes into this idea of territoriality and especially important to include home range in what one is talking about.

I really like to regard territory *more* generally than Dr. Walther did, and would not even mind, when speaking about mammals, if we include home range and strict territory under the general term of territory.

The reason is that one so often finds that in home range behaviour, an animal or group of animals are using a certain area and there is this overlap which we've mentioned already. Also, it is characteristic that, within the home range of a given group, there is an area that only those animals in that group use.

This applies to several species of birds, especially waders, such as described by Catelko in the Arctic, which, I remember, had this kind of behaviour (speaker refers to diagram). There was a zone which was exclusive to them. And it could be that it is this element of exclusiveness which is the central idea of territoriality and of possessing a territory.

I know that Schaller, for example, described gorillas as completely overlapping in home ranges but I would guess he probably didn't know enough about those groups and their relationships to know what was really happening. And in the sheep that I've studied, for example, it is very clear indeed and I have called this area the "monopolized zone". As I see it, there is a whole range of behaviour which should be called territoriality, it is territorial behaviour, something the animal does. It may express itself as a home range, and usually within this will be a monopolized zone. You will then have territories of the kind described as examples by Dr. Walther. At the other extreme, you could have the kind of arrangement that I have described in topi, where there is no actual space, there isn't a territory. It is something around the animal that goes with him, but which I think is, well, from its behaviour, is certainly territoriality. That's why this covers everything, and I don't really like the ideas that Dr. Walther expressed. I called it a "ward", for want of a better word (I don't like that either), but it was to indicate that there is something common to these, and, as I've said, I really wouldn't mind if you called all this territory. I found it less and less useful to distinguish between home range and territory. More and more examples come up, and you find what a continuous spectrum it is. But there does seem to be something a bit different when the animal has no place on the ground to mark or relate himself to at all. He has an area around him, and yet it's very distinctive territorial behaviour, that's why I suggested this term.

One sees all degrees of this kind of behaviour, and one is very often involved with a male showing strict possession of territory and females also probably showing territorial behaviour, but having what we used to call a home range for them. Waterbuck are a good example. The males have territories with very good boundaries, the females wander over several, but Spinage describes quite specifically in his paper the fact that these groups of females are rather antagonistic to other females and tend to push them out. So they have a home range, but there's an element of defence in it towards other females. When one has this kind of combination of activities between the sexes within a single species, it gives, I think, even more credence to my feeling that one should see these all as a spectrum of expressions of the same kind of thing. But one should return to the fact that it is all territoriality, something that the animal is doing, an aspect of its behaviour, and seen that way, I think that a good many of the differences of opinion that we've had expressed do disappear. There was one particular point I noted in what Dr. Walther said and that was his statement that he thought the home range didn't have a boundary. Now the boundary is a very difficult concept, and as you know some very good statistical concepts of home range have been developed, particularly for small mammals, relating home range to the use of the area and distance from the centre. The animal uses it less and less, there's no actual boundary, it just sort of tails off – but I believe in many species one does see a boundary to home range because the animals, although they overlap in their home ranges and so on, very definitely don't go beyond a certain area and even behave somewhat apprehensively if they do. A good example of this is baboons, probably, and coyotes, which Kaufman studied and he described this very well. So I guess home ranges can have a boundary which the animals recognise and this again is one of the difficulties of distinguishing between home range and territory.

DR. H. KLINGEL: One question to Professor Walther first: Did you say the flight distance in the territory is greater than outside the territory?

PROF. WALTHER: The flight distance is less.

