VOL. 52, NO. 1 March, 1977

THE QUARTERLY REVIEW *of* BIOLOGY

ON TERRITORIALITY IN UNGULATES AND AN EVOLUTIONARY MODEL

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ABSTRACT

The behavioral characteristics of territorial ungulates are reviewed and compared with non-territorial species in terms of social distribution, spatial dispersion, and interaction patterns. Territoriality is related proximally to dominance and ultimately to mating enhancement. Alternative male mating strategies are categorized. Selective gains are estimated by the potential mating enhancement factor (PMEF) and costs by reduced chances of survival. The likely lifetime mating enhancement (LLME) resulting from territorial versus roving/rank dominance strategies are calculated for model populations. Ecological conditions favoring territoriality are discussed, and a comparison is made with territorial systems in other animal groups. There is a need for more empirical data.

INTRODUCTION

TERRITORIALITY is a widespread behavioral phenomenon. Its existence has been reported from every vertebrate class, and in several invertebrate orders (see review by Brown and Orians, 1970). The term is being applied increasingly, both by popular writers and social psychologists, to aspects of human behavior (Ardrey, 1967; several papers in Esser, 1971), without any general agreement among zoologists as to the general characteristics or functions of territoriality.

The definition most widely followed is that due to Noble (1939): a territory is simply *any defended area*. Burt (1943) suggested the modification, at least for mammals, that a territory should be both *defended* and to some degree *exclusive*. Pitelka (1959) held that the ecological importance of *exclusive areas* should be emphasized, rather than the mechanisms by which such exclusion was maintained. Emlen (1957) criticized the teleological implications of "defence," and contended that a territory was simply the area within which an individual was *aggressive and supremely dominant* with respect to certain categories of intruder. Marler and Hamilton (1966) proposed that territories arose when an external reference for *dominance was fixed in space*, and emphasized some degree of *exclusive occupancy* as an important ecological consequence. Schenkel (1966), considering mammals, proposed substituting for "defence" a criterion of *intolerance within a fixed spatial area,* but added that it should be possible for the occupant to maintain surveillance over this area so as to be able to intercept intruders. Jay (1968), discussing primates, suggested that a defended territory be regarded as a special case of spatial exclusion. Walther (1972a), for ungulates, pointed out that behavioral interactions readily interpreted as examples of defence might be highly infrequent, and emphasized the importance of a *subjective boundary* modifying behavior inside and outside the delineated area. Wiley (1973) considered that territoriality occurred where *dominance depended on location*, and contrasted the *reciprocity of dominance* among neighboring territory holders with the fixed dominance relationships prevailing in hierarchal systems.

While it seems to be agreed that a territory is a geographically fixed spatial area, attempted definitions place varying emphasis on behavioral relationships with this space expressed in terms of concepts of *defence*, *exclusion*, and *dominance*. Each of these criteria is open to criticism. Communicatory signals such as vocal advertisements or scent marks may be more important in maintaining territorial exclusion than the active interception and driving out of intruders. While the former can be regarded as constituting "indirect defence," similar behavior is exhibited by non-territorial species; a repulsive effect on rivals cannot automatically be assumed. Furthermore, it may be difficult to distinguish aggressive displays, putatively functioning to defend a territorial space, from similar actions related instead to defence of a female, access to a social group, or simply defence of dominant status — except by the concurrent observation that recipients avoid intruding into the area occupied by the aggressor. On the other hand, exclusive occupancy could arise not only through active social inhibition, as implied in the original definition, but merely as a result of physical barriers, preference for an unexploited food supply, or passive avoidance of strangers (Brown and Orians, 1970). Dominance is itself a complex phenomenon, with its own problems of definition. It may be identified by consistent success in aggressive interactions, spatial displacements, priority of access to desirable objects, or by constraints on the behavior of subordinates. However, rankings determined by different measures do not necessarily agree (Gartlan, 1968; Bernstein, 1970).

Part of the confusion arises from varying emphasis placed on the different levels of functional interpretation: (i) *immediate effects* of a display in terms of the response shown by a recipient; (ii) *proximate consequences* in terms of the subsequent structuring of social relationships among individuals; and (iii) *ultimate results* in terms of differential genetic success.

Consideration of genetic advantages is usually limited to suggesting possible benefits, either to the individual or to the species, without any critical examination in the light of modern evolutionary theory. Proposed species benefits invoke interdemic or "group" selection (Wynne-Edwards, 1963), but the weight of modern opinion is that such processes could not outweigh individual selection except under very unusual conditions (Williams, 1966; Wilson, 1973). Thus, any advantages for the species, or local populations thereof, are merely coincidental. The shortcomings of models based on individual selection are due to failure to take a sufficiently farsighted perspective. It is not just individual survival value that needs to be considered, or even reproductive success, but rather the long-term viability of gene combinations within a particular ecological and social milieu. Selection operates directly on the phenotypic expression, both morphological, behavioral, and organizational, of a genotype. This itself is subject to environmental modification.

Individual genetic success is influenced by four processes, operating simultaneously but, potentially, to varying degrees: (i) differential *survival*, related to access to food, shelter sites, or other maintenance needs; (ii) differential *reproductive* output, through variable mating contributions by males and litter or clutch size of females; (iii) differential *progeny viability*, resulting from nutritional regime, predator protection, and other processes influencing the survival of offspring from conception through to reproductive age; (iv) *progeny quality* at maturity, based on both physical and social attributes affecting relative competitive capabilities (see Crook, 1972; Goss-Custard, Dunbar, and Aldrich-Blake, 1972). A useful perspective is given by game theory. The final measure of success, or "goal" of behavior, can be viewed as the maximization of the relative genetic contribution to subsequent generations. The pattern of deployment of particular behaviors in certain contexts constitutes a strategy potentially enhancing success in one or more of the above processes. This does not require any conscious teleology, but is simply a teleonomic (Pittendrigh, 1958) response to the conditions of life. The phenotypic characteristics of individuals that have made the greatest genetic contributions in the past are those prevailing in the extant population.

Previous reviews of territoriality have been based largely on avian models (e.g., Hinde, 1956; Brown and Orians, 1970). Until recently, only a few examples of mammalian territoriality were known, and most of these were poorly documented (see Eisenberg, 1965). Field studies completed within the last decade have revealed that territoriality is also a widespread behavioral trait in mammals, particularly among ungulates (see, for example, various papers in Geist and Walther, 1974). Certain features of mammalian territorial systems point to the need for a reappraisal of traditional concepts in the light of this new knowledge.

This is what I propose to undertake here for one particular taxonomic grouping, the ungulates (which I will take to include members of the orders Artiodactyla, Perissodactyla, and Proboscidea). My approach will be first to consider the behavioral and social characteristics of territorial species, contrasting these with those of non-territorial representatives. Rather than superimpose any preconceived definitions, I will accept as exhibiting territoriality those species so regarded by their principal investigators. Controversial cases are discussed in the text. This will lead to an evaluation of criteria of territoriality based on proximate functional consequences. Next, the likely genetic results of territoriality will be examined, and this examination will lead to the development of an evolutionary model. From this basis, the ecological conditions likely to favor territoriality will be assessed. Finally, the conclusions reached for ungulates will be related to the wider phenomenon of territoriality in other animal groups. This paper expands some ideas expressed briefly in a previous publication (Owen-Smith, 1972).

TERRITORIALITY IN UNGULATES

Incidence

Territoriality is of widespread occurrence, but of varying incidence, among the different ungulate families. It seems prevalent among most of the so-called antelopes of the subfamily Bovinae. It appears also in some equids, rhinoceroses, camelids. and in the sole extant antilocaprid (Table 1). It is generally absent, with a few interesting exceptions, in the wild cattle tribe (Bovini), among sheep and goats (Caprinae), and in deer (Cervidae) (Table 2). For remaining families, evidence remains scanty.