DR. H. KLINGEL: I would like to criticise a few things which Prof. Walther has mentioned here. First, the moving territory. This term has certainly been used wrongly, but I think there is some evidence for moving territory. We should try to stick to some sort of definition for the word territory, otherwise this term is completely useless and if everybody is using it in a different sense then we would have to call it territory (Jewell) or territory (Walther) but *not* territory (Klingel), because I'm trying not to make a new definition of it. But I think there's a reasonable definition which is very simple and which applies to all cases I can think of. And that is a definition which has been given by Nobel in, I think, 1937 – and this says, 'territory is a defended area'. Now this naturally would include quite a number of other things and one might have to define it more clearly, but then you have the difficulty that not everything that is territoriality and not everything that is a territory does fit in. Now let me discuss one particular point which Prof. Walther has mentioned – the individual distance. The individual distance is a space which is usually very well defined by the distance from the animal to the edge of it, which the animal always carries around with it. This individual distance has to be overcome within a species and under certain conditions, for example when two individuals of a species have to take up a closer contact during social grooming or copulation. There are also different mechanisms which serve to overcome this individual

distance and to prevent the animals from fighting each other, which they normally do when another animal comes within this space which surrounds the animal.

Now, what I want to criticise is that individual distance could be the limitation for the boundaries of a territory. I think this is completely wrong and it can't be in this way, because, first of all, the individual distances of all these animals which you have described and all these animals which we are talking about, are much smaller than the territories, maybe with the exception of the Uganda Kob, but probably not even in that case. The individual distance is kept by the territorial animals when they are at the edge of their territory.

PROF. WALTHER: I spoke about the enlarged individual distance which may precede territoriality – I'm well aware that the individual distance is very small, much smaller, but it comes to the same, we can observe that before he becomes territorial, such a male is easily angered, and chases other males out of the way, and then he has a space around him of 50 yards, 100 yards, even more, but he is not yet territorial. He carries this distance with him, what I call enlarged individual distance. This proceeds, in some instances, to becoming territorial.

DR. H. KLINGEL: Well, I did see that point before but still I don't see that the individual distance is enlarged, because, individual distance, the space around the animal, does not apply to conspecifics alone, it applies to every other animal around it.

PROF. WALTHER: The individual distance between males is usually higher than between females. When you have two females, the individual distance depends largely on the activity; it is larger during grazing, for example, than in resting. Between females you have a smaller individual distance than in males. So you compare grazing males with grazing females; resting males with resting females. And before becoming territorial, this male keeps the other males at an even larger individual distance, but it may proceed to territoriality, and I see a connection between territoriality and the so-called moving territory, but this I wouldn't call territoriality in its true sense.

DR. H. KLINGEL: Yes, I see this point, but as far as I'm informed, individual distance does not apply to conspecifics alone. Now if you use this term 'individual distance' only as a sort of . . .

PROF. WALTHER: But how far do you make it then? For example, we have tick-birds on certain animals, they can sit on the back of the animals, there's obviously no individual distance.

DR. H. KLINGEL: Oh yes, but as far as I know, this term has been used for the space which is cleared by the animal which is standing in the middle, and normally, among animals of the same size with which it hasn't got any special relationship. In the case of the tick-birds, of course, it is a completely different matter. If you want to employ this term here, it loses its value because again, like the term territory, it is used for different things.

PROF. WALTHER: I always consider individual distance mainly applied to animals of the same species.

DR. H. KLINGEL: I want now to get on to Dr. Jewell's remarks about the monopolized zone. I do not see any difference between your monopolized zone and what many people, including myself, call a territory. If we stick to the definition that a territory is a defended area then here (diagram) is, in fact, a territory, but this does not say that the animals are restricted to that territory, they may have additional range, additional home range, and this is what is overlapping. To my mind, especially in the case of the sheep, there is no basic difference, and you have this in many other species as well. There's a well-defined territory which is defended, and in addition to that, there is, in between the territories, a neutral zone which either member of the population can use at any time. And this is exactly what you have. The second point is about your "wards" which are kept by "wardens" who are occasionally "rewarded" by the presence of females there. These wards are defended, aren't they? (Dr. Jewell signifies agreement.) They are defended for some time. The term territory does not imply that the territory is kept for any length of time, it says it is *kept* – for minutes, for hours, for years, though it doesn't say so in the definition, so why don't we call it a territory? And this now, to come back to Prof. Walther's idea, this would be a territory which is moving, it is defended all the time. It is not the territory actually, which is moving, it is always a new territory which is established. But since it is partly established over the same range as the old territory we can call it a moving territory. The *pseudo*-territories have been mentioned before, they have been described by Watson as such in the wildebeest and they come into this context again. They are not moving territories as in the topi, because there it's definitely a very limited area which is only defended for a very short time, so the territory itself is, in fact, left behind, and when the animal moves along with the herd, it starts a new territory. This is a major difference so in this instance we would not need to call it anything else but a territory, it would not be a moving territory. I would not equate this with the "ward" – I would make a slight difference there, since the new wards are in fact covering a large portion of the old ward, I would call this a moving territory. But not in the wildebeest, because they migrate for several kilometres, up to 10 kilometres, before establishing a new territory, and they don't have a territory while they are migrating, they make a new one and in between they are non-territorial, so there we just have territories.