Social Distribution

Almost without exception, territoriality is exhibited only by adult males. In a few species, females restrict their movements to individual male territories, but do not manifest other behavioral characteristics of territoriality, e.g. dikdik (Hendrichs and Hendrichs, 1971); klipspringer (Dunbar and Dunbar, 1974). (Scientific names listed in Tables 1 and 2 will not be repeated in the text.) Suggestions that females might hold territories independently of males in steenbok (Jarman, 1974; M. Cohen, pers. commun.), and possibly in other small antelope species remain unconfirmed. For the Indian rhinoceros, Üllrich (1964) has claimed, from observations in Assam, that individuals of both sexes hold separate small feeding territories on the meadows surrounding ponds. However, Laurie (pers. commun.) has found no evidence of such territories in Nepal, and the Assam situation needs further investigation.

At any one time only a proportion (between one-third and two-thirds) of the adult male segment of the population exhibits territoriality. In the more sociable species, the two classes of adult males are readily distinguished by their grouping patterns. Territorial males are either solitary or attached to female groups, whereas so-called "bachelor males" are associated in all-male groups, along with a proportion of subadults. In less sociable species, such as the white rhinoceros, non-territorial males are also solitary, and are distinguishable only by behavioral criteria. Failure to consider this possibility could account for the reported absence of territoriality in East African populations of black rhinoceros (Schenkel, 1966; Goddard, 1967) and bushbuck (Alsopp, quoted by Leuthold, 1974; Waser, 1974). In Zululand, black rhinoceroses exhibit a similar pattern to that in the white rhinoceros, with dominant and subordinate bulls coinhabiting the same territory

TABLE 1

Ungulate species reportedly exhibiting territoriality

		POP. DENS.	GROUP SIZES			
		/km^2 local,	male		female	
SPECIES	AREA	overall	terr.	bach.	no. ♀s	aggreg.
PERISSODACTYLA						
Rhinocerotidae						
Ceratotherium simum	Umfolozi,	5.7	1	1	1	2
white rhinoceros	S. Africa	3.2	—	—	1-2	1-7
*_Diceros bicornis_	Hluhluwe,	0.9	1	1	1	2
black rhinoceros	S. Africa	0.8	—	—	—	—
	Ngorongoro,	0.3	1	1	1	2
	Tanzania	—	—	—	1-2	1-5
	Tsavo,	—	1	1	—	—
	Kenya	—	—	—	1-2	1-4
*_Rhinoceros unicornis_	Kaziranga,	—	—	1	1	2
Indian rhinoceros	India	0.8	—	—	—	—
Equidae						
Equus asinus	Danakil,	—	—	—	—	—
African wild ass	Ethiopia	—	—	—	—	—
Equus grevyi	N.F.D.,	6+	1	2.1	5.6	8
Grevy's zebra	Kenya	—	—	1-9	1-26	1-450
ARTIODACTYLA						
Tayassuidae						
*_Dicotyles tajacu_	Arizona &	20	—	—	—	8
collared peccary	Texas,	—	—	1-4	1-6	2-50
	U.S.A.			(♀s)		
Camelidae						
Lama vicugna	Peru	30	1	—	—	—
vicuna		—	(+ ♀s)	1-25	—	5-10
Cervidae						
Capreolus capreolus	England	28	1	1	1	2
roe deer		—	—	—	—	—
	Swiss	24	1	1	1	2-3
	plateau	—	—	—	—	1-10
Antilocapridae						
Antilocapra americana	Montana,	1.6	1	2.4	—	—
pronghorn	U.S.A.	—	—	—	—	4-23
Bovidae						
Rupicaprinae						
*_Rupicapra rupicapra_	Switzerland	40	1	sev.	—	—
chamois		—	—	—	—	5-25
Bovinae						
Cephalophini						
Sylvicapra grimmia	E. Transvaal,	—	1	—	1	—
grey duiker	S. Africa	—	—	—	—	—
Neotragini						
Madoqua kirkii	Serengeti,	20+	1	—	1	1-3
dikdik	Tanzania	—	—	—	—	—

TABLE 1 (Continued)

HOME RANGE SIZES (km^2)				SCENT	MALE	
male		female			MATING	
terr.	bach.	seasonal	annual	MARKS	SYSTEM	SOURCE
1.6	1.6	11.6	16.2	dung	terr.	Owen-Smith, 1975
0.7-2.6	—	8.9-14.7	8.9-20+	urine		
4.1	4.2	6.7	6.7	dung	terr.	Hitchins, 1971; pers. commun.
—	—	—	—	urine		
—	15	—	14.5	dung	?	Goddard, 1967
—	2.5-43	—	2.5-25			
—	—	—	—	dung	?	Schenkel, 1966; Schenkel & Schenkel-Hulliger, 1969
—	—	—	—	urine		
—	—	—	—	dung	?	Ullrich, 1964
—	—	—	—	urine		
10+	—	—	—	—	terr.	Klingel, 1972
—	—	—	—			
5.8	—	—	—	dung	terr.	Klingel, 1974
2.7-10.5	—	—	—			
—	0.5-3.8	0.5-3.8	—	dung	?	Ellisor & Harwell, 1969; Sowls, 1974
—	—	—	—	gland		
—	—	—	—	dung	terr.	Franklin, 1974
0.07-.30	—	0.07-0.30	—		harem	
—	—	—	—	gland	terr.	Bramley, 1970
0.04-0.16	0.07-0.40	0.05-0.15	—			
0.14	0.28	0.49	—	gland	terr.	Kurt, 1968
—	—	0.3-1.8	—			
—	—	—	—	dung	terr.	Bromley, 1969;
0.2-4.3	—	—	—	gland		Kitchen, 1974
(0.07)	—	4.5	—	gland	(terr.)	Krämer, 1969
—	—	—	—			
—	—	—	—	—	terr.	Sommerlatte, pers. commun.
—	—	—	—			
—	—	—	—	dung	terr.	Hendrichs & Hendrichs, 1971
0.03-0.12	—	0.03-0.12	—	gland	pair	

TABLE 1 (Continued)

SPECIES	AREA	POP. DENS. /km² local, overall	GROUP SIZES male terr.		GROUP SIZES female no. ♀s	aggreg.
			terr.	bach.	no. ♀s	aggreg.
Oreotragus oreotragus	Semien,	13-47	1	—	1-2	2-3
klipspringer	Ethiopia	—	(+ ♀s)	—	—	—
Ourebia ourebi	Albert,	—	—	—	—	—
oribi	Zaire	—	—	—	—	—
Raphicerus campestris	Kruger,	—	1	—	1	1-2
steenbok	S. Africa	—	—	—	—	—
Boselaphini						
Boselaphus tragocamelus	Kanha,	—	1	—	—	—
nilgai	India	—	—	2-18	2-10	—
Tragelaphini						
**Tragelaphus scriptus*	Rwenzori,	26	1	1	1	2
bushbuck	Uganda	—	—	—	1-2	1-3
	Nairobi,	—	—	—	—	—
	Kenya	—	—	—	—	—
	Chobe,	18	1	1	1	1-2
	Botswana	7	—	—	—	—
	Sengwa,	—	1	1	1	1-2
	Rhodesia	—	—	—	—	—
Antilopini						
Antilope cervicapra	Kanha,	—	1	—	—	—
blackbuck	India	0.04	—	1-3	2-5	—
Antidorcas marsupialis	Etosha,	—	1	—	9	19
springbok	S.W. Africa, & N. Cape	—	—	2-50	2-35	19-250
Gazella granti	Ngorongoro,	—	1	10	—	16
Grant's gazelle	Tanzania	6	—	—	—	12-31
	Serengeti,	—	1	4.6	6.1	46
	Tanzania	0.16	—	2-37	2-37	3-428
Gazella thomsoni	Ngorongoro,	70	1	13	—	23
Thomson's gazelle	Tanzania	14	—	—	—	—
Litocranius walleri	Tsavo,	—	1	1	—	2.1
gerenuk	Kenya	—	—	—	—	1-10
Reduncini						
Aepyceros melampus	Nairobi,	30	1	—	—	—
impala	Kenya	8	—	2-38	3-39	1-67
	Serengeti,	40	1	—	—	—
	Tanzania	—	—	3-60	—	10-100+
Kobus defassa	Rwenzori,	10	1	5.3	5	—
defassa waterbuck	Uganda	2.1	—	—	—	—
	Nairobi,	—	1	—	—	—
	Kenya	0.8	—	—	—	—
	Kafue,	—	1	—	—	—
	Zambia	—	—	—	—	—
Kobus elypsiprimnus	Sabi-Sand,	—	1	—	—	—
common waterbuck	S. Africa	1.5	—	—	—	1-23
Kobus kob	Toro,	—	1	—	—	—
kob	Uganda	40	—	450-600	—	2-1000