PROFESSOR IMMELMAN: Before we go on discussing the different types of territoriality which occur in animals we should arrive at a common definition of territory. Being an ornithologist, I have noticed that mammologists have been talking about territory in quite a different way than we do, and so I would like to comment on several things which have been said during the last few minutes and during the last days to try to solve several things arising out of the definition of territory – just given by Dr. Klingel – that territory is any defended area.

(1) In many papers it was said that territoriality is mainly an affair of the male and of course this is very different in the different groups of animals. There are species in which only the males are territorial, in other species males and females have got their own territories, at least outside the breeding season, like the European robin, or within the breeding season, like in the humming-birds. There are species where male and female together defend a territory, like in many birds, especially tropical birds, and then there are species in which a whole group defends a territory together like, for example, in many species of babblers. So the participation in territoriality of course doesn't go into the definition.

(2) Then there's the question of time. There are species which are territorial all their lives,

there are other species which are territorial only for the breeding season, and there are species which defend territory for a very long time, and there are others which defend territory only for days or hours or minutes, and so we come to this question of a moving territory. In birds, there are several examples of territories being held very, very briefly, i.e. in migrating birds. It has been observed in recent years that many of our European passerine birds which migrate south do defend a small territory as soon as they arrive at a place where they are going to rest. This may be for two days, it may be for a week, it may be for five minutes – but still they establish a territory and at least on their way back to Europe, they sing at their territory, this means they mark that territory. It has also been found that some of these birds come back to the same resting place year after year, so they have got a definite territory which they inhabit and which they defend, perhaps two days per year or three hours per year, but they come back next year and defend the same territory. So time doesn't go into the definition of territory.

(3) The size of the territory, of course, can be very different in different groups of animals. It can be very large in reptiles, or as Dr. Klingel said, yesterday, in the wild ass. It can be very small, and in fact, territory can be as small as the individual distance which is the case for example in many colonial breeding birds, which defend a territory round their nest, which is just as big as the birds can reach with their beak – that's just the individual distance.

(4) Then the object of defence can be very different again in some species. Only other males are driven out of the territory, as we've heard in several of the lectures. In others, males and females are driven out and now I come to your point, territoriality is not restricted to conspecifics. At least in birds we have got examples for interspecific territoriality. There was a recent paper by a man, I think his name was Cody in "Condor". He showed that in several species of North American Woodpeckers, there is definite interspecific territoriality. These woodpeckers obviously inhabit the same ecological niches and so there has to be interspecific territoriality. So if you are looking for a general definition of territory, we cannot restrict it to conspecifics, in some cases there are other species against which the territory is also defended.

(5) The purpose of the territory does not go into the definition at all, because as you know, there are feeding territories, breeding territories, roosting territories and so on.

(6) Even being stationary or not, could not go into a definition of territory because as Dr. Klingel mentioned on Monday afternoon in the wildebeest, for example, the animals establish a small territory wherever they are, so they have got some sort of a moving territory but it's not really a moving territory, it's a new territory everywhere. And the expression 'moving territory' – I think it was introduced by Peter Mahler – really means the individual distance.

Now at the end I come to the difference between individual distance and territory. Something has been said about this already by Dr. Klingel, but one essential difference, I think, is that in the individual distance the thing which is defended is always the individual, while in territory it is something else *also*. It is food or it is the female, or it is a certain area, and so on. It is not only the individual itself. Of course the individual itself is defended also, but it also defends something else, at least an area where something else may intrude. Like the migrating birds which take up a territory and defend nothing else than the territory and the females enter later. And then, I think, defence is really the main characteristic of a territory but not only defence of the individual itself, but the defence of something else. And you said, defence is not so very characteristic for territoriality.