TABLE 1 (Continued)

HOME RANGE SIZES (km^2)					MALE	
male		female		SCENT	MATING	
terr.	bach.	seasonal	annual	MARKS	SYSTEM	SOURCE
0.08	—	0.08	—	dung	terr.	Dunbar & Dunbar, 1974
—	—	—	—	gland	pair	
—	—	—	—	gland	terr.	Hediger, 1951
—	—	—	—			
—	—	—	—	gland	terr.	M. Cohen, pers. commun.
—	—	—	—			
—	—	—	—	dung	terr.	Schaller, 1967
—	—	—	—			
—	—	—	—	?	?	Waser, 1974, 1975
0.15-0.25	—	0.06-0.20	—			
—	0.0056	0.0025	—	?	?	Alsopp, in Leuthold, 1974
—	—	—	—			
—	—	—	—	(gland)	(terr.)	Simpson, pers. commun.
0.05-0.1	—	—	—			
0.06	—	—	—	—	terr.	Jacobsen, 1974
—	—	—	—			
—	5	—	—	dung	terr.	Schaller, 1967
0.8-1.4	—	1-2+	—	gland		
—	—	—	—	dung	terr.	Bigalke, 1972
—	—	—	—			
0.9	1-2	4	—	(dung)	terr.	Walther, 1965; Estes, 1967
—	—	—	—			
—	—	—	—	(dung)	terr.	Walther, 1972b
0.4-3.0	—	—	—		(harem)	
—	9	—	—	dung	terr.	Walther, 1964, 1974; Estes, 1967
0.01-0.04	—	1-9	—	gland		
—	—	—	—	gland	terr.	Leuthold, 1971
4.6-6.4	—	2.4-4.5	—			
—	—	—	—	?	terr.	Leuthold, 1970
0.2-0.9	2.0-5.0	4.5-5.7	—			
0.5	5	5	—	dung	terr.	Jarman, 1970; Jarman & Jarman, 1974
—	—	—	—	gland		
—	1.0	6.5	—	none	terr.	Spinage, 1969, 1974
0.8-2.2	—	—	—			
—	—	—	—	—	terr.	Kiley-Worthington, 1965
0.6-2.5	—	—	—			
1.2	—	—	—	—	terr.	Hanks et al., 1969
—	—	—	—			
—	—	—	—	—	terr.	Herbert, 1972
—	—	—	—			
—	—	—	—	none	terr.	Buechner, 1961 & 1974; Leuthold, 1966; Buechner and Roth, 1974
0.0002-0.03	—	—	—			

TABLE 1 (Continued)

SPECIES	AREA	POP. DENS. /km^2 local, overall	GROUP SIZES male terr.	bach.	female no. ♀s	aggreg.
Kobus leche	Kafue,	—	1	—	—	—
lechwe	Zambia	45	—	—	2-23	—
	Okavango,	50	1	—	—	—
	Botswana	—	—	—	—	—
Kobus vardoni	Luangwa,	—	1	—	5.5	—
puku	Zambia, &	—	—	—	1-28	—
	Chobe,					
	Botswana					
Redunca arundinum	Kruger,	—	1	—	1	2
common reedbuck	S. Africa	—	—	—	—	—
Redunca fulvorufula	Loskop,	—	—	—	—	—
mountain reedbuck	S. Africa	—	—	—	—	—
Hippotragini						
Hippotragus niger	Kenya and	—	1	1	—	18
sable antelope	Angola	—	—	—	—	—
	Matopos,	3	1	—	8	15
	Rhodesia	—	—	2-12	—	—
Alcelaphini						
Alcelaphus buselaphus buselaphus	W. Pretorius,	—	1	9	—	—
red hartebeest	S. Africa	2	(+ ♀s)	—	—	4-17
Alcelaphus b. cokei	Nairobi,	22	1	—	—	—
Coke's hartebeest	Kenya	13	—	—	—	—
Alcelaphus b. lelwel	Garamba,	—	1	—	—	—
Lelwel hartebeest	Zaire	—	(+ ♀s)	—	—	7-15
Alcelaphus b. lichtensteini	Kafue,	1	1	sev.	—	—
Lichtenstein's hartebeest	Zambia	—	(+ ♀s)	—	1-9	—
Connochaetes gnou	W. Pretorius,	20	1	—	—	30
black wildebeest	S. Africa	—	—	—	—	—
Connochaetes taurinus	Ngorongoro,	—	1	—	—	10
wildebeest	Tanzania	30	—	50-500	—	—
	Serengeti,	—	1	—	—	28
	Tanzania	10	—	—	—	2-150
Damaliscus d. dorcas	Swellendam,	10	1	75	3	—
bontebok	S. Africa	—	—	—	—	—
Damaliscus d. phillipsi	Rietvlei,	50	1	—	—	—
blesbok	S. Africa	—	—	—	—	—
	Jack Scott,	50	1	—	8	—
	S. Africa	—	—	—	1-38	—
Damaliscus l. lunatus	Kruger,	—	1	—	—	8
tsessebe	S. Africa	0.04	(+ ♀s)	1-3	—	—
	S.E.	4-7	1	—	—	7
	Rhodesia	—	—	—	—	2-12
Damaliscus l. korrigum	Rwenzori,	—	1	7	7	—
topi	Uganda	50	—	2-23	1-24	—

TABLE 1 (Continued)