DR. WALTHER: It is not *the* single characteristic . . .

Well, I will comment on this because defence in many mammals might not be as obvious as it is in many birds because mammals and birds have got different ways of marking their territories. Some species in both classes mark them optically, although that's rather the exception. But the main method of marking in mammals is of course, smell, and in birds, acoustically. So a bird which marks its territories has always to stay within its territory and has to be singing while a mammal may deposit its scent mark and may even leave the territory, and there's still this marked boundary which is completely absent in birds as soon as the individual leaves the territory. So this marking and defending may be less obvious in mammals than it is in birds, but still it is there, at least at the time of establishment of territory. And I think therefore that for finding a common definition of what we are talking about, we have to rely on Hinde's definition: 'Territory is any defended area' and one might add: Any defended area where not only the individual itself but something else is defended. This definition of course is very very broad and within it there are very many types of territoriality.

CHAIRMAN: Would you include in your definition of something else besides the animal, the animal's social status as a possible something else?

PROF. IMMELMAN: That's a question which is very difficult to answer. I saw Dr. Walther shaking his head when I said 'food' because a fight going on at a feeding-dish – is this territoriality or is it not? Even with this broad definition of cause there is no sharp limit: This is territoriality and this is not. Well, I wouldn't include it. This broader situation is where you really can argue.

CHAIRMAN: Professor Immelman has looked at this across taxonomic boundaries and tried to broaden this to include a number of expressions of this kind of behaviour.

MR. RIBBINK: Of the three speakers, I would choose to support Dr. Walther and bring in yet a further discipline in terms of introducing fish. Firstly, concerning individual space, when fish begin the reproductive season, these fish would no longer school but would remain in the surface waters and they would not tolerate the usual distance between themselves and other fish. This is not yet, as I see it, territoriality, but it is intentioned territoriality because for these fish, and I am dealing primarily with cichlids, to have a territory they must claim a space on the substrate. These fish do not tolerate the individual distances or the individual proximity of others in the surface water. I feel this is a form of intentioned territoriality. This is, I think, in agreement with Dr. Walther.

Now, the second point that I want to make, also refers to something that Dr. Jewell raised and he can possibly supply me with suitable terminology. A territory in these fish is guarded and defended and it is into the territory that males encourage females, very much as Thomson's gazelles do. However, these territories have a definite boundary and by scuba-diving we noticed that this boundary, which was also suggested by Dr. Walther, is recognised by not only the fish within his territory, but also by those which flank his territory. As in the Thomson's gazelles, the two fish will come to the boundary and they will have a specific form of boundary fighting which establishes the boundary. As with Thomson's gazelle, we also find, not a dung-heap or anything of such nature, but a plant will in fact mark the centre of the territory. We found that there is also an inner-territory or monopolised zone and it is towards this inner-territory that the females are

encouraged and it is only in this territory or monopolised zone that the actual courtship takes place and spawning takes place. It is within this that the eggs are laid and nests are built. These are small depressions in the sand cleared by the mouth in most cichlids. We can consider all these territories to be within a home range. During courtship, the females roam and they are encouraged towards the inner-territory, whereas all males are rejected.

Now, the time-aspect which Dr. Walther introduced, is also very important. From laboratory studies, not field studies, we found that initially, in the establishment of a territory, the male will reject or chase away all other fish, be they male or female. Later on at the peak, which was suggested by Dr. Walther, they will encourage females, not chase them away but most definitely act aggressively towards other males. And a very interesting phenomenon which we found at Lake Sibaye while diving – it has never been found in cichlids – is that at about 11.30 each day the territories break down. Males will tolerate both males and females and then by about midday one finds that these fish will feed communally, four males at a time, possibly more, from a single feeding zone. Therefore, as Dr. Walther suggested, it is important when discussing territoriality, to define the time at which one is making one's observations, the initial period the peak or the breakdown.