HOME RANGE SIZES (km^2)				MALE		
male		female		SCENT MARKS	MATING SYSTEM	
terr.	bach.	seasonal	annual			SOURCE
—	—	—	—	none	terr.	DeVos and Dowsett, 1966
0.2-0.8	—	—	—			
0.7	—	—	—	—	terr.	Lent, 1969;
—	—	—	—			Child and Richter, 1969
—	—	—	—	—	terr.	DeVos, 1965; DeVos and Dowsett,
0.05-0.2	—	—	—			1966; Child and Richter, 1969
—	—	—	—	?	terr.	Jungius, 1971
0.35-0.63	—	0.35-0.63	—			
—	—	—	—	—	terr.	Irby, per. com.
—	—	—	—			
2.5+	—	—	—	—	terr.	Estes and Estes, 1974
—	—	7.5-50	—			
—	—	2.6	—	—	terr.	Grobler, 1974
0.25-0.4	—	—	—			
—	0.6	—	—	dung	terr.	Kok, 1975
0.3-1.1	—	0.3-1.1	0.3-1.1	gland	harem	
0.31	—	—	—	dung	terr.	Gosling, 1974
—	6.7-10.3	3.7-5.5	—	gland		
3	—	3	—	—	terr.	Backhaus, 1959
—	—	—	—		harem	
—	—	—	—	gland	terr.	Dowsett, 1966
1.5-5	1.0-2.8	1.5-5	—		harem	
—	—	—	—	dung	terr.	Richter, 1972
0.025-0.16	—	—	—	gland		
0.012	—	2.5+	—	dung	terr.	Estes, 1969
—	—	—	—	gland		
—	—	—	—	—	terr.	Estes, 1969; Watson, 1969; Talbot &
—	—	—	—			Talbot, 1963
—	—	—	—	—	terr.	David, 1973
0.1-0.4	—	0.2-7.0	—			
0.016	—	—	—	—	terr.	Lynch, 1974
—	—	—	—			
0.023	—	—	—	dung	terr.	Novellie, 1975
0.009-0.014	—	—	—	gland		
—	—	—	—	dung	terr.	Joubert, 1972
2-4	—	2-4	—	gland	harem	
—	—	—	—	—	terr.	Grobler, 1973
—	—	—	—			
0.7	—	—	—	none	(terr.)	Jewell, 1972
—	—	—	—			

TABLE 1 (Continued)

		POP. DENS. $/\text{km}^2$, local, overall	GROUP SIZES			
			male		female	
SPECIES	AREA		terr.	bach.	no. ♀s	aggreg.
Bovini						
Bubalis bubalis	Wilpattu,	—	1	—	—	6-9
water buffalo	Ceylon	—	—	—	—	—

For group and home range sizes, the upper figure represents the mean or mode, and the lower figures the range of values reported.

Tentative data are in parentheses.

* Assessment is somewhat tentative.

terr., territorial.

bach., bachelor.

aggreg., all individuals present, including short-term associations.

TABLE 2

Ungulate species reportedly non-territorial

		POP. DENS. $/\text{km}^2$ local, overall	GROUP SIZES			
			male		female	
SPECIES	AREA		dom.	bach.	no. ♀s	aggreg.
PROBOSCIDEA						
Elephantidae						
**Elephas indicus*	Yala,	—	1		—	—
Asiatic elephant	Ceylon	0.2	1-7		2-22	—
Loxodonta africana	Kabalega,	—	3		1-3	6.6
African elephant	Uganda	3	1-11		—	5-1000
	Tsavo,	—	1-4		1-3	13
	Kenya	1.2	1-35		—	5-700
	Serengeti,	—	4		2	—
	Tanzania	0.17	1-20		1-4	10-20
	Manyara,	5.5	2.1		3.4	11
	Tanzania	—	1-10		—	2-24
PERISSODACTYLA						
Equidae						
Equus caballus	New Forest,	14	1		1-2	—
horse	England	—	(+ ♀s)		1-6	—
Equus burchelli	Ngorongoro,	—	1	2.9	2.8	—
plains zebra	Tanzania	22	(+ ♀s)	1-9	1-6	1-16
	Serengeti,	—	1	2.7	2.2	—
	Tanzania	5	(+ ♀s)	1-6	—	1-11
	Kruger,	—	1	3	—	4
	S. Africa	1.1	(+ ♀s)	1-7	—	1-11
Equus zebra	S.W.	—	1	6	2-3	5
mountain zebra	Africa	—	(+ ♀s)	1-15	1-6	1-13
	Cradock,	2.2	1	—	—	—
	S. Africa	—	(+ ♀s)	—	1-5	—

TABLE 1 (Continued)

HOME RANGE SIZES (km^2)				MALE		
male		female		SCENT	MATING	
terr.	bach.	seasonal	annual	MARKS	SYSTEM	SOURCE
—	—	—	—	—	terr.	Eisenberg & Lockhart, 1972
—	—	—	—	—		

TABLE 2 (continued)

Ungulate species reportedly non-territorial

HOME RANGE SIZES (km^2)				MALE	
	female		SCENT	MATING	
male	seasonal	annual	MARKS	SYSTEM	SOURCE
—	—	—	gland	?	Kurt, 1974
—	—	—			
—	—	—	—	?	Buss & Smith, 1966; Laws et al., 1970; Laws, 1974
—	—	—	—		
—	—	—	—	?	Laws, 1969, 1970, 1974; Leuthold & Sale, 1973
300-1200	—	330-3120			
300	—	—	—	?	Hendrichs, 1971; Croze, 1974
—	—	—			
—	—	—	none	rank	Douglas-Hamilton, 1971, 1972
—	14-52	—			
—	—	—	—	harem	Tyler, 1972
—	0.8-10.2	—			
—	—	—	(dung)	harem	Klingel, 1967, 1969
80-250	80-250	—			
—	—	1000+	—	harem	Klingel, 1967, 1969
300-600	300-600	—			
—	—	—	—	harem	Smuts, 1972, 1974
—	—	570			
—	—	—	—	harem	Klingel, 1968, 1969; E. Joubert, 1972
10-20	10-20	—			
9.4	9.4	—	none	harem	Penzhorn, 1975
3.1-16.0	3.1-16.0	—			

TABLE 2 (Continued)

		POP. DENS. $/km^2$ local, overall	GROUP SIZES		
			male	female	
SPECIES	AREA		dom. bach.	no. ♀s	aggreg.
ARTIODACTYLA					
Suidae					
**Phacochoerus aethiopicus*	Nairobi,	—	1	1	—
warthog	Kenya	1.8	1-2	1-2	—
	Sengwa,	8	1	1	5-6
	Rhodesia	3	1-6	1-3	1-16
Giraffidae					
Giraffa camelopardalis	Nairobi,	0.7	1	—	—
giraffe	Kenya	—	sev.	—	1-18
Cervidae					
Cervinea					
Alces alces	British Columbia,	—	1	1	2
moose	Canada	—	—	1-3+	—
	Grand Tetons,	—	1	1	2
	U.S.A.	0.1	1-2	—	—
Cervus axis	Kanha,	24	1	—	—
chital	India	3	2-5	—	5-10
Cervus canadensis	Banff,	—	1	—	—
American elk	Canada	—	2-4	5-20	10-30
	Montana,	8	1	5	—
	U.S.A.	2.5	2-6	2-21	—
Cervus duvauceli	Kanha,	—	5-9	—	—
barasingha	India	0.3	1-16	—	13-19
Cervus elaphus	Scotland	—	—	—	40
red deer		—	—	—	—
	Rhum,	1.7	—	—	9
	Scotland	—	—	—	—
**Cervus unicolor*	Kanha,	—	1	—	—
sambar	India	0.8	1-2	1-3	—
Rangifer tarandus	Alaska,	7	sev.	—	—
caribou	U.S A.	—	—	—	20-30
	Newfoundland,	—	—	—	—
	Canada	—	1-16	3-5	2-176
Odocoilinea					
Odocoileus hemionus	California,	50	1	1	—
mule deer	U.S.A.	—	—	—	1-5
Odocoileus virginianus	Illinois &	40	1	1	—
white-tailed deer	Texas, U.S.A.	—	2-4	—	1-3
Bovidae					
Caprinae					
Capra ibex	Switzerland	—	1	5	—
ibex		—	1-30	1-15	—
Capra walie	Ethiopia	—	1	3	—
walia ibex		—	1-4	1-7	—
Ovis canadensis	Canada	—	sev.	sev.	—
bighorn sheep		—	—	—	—
Ovis orientalis	Pakistan	—	—	—	—
Urial sheep		1-6	1-3	1-2	—

TABLE 2 (Continued)

HOME RANGE SIZES (km^2)			SCENT MARKS	MALE MATING SYSTEM	SOURCE
	female				
male	seasonal	annual			
— —	— —	— —	none	?	Frädrich, 1965
1.8 0.7-3.7	1.7 0.6-3.4	1.7 0.6-3.4	gland	?	Cumming, 1975
85 —	— —	— —	none	(rank)	Foster & Dagg, 1972
— —	— —	— —	—	roving	Geist, 1963
— 2.5-5	— 2.5-5	— —	—	—	Houston, 1974
— 5-7	2 —	— —	gland	roving	Schaller, 1967
— —	— —	— —	gland	harem	Struhsaker, 1967
— 3.7-37	— 3.7-37	(75) —	—	(terr. harem)	Knight, 1970
— —	— —	— —	gland	rank	Schaller, 1967
— —	— —	— —	—	harem	Darling, 1937
5 —	4 —	— —	—	harem	Lowe, 1966; Lincoln et al., 1970
— —	— —	— —	gland	?	Schaller, 1967
— —	— —	— —	—	roving	Lent, 1965
— —	— —	— —	—	roving	Bergerud, 1974
— 0.6-1.8	— 0.4-1.6	— —	—	roving	Linsdale & Tomich, 1953; Dasmann & Taber, 1956
— —	— —	— —	—	roving	Severinghaus & Cheathum, 1956; Hawkins & Klimstra, 1970; Brown, 1974
— —	— —	— —	—	roving	Nievergelt, 1966
— —	— —	— —	—	(roving)	Nievergelt, 1974
— 2-25	— 2-25	— —	none	roving	Geist, 1971
— —	— —	— —	—	roving	Schaller & Mirza, 1974

TABLE 2 (Continued)

SPECIES	AREA	POP. DENS. $/km^2$ local, overall	GROUP SIZES male dom. bach.	female no. ♀ s	aggreg.
Ovis musimon	Hirta,	—	1	—	—
Soay sheep	England	100-250	1-5	25-35	—
Ovibovinae					
Ovibos moschatus	Thelon,	—	1	—	11
musk ox	Canada	—	1-7	2-13	2-65
Rupicaprinae					
Oreamos americanus	British Columbia,	—	—	—	—
Rocky Mountain goat	Canada	—	1-2	1-5	—
Saiginae					
**Saiga tartarica*	U.S.S.R.	43	—	—	—
saiga		3.4	1-10+	2-25	2-100
Bovinae					
Tragelaphini					
**Tragelaphus buxtoni*	Tsavo,	—	1	—	—
lesser kudu	Kenya	—	—	1-3	—
**Tragelaphus angasi*	Zinhave,	10	1-3	—	3
nyala	Mozambique	—	1-6	1-3	1-12
	Hluhluwe,	10+	1	1	2-3
	S. Africa	—	1-6	1-3	1-7
**Tragelaphus strepsiceros*	Chobe,	14	—	—	—
greater kudu	Botswana	4.5	—	—	1-16
	Kruger,	2-3	1-4	4	9
	S. Africa	1	1-10	1-7	2-15
Taurotragus oryx			—	—	—
eland			—	—	—
Hippotragini					
**Hippotragus equinus*	Kruger,	—	1	—	—
roan antelope	S. Africa	0.03	(+ ♀s)	—	6-12
Bovini					
Bison bison	Yellowstone,	5	4	—	23
American bison	U.S.A.	0.3	1-12	7-10	3-480
	Montana &	11	—	—	40-80
	California, U.S.A.	2.7	35	—	150
Bos gaurus	Kanha,	—	—	—	10
gaur	India	0.6	1-6	—	8-38
Syncerus caffer	Tsavo,	4	—	—	350
African buffalo	Kenya	—	—	—	—
	Serengeti,	—	—	—	—
	Tanzania	2	—	—	50-2000

For group and home range sizes, the upper figure represents the mean or mode, and the lower figures the range of values reported.

Tentative data are in parentheses.

* Assessment somewhat tentative.

dom., dominant.

bach., bachelor.

aggreg., all individuals present, including short-term associations.

TABLE 2 (Continued)

HOME RANGE SIZES (km²)			SCENT MARKS	MALE MATING SYSTEM	SOURCE
	female				
male	seasonal	annual			
—	—	—	—	roving	Grubb & Jewell, 1966; Grubb, 1974; Jewell et al., 1974
0.01-0.25	0.01-0.25	0.01-0.25			
—	—	—	—	harem	Tener, 1965
—	—	—			
—	—	—	gland	roving	Geist, 1964
—	—	—			
—	—	—	gland	(harem)	Bannikov et al., 1967
—	—	—			
2.2	1.8	—	none	?	Leuthold, 1974
—	1-3.5	—			
10	10	—	none	?	Lobao Tello & Van Gelder, 1975
—	—	—			
3	1	—	(none)	?	Anderson, pers. commun.
—	—	—			
15	15	—	(gland)	?	Simpson, 1972, pers. commun.
—	—	—			
15+	6.6	—	none	?	Owen-Smith, in prep.
—	4-12	—			
—	—	—	—	(rank)	Estes, 1974
—	—	—			
—	—	—	dung	(harem)	Joubert, 1974
64-104	—	64-104			
30	30	90	—	rank	McHugh, 1958
—	—	—			
—	—	—	—	rank	Lott, 1974
—	—	—			
75	75	75	none	roving	Schaller, 1967
—	—	—			
50	50	85	—	—	Leuthold, 1972
—	—	—			
180	180	400	—	rank	Sinclair, 1974
—	—	—			

(Hitchins, 1971 and pers. commun.). For bushbuck, both Jacobsen (1974) and Simpson (pers. commun.) concluded from observations in southern Africa that territoriality existed, though their evidence is equivocal.

The existence of the bachelor male segment cannot be ascribed merely to the saturation of all available space for territories. It persists even when vacant areas are readily available, for example in blackbuck (Schaller, 1967) and bontebok (David, 1973). Waterbuck and sable bachelor herds consist only of subadult or young adult males (Spinage, 1969; Estes and Estes, 1974; Grobler, 1974), but in most species a number of prime adults are also included. However, more subtle age distinctions may exist. For example, in Serengeti impala prime males aged 4½ to 6½ years occupied territories mostly during the peak conception period, whereas younger and older males were territorial earlier or later (Jarman and Jarman, 1974).

Where the breeding season is extended, as is usually the case under tropical conditions, territories are frequently occupied year-round, except for temporary abandonment under unusually harsh conditions. This is also the case for wildebeest in Ngorongoro Crater, Tanzania (Estes, 1969) and in southern African populations of bontebok and tsessebe (David, 1973; S. Joubert, 1972), despite restricted breeding seasons. However, individual males may interchange between the categories of territorial and bachelor male more frequently. For example, Uganda kob males holding prime territories on territorial grounds are displaced about every ten days (Buechner and Roth, 1974). In contrast, in waterbuck, sedentary wildebeest, and white rhinoceros, individual males can hold the same territories for several consecutive years (Spinage, 1969; Estes, 1969; Owen-Smith, 1975). In other cases where there is a prolonged non-breeding season, the division between territorial and bachelor males breaks down during this period; in effect all males revert to bachelor status, e.g. pronghorn (Kitchen, 1974), roe deer (Kurt, 1968; Bramley, 1970).

Among non-territorial species, a two-fold division of the adult male segment occurs in the zebras *Equus burchelli* and *E. zebra*. Individual "harem" stallions are attached to female-young units, while remaining stallions associate in all-male "bachelor" groups (Klingel, 1967; E. Joubert, 1972). "Bachelor" male groups are reported also for the African buffalo, but these comprise only 15 per cent of the adult male population and consist mostly of senile individuals (Sinclair, 1974). The majority of males remain permanently attached to the large female herds. Among cervids and caprines, males are aggregated in all-male groups only during the non-breeding season. During the rut they roam independently, forming temporary attachments to individual females or female groups.