MR. BOULTON: I'm very much interested in the last speaker's and Dr. Immelman's observations, because they have, in a sense, politely stolen my thunder. I don't want to end this controversy which has pretty well been dominated by studies of ungulates. I would like to make two points only. The first was pointed out by the last two speakers. Territoriality is a concept; it occurs in a great number of different kinds of animals, including insects.

The second point is that words are for the purpose of inter-communication between humans. Therefore, before we proliferate terms without defining them, we ought to nail down the concepts, so that what was territory in the literature of 1930 and 40, does not become something else in the literature of 1970. These are really the main points that I wish to make. I don't want to take time and bore you with a lot of details but there are a couple of points, especially that Dr. Immelman made. Territoriality in colonial birds exists but there are really no colonial mammals, or very few, perhaps the gorilla might be called a colonial mammal in its breeding habits, but certainly most of the territoriality which has been discussed so far does not involve colonial breeding species. So, as Dr. Immelman said, a territory can be only a metre in diameter for a bird which physically occupies a very large part of that space. Territoriality is a concept, not a succession of words.

PROF. BROEKHUYSEN: It is pretty obvious to me that we will not come to a conclusion about what territoriality is. Also I would like to have this concept divided, perhaps in the future. Firstly, where an animal has got a particular area – which is of course there, and is defended by the male or female – then we could perhaps call this 'territory maintaining behaviour'. In other words, through that behaviour, the territory is maintained, it is kept there. Any other behaviour, as in these very interesting cases, pointed out by Dr. Walther and others, where the animals move and they defend the area around them, having a moving territory and not an established one, we can perhaps call territorial behaviour. We then make a distinction between territory maintaining behaviour, which is a stationary thing, and territorial behaviour. Territorial behaviour, therefore, is behaviour which would be applied also in territory maintaining behaviour. We will never be able to give a general definition of territorial behaviour if we don't split this up.

If I may just say a few words on migrating birds which Dr. Immelman mentioned and which I would like to correct. It is quite true that a lot of palearctic waders do come back to the same area. I don't think it has been established that those birds which come back to the same area here, like the Steppe Buzzard which, having twice flown to Russia, came back within two miles of the same area, exhibit territorial behaviour. I have studied the Steppe Buzzard carefully and I have not discovered any territorial behaviour. They are there, but they allow others to come in as well, they come to the same place, but they don't defend it against others. Therefore, I feel that this is not territorial behaviour although they come back to the same wintering place.

MR. OWEN-SMITH: We can all agree on what territorial behaviour is, we might quibble a little bit about different definitions, whether it is defence of an area, or intolerance or dominance. I personally prefer the definition spatially localised dominance, in that I don't see my animals chasing away other animals from the area. There is a variety of interactions which take place within that area which are related to maintaining dominance within a fixed piece of space. What we are arguing about is when a territory is not a territory. Territorial behaviour is characteristic with species. Whether a territory exists or not, is something to be looked at. One population of that species might be territorial, another population existing elsewhere, might not be. The existence of territories is a system of population organisation which is super-imposed, which is the result of behaviour patterns between individuals. It is therefore highly flexible to the particular ecological circumstances operating in that particular study population. If it is possible for individuals in the population to maintain a fixed location within a fixed area, you may have a fixed territory. If they have to migrate or move, you may get diminishing degrees of localisation, you may get temporary territories, you may get moving territories or you may get a shifting field of dominance occurring, depending on how the population moves and therefore you have a gradient leading from a fixed territory to a moving territory. The other possibility is that territorial expression is also related to population density. This seems to be the significant difference between populations of primates, such as the vervet monkey and the grey langur in which one population is territorial and the other one is not territorial. As population density diminishes, so the likelihood of interactions between neighbouring individuals decreases, so the density of marks of that individual, if it is a mammal, decreases, so the audibility of its vocal signals decreases outwards. You can therefore have a trend from the strictly exclusive territory to a broader stage, a bigger territory in which some overlap occurs in the borders and you might have a monopolised zone in the centre. If the individuals meet so seldom, then you might just have a system of overlapping home ranges.