Spatial Dispersion

The striking feature of territorial species is the regular spacing out of the territorial males (well illustrated for wildebeest by Estes, 1969). Each territorial male limits his movements mostly to a fixed spatial area, discrete from those occupied by other such males. These geographic areas, each occupied by a single territorial male, are referred to as territories. To some degree they exist independently of the occupying individual: territory limits may persist intact even when the former occupant is displaced by a new male, and if the resident male dies or disappears a vacant territory awaits occupation by another individual.

In some species, territories are centripetally focussed: males spend most of their time on central "stamping grounds," and the borders between neighboring territories are diffuse, e.g. wildebeest (Estes, 1969), bontebok (David, 1973). This situation seems associated with species occupying open grassland habitats where neighbors are constantly visually apparent to one another. In others, territories are boundary-orientated, with males engaging in regular patrols along a fairly sharply defined border zone separating adjacent territories, e.g. white rhinoceros (Owen-Smith, 1975), Thomson's gazelle (Walther, 1972a), and Coke's hartebeest (Gosling, 1974). For such species, scent marking is usually prominent. In a third variant, territories are separated by an unoccupied "no-man's land," e.g. Grant's gazelle (Walther, 1972b) and pronghorn (Kitchen, 1974). In Nairobi Park waterbuck, territories are arrayed in a single layer chain flanking watercourses (Kiley-Worthington, 1965), while in a blesbok population, Novellie (1975) found territories aligned along a roadside burn.

Intrusions into neighboring territories may occur in special circumstances. During the dry season territorial males may be forced to make regular excursions to water, traversing other territories on the way, e.g. waterbuck (Spinage, 1969), wildebeest (Estes, 1969), and white rhinoceros (Owen-Smith, 1975). Common reedbuck males sometimes feed within neighboring territories for periods of several hours (Jungius, 1971). During the dry season, Ngorongoro wildebeest males may leave their territories to feed elsewhere during the day, returning only at night (Estes, 1969). Wildebeest and bontebok males also invade neighboring territories regularly to engage in challenge rituals (Estes, 1969; David, 1973). In vicuna, territorial males, together with their female harems, abandon their territories each evening to retire to separate sleeping areas on higher ground (Franklin, 1974). Quantitative estimates of the degree of territory fidelity are available for three species only. White rhinoceros territorial males were encountered outside their home territories on only 0.6 per cent of sightings under wet season conditions, but this increased to 7 per cent once water sources ran dry (Owen-Smith, 1975). Wildebeest territorial males were discovered more than 100m from their stamping grounds on 11 per cent of occasions seen, much of this arising from challenge rituals (Estes, 1969). In Coke's hartebeest, absenteeism even in the most favorable territories averaged 13 per cent year-round (Gosling, 1974).

Territory sizes vary widely, from as little as 150 sq m in the case of central territories on Uganda kob territorial grounds (Buechner and Roth, 1974) to 10 sq km or more in Grevy's zebra and African wild ass (Klingel, 1972). There is no close relationship with body size. For example, in Ngorongoro Crater wildebeest (mass 100 kg) hold territories about 1 ha in area (Estes, 1969), while territories of Thomson's gazelle (mass 12 kg) cover 4 to 6 ha (Estes, 1967). Small territories tightly clustered together in certain localities (termed territorial grounds) are strikingly exhibited by some populations of kob, but a similar tendency occurs in lechwe (DeVos and Dowsett, 1966), puku (DeVos, 1965) and wildebeest (Estes, 1969). Notably, these are species occupying highly productive habitats at high local population densities. In migratory populations, the fixity of territory locations is necessarily attenuated. Serengeti wildebeest occupy fixed territories for periods of only a few hours or days, then abandon these to keep up with the shifting female aggregations (Estes, 1969; Watson, 1969). In Uganda topi, males occupy so-called "wards" which drift slowly in location following the general movement of the female segment (Jewell, 1972).

Bachelor males generally move over a wider area encompassing several territories. Where small territories are clustered in particular localities, bachelor males are usually excluded from the territory mosaic. In other cases they may be tolerated within territories to varying degrees, e.g. Grant's gazelle (Walther, 1972b), impala (Jarman and Jarman, 1974), and Grevy's zebra (Klingel, 1975). In the white rhinoceros, and in the black rhinoceros at least in Zululand, there is an unusual situation in which bachelor males restrict their movements largely to the territories of individual territorial males (Owen-Smith, 1975; Hitchins, 1972).

Individual females or female groups range over the area of several male territories in most species. Exceptions include vicuna, dikdik, klipspringer, and common reedbuck, in which females coinhabit individual male territories (Franklin, 1974; Hendrichs and Hendrichs, 1971; Dunbar and Dunbar, 1975; Jungius, 1971). A similar situation occurs in certain populations of tsessebe, hartebeest, and Grant's gazelle, but is not a species-specific feature (see S. Joubert, 1972; Grobler, 1973; Backhaus, 1959; Dowsett, 1966; Gosling, 1974; Walther, 1972b). Evidently it arises where suitable habitat is localized in extent, and disappears where more extensively favorable habitats are occupied. In grey duiker, two or three females occupy fairly discrete home ranges within each male territory (Sommerlatte, pers. commun.). A similar situation has been described for muntjacs (*Muntiacus reevesii*) under semicaptive conditions (Dubost, 1970), but little is yet known about other small antelopes and deer in the wild.

In most species, female home ranges exhibit considerable overlap. In Soay sheep and warthog, "home range groups" or "clans" of females may be distinguished, occupying areas largely discrete from other such home range groups (Grubb and Jewell, 1966; Cumming, 1975). In sable and roan antelope, the home ranges of the cohesive female groups show relatively little overlap (Estes and Estes, 1974; S. Joubert, 1974); this may also be the case for African buffalo herds (Sinclair, 1974). In roan antelope in Kruger Park, a single male is usually attached to the group of females (S. Joubert, 1974), and it is a matter of interpretation whether this represents a harem association by the male, or territoriality at low population density. Behavior patterns otherwise resemble those of the closely related sable antelope, which exhibits clear male territoriality (Estes and Estes, 1974; Grobler, 1974). Spacing among female groups could be derived merely from matrilineal traditions of group membership. Notably, no such spacing occurs in plains zebras, in which young females are abducted out of their maternal groups (Klingel, 1967).

Among non-territorial deer and caprines, males commonly abandon their usual home ranges during the rut and move on to the female home ranges. Red deer and American elk stags may localize their rutting activities in particular areas, a behavior giving rise to suggestions of territoriality (Burkhardt, 1958; Knight, 1970). However, other observers have emphasized that the areas occupied do not have fixed spatial limits (Lincoln, Youngson, and Short, 1970; Bützler, 1974; Struhsaker, 1967). Rutting territories were described for chamois on the basis of spatial localization by certain "platzbocke" (Krämer, 1969); but this interpretation has been questioned by Geist (1974), who has suggested that the situation is simply an artefact of abnormally high population density.

Interaction Patterns

For territorial species, the behavior patterns exhibited in encounters with other conspecifics cannot be interpreted without knowledge of the spatial framework. The responses of a territorial male depend not only on the social status and actions of the other individual, but also on the location of the meeting relative to his own home territory.

Within his own territory, a territorial male responds, upon detecting another conspecific individual, usually by approaching. In some species, the approach may be preceded or accompanied by vocal emphasis of presence, e.g. wildebeest (Estes, 1969) and pronghorn (Kitchen, 1974). If the other individual is a male, the approach is likely to give way at close quarters to displays emphasizing horns, e.g., Grant's gazelle (Walther, 1972b), body size through lateral presentation, e.g., pronghorn (Kitchen, 1974), or simply presence by actions such as horn thrashing, e.g., white rhinoceros (Owen-Smith, 1975) and kob (Leuthold, 1966). If the intruding male flees, the territorial male is likely to chase after, in some cases simultaneously emphasizing his presence vocally, e.g., white rhinoceros (Owen-Smith, 1975) and Thomson's gazelle (Walther, 1974). Usually the pursuit is broken off when the intruder crosses over the territory's boundary. If the intruder stands his ground and gives a submissive display (among antelopes, commonly holding the head lower, but in the white rhinoceros making a fierce looking "snarl"), the territorial male either perseveres threatening displays until the other male eventually leaves the territory (e.g., bontebok, David, 1973), or moves away himself subsequently ignoring the other male (e.g. white rhinoceros, Owen-Smith, 1975). Threatening actions may be ineffective when a large group of bachelor males has penetrated a territory, but attacks rarely occur. If, however, the intruder stands his ground and gives matching displays, there ensues either a vigorous (though usually brief) fight (e.g., Thomson's gazelle, Walther, 1974), or some more ritualized testing of relative confidence, strength, or both (e.g., Grant's gazelle, Walther, 1972b). If the intruding male is able to demonstrate superiority, he remains, and assumes the status and behavior of territorial male in that territory. The former territory holder usually leaves and joins a bachelor herd. However, in the white rhinoceros the defeated male may remain within the territory, simply assuming the behavior patterns of a bachelor male there.

Outside his home territory, as when proceeding to water, a territorial male attempts to avoid meetings with resident territorial males. If accosted, he either retreats or responds submissively (e.g., white rhinoceros, Owen-Smith, 1975; waterbuck, Spinage, 1969). In Grant's gazelle in open plains habitats, territorial males may wander into another territory in association with a bachelor herd. Upon leaving his own territory, a male immediately behaves submissively towards the male whose territory has been entered, without there being any intervening contest (Walther, 1972a, b). Similar behavior occurs in pronghorns during the post-rut period (Kitchen, 1974). In the white rhinoceros, a submissive response is shown on distant territories, but a male accosted within the territory of a neighbor gives the displays typical of resident territorial males, coupling these, however, with steady backing away (Owen-Smith, 1975). Though undescribed, a similar distinction may apply in other species.

Since territorial males rarely wander, the most usual type of meeting between territorial males involves neighboring territory-holders at a mutual boundary. In such confrontations, both males give matching displays, but aggressive actions are highly ritualized and seldom lead to fights. Chasing reversals across the border occur, for example, in pronghorns (Kitchen, 1974), while in the white rhinoceros a ritualized sequence of advances and retreats is a striking feature (Owen-Smith, 1975). Generally border encounters are broken off without any clear winner or loser being evident. In both wildebeest species and in bontebok, territorial males penetrate neighboring territories to engage in challenge rituals, then return to their own territories (Estes, 1969; Richter, 1972; David, 1973). In contrast, in a blesbok population studied by Novellie (1975), territorial males met only at boundaries.

Towards females, the initial approach of a resident territorial male gives way at close quarters to either an olfactory investigation or courtship displays. Frequently, the latter retain elements of the aggressive displays exhibited towards other males (see Walther, 1974). Dikdik and vicuna are exceptional in that territorial males respond threateningly even to intruding females (Hendrichs and Hendrichs, 1971; Franklin, 1974). More usually, the territorial male attaches himself to a particular female or female group, and attempts to prevent their leaving his territory by blocking their movements at boundaries. If unsuccessful, the male does not follow for more than a short distance beyond his own territory limits, and the females are likely to be joined instead by one of the neighboring territorial males. In most species, territorial males do not interfere with matings by neighboring territorial males. Where this sometimes occurs, as in Coke's hartebeest (Gosling, 1974), the intruding male is readily chased back by the resident. In wildebeest, territorial transgressions may be frequent during the "frenzied activity" of the brief rut (Estes, 1969), but a detailed description of behavior during this critical period is unfortunately lacking.

Bachelor males everywhere behave submissively towards any territorial male whose territory they may have entered. They associate only transiently with females, and rarely perform courtship or mating. This does not seem to be due to any physiological incapacity on their part, but rather to the almost invariable presence of a territorial male with any receptive female. Notably, a white rhinoceros bachelor male consorted with an estrous female when the resident territorial bull happened to be engaged with another female; but later the territorial bull displaced him and mated with this female (Owen-Smith, 1975). In Grevy's zebra, several bachelor males attempted to mate with an estrous female located outside the territory mosaic, with much fighting (Klingel, 1975). Where tolerated within territories, bachelor males are merely kept a short distance away from any estrous females, and seem readily intimidated by territorial males.

Among females of most species, aggressive interactions are rare. Dominance interactions among group members have been described clearly only in species forming cohesive female groups, such as sable and roan (Estes and Estes, 1974; S. Joubert, 1974). When different groups meet, females generally respond passively. Strong aggressive responses towards strange females have been reported only for moose (Houston, 1974) and mule deer (Miller, 1974), though they may occur in other solitary species.

Males of non-territorial species respond with very similar types of behavioral display in encounters. The significant difference is simply the lack of any spatial constraint on their performance, at least in relation to any particular geographic area. They may, however, be influenced by spatial proximity to certain other individuals, such as estrous females or superior males.

Indirect Manifestations of Presence

Individuals may become aware of the presence of other conspecifics without a direct meeting by detecting visual, auditory, or olfactory signs of their presence.

Special postures termed "static-optic advertising" are typical of territorial males occupying open habitats, where such visual signals may be apparent over some distance in space (e.g., wildebeest, Estes, 1969; tsessebe, S. Joubert, 1972). Advertising calls are made for example by territorial male wildebeest and kob (Estes, 1968; Leuthold, 1966).

Scent marks can emit a signal persisting over some interval in time. Fecal accumulations at particular sites are striking in several territorial species, including the white rhinoceros (Owen-Smith, 1975), Grevy's zebra (Klingel, 1975), vicuna (Franklin, 1974), Coke's hartebeest (Gosling, 1974), bontebok (David, 1973) and dikdik (Hendrichs and Hendrichs, 1971). In some species dung piles seem to be the product mostly of territorial males, but in others females and bachelor males may also contribute to these. However, only territorial males exhibit special defecation rituals, commonly including kicking or pawing in the dung pile. In Coke's hartebeest, both neighboring territorial males defecate and paw at the same dung pile during challenge rituals (Gosling, 1974). In transfer experiments, a dikdik male scraped and defecated over the dung of both neighboring and strange males located within his own territory, but only over the dung of a stranger in a boundary region (Hendrichs and Hendrichs, 1971). Especially prominent dung piles may occur at territory borders in some species — e.g., white rhinoceros (Owen-Smith, 1975) and Grevy's zebra (Klingel, 1975) — but generally dung accumulations are not limited to such locations. Extensive urine marking seems restricted to rhinoceroses, though in antelopes, such as gazelles, linked urination-defecation may occur at particular sites (Walther, 1964, 1965). In the white rhinoceros only territorial males spray-urinate, and only within their own territories. While repeated spray-urination accompanies boundary patrols, spray-urination is also performed elsewhere in the territory, so that such scent marks are scattered throughout (Owen-Smith, 1975). Among antelopes, territorial males commonly deposit preorbital gland secretion on vegetation, and likewise such scent marks are not restricted to border regions (e.g., Thomson's gazelle, Estes, 1967). Pronghorns mark with subauricular gland secretion (Kitchen, 1974), while roe deer and impala rub a glandular forehead patch on plants (Bramley, 1970; Jarman and Jarman, 1974). Among bachelor males, scent marking is performed in attenuated fashion (e.g., Thomson's gazelle, Walther, 1964). In females, scent glands are usually reduced in size and are non-functional, but Coke's hartebeest is an exception (Gosling, 1974). Scent marking seems to be absent or only weakly expressed in species such as kob (Leuthold, 1966) and wildebeest (Estes, 1969), where territorial males are in close visual and auditory contact. Puzzlingly, it is also lacking in waterbuck (Spinage, 1969) and Grant's gazelle (Walther, 1972b), despite fairly large territories and the absence of auditory advertising.

Among non-territorial species, males commonly advertise their presence with special calls or visual displays during the rut. Plains zebra males sometimes defecate on the dung of other conspecifics, but because of their wide-ranging habits significant accumulations do not result (Klingel, 1967). Preorbital and forehead glands occur in Old World deer, and their secretion may be deposited in the environment, especially by males during the rut (see Struhsaker, 1967). In Rocky Mountain goats and chamois, both sexes mark with occipital gland secretion (Geist, 1964; Krämer, 1969). It is not the occurrence of scent marking that distinguishes territorial species, but rather the concentration of scent marks and other signs of a particular individual within the local extent of a territory.

Relationship between Behavior and Social Structure

We are now in a position to consider how social structure arises as a proximate consequence of behavior patterns.

While some degree of spatial exclusion is always a feature of territoriality, it generally exists only among the set of territorial males. Furthermore, by adopting the submissive actions characteristic of bachelor males, territorial males may sometimes penetrate other territories, and in some cases even remain within them for extended periods. On the other hand, a male that reciprocates the threatening gestures of the resident territory holder is likely to be attacked, unless he soon leaves the area. Hence territorial exclusion follows largely as a consequence of the choice of action adopted by other males. Under normal circumstances, territorial males keep within their own territories and thereby avoid the drain of time and energy and possible risk of injury associated with challenges. Bachelor males, if harassment is sufficiently great, will tend to avoid the territory mosaic, provided areas unoccupied by territorial males are available. Persistent aggressive challenges are usually not directed against females, and hence females wander relatively freely through the male territories in most species.

Scent marks, by providing evidence of the presence of a resident territorial male in the area, may help inhibit intrusions. The deterrent effect is not intrinsic to the scent mark, however, but depends upon the relationship between the individuals concerned. A neighboring territorial male might turn back, a bachelor male could continue on cautiously, and a receptive female would perhaps be attracted to remain in the area. This does not preclude additional functions in patterning the home area for the originator of the scent (Schenkel, 1966; Klingel, 1975). Nevertheless, it seems noteworthy that scent marks and other advertisements of presence are exhibited most strikingly by territory-holding males.

To the displays of resident territorial males, other males usually respond by avoidance, withdrawal, or submission. This is the basis used to identify the existence of a dominance-subordinance relationship. By consistently directing aggressive displays towards all other individuals, a resident territorial male in effect manifests a claim to supreme dominance within his own territory. This claim may occasionally be challenged, and, if the challenger is victorious in the ensuing contest, he assumes dominance within the spatial limits of that territory. Usually the loser is subsequently driven from the territory, but in the white rhinoceros a dominance reversal occurs without spatial displacement (Owen-Smith, 1975). In Coke's hartebeest and impala, males reported first exhibit top-ranking dominance over associated bachelor males before challenging for territorial dominance (Gosling, 1974; Jarman and Jarman, 1974).

Territoriality is simply one possible form that can be taken by the social ordering of dominance relationships, distinguished by the dependence of relative dominance on spatial location. The need to refer to particular spatial areas in interpreting social structure is the basic justification for introducing the word *territory*. The resulting form of population organization, based on space-correlated dominance relationships among a set of individuals, is approximately referred to as *territoriality*. The term *territorial behavior* encompasses the various actions by which the spatially localized dominance is maintained, including limitation of movements, aggressive challenges directed towards intruding individuals, self-advertisement, and the blocking of females at boundaries. Characterization in terms of behavior exemplifying "defence" of the territory is both unnecessary and misleading. As a motivational model, this characterization implies that aggressive behavior by the territory holder will continue until an intruding individual has vacated the area of the territory. But in many cases aggression is subdued or terminated as soon as the intruder responds submissively. As a functional model, it implies that spatial exclusion arises directly as a consequence of the aggressive displays of territory holders. However, whether threatening displays have this effect in particular instances depends on the responses adopted by recipients.

Ultimate Genetic Results

Dominance is of genetic significance to the extent that it enhances access by the more dominant individuals to some limited resource influencing survival, reproductive success, or the successful rearing of quality progeny. Potentially significant resources include food, shelter sites or other loci of significance, and mates.

Food

An adequate food supply is a basic survival requisite for all animals. Variations in quantity and quality can influence both individual survival and that of dependent progeny. By excluding other territorial males from utilizing his territory, a territory holder potentially reduces pressure on its food reserves. However, food reserves are generally shared with females and immature animals and sometimes also with bachelor males. Since territorial males comprise only about 10 per cent of the population, the effective reduction in population biomass within the territory will be small. It was estimated to amount to only 5 per cent in the white rhinoceros (Owen-Smith, 1975). There is no evidence to suggest that the survivorship of territorial males is increased as a result of any food gains. On the contrary, wildebeest territorial males in Ngorongoro Crater lost condition faster than bachelors, despite the relegation of the latter to supposedly less favorable habitats (Estes, 1969). A similar situation has been noted in Uganda kob (Leuthold, 1966) and impala

(Jarman and Jarman, 1974). Where territories are held seasonally, occupation occurs during the summer or wet-season months of food abundance. Even where territories are held year-round, males commonly abandon their territories to feed elsewhere during critical periods of food shortage.

Alternatively, the slight reduction in population biomass within the territory could increase energy flow to females feeding there, some of which are likely to be bearing the progeny of the territorial male concerned. However, a quantitative estimate made for impala (Jarman and Jarman, 1973) indicated that this gain is very small, of the order of 3 to 5 per cent. Moreover, territorial exclusion is most strict during the rut rather than during the most critical periods for the survival of offspring, periods which usually occur at the opposite season of the year. Furthermore, the biomass reduction would benefit equally a proportion of females bearing the offspring of other males, except in those few species in which females are confined to individual male territories. Notably, these exceptions occur in species which are either highly selective feeders on particular plant parts, such as dikdik; or for which favorable feeding areas are patchily distributed, for example, vicuna (Franklin, 1974), and Grant's gazelle in woodland habitats (Walther, 1972b). In these few cases, the selective consequences for progeny survival may be important. However, most of the larger ungulates feed on plant foliage that is widely distributed and is of a relatively uniform quality over extensive areas. It thus constitutes an "undefendable" resource in terms of energetic gains in relation to costs (J. L. Brown, 1969). Notably, spatial restrictions on feeding are generally absent among females, though resultant food gains would enhance not only their own individual survival but also that of their offspring.

Shelter Sites or Other Loci of Significance

For most ungulates, there are no localized sites of importance comparable to the nest sites of birds or burrows of rodents. The various wild pigs (Suidae) form a possible exception, but territorial dominance associated with particular sleeping nests or holes has not been demonstrated in any species (Frädrich, 1974; Cumming, 1975).

Male Access

Virtually all matings are performed by territorial males. In pronghorns, the bachelor male segment accounted for only 8 per cent of copulations (Kitchen, 1974). In other species, in which the breeding season is more prolonged, the proportion seems to be even less. Thus, the reproductive success of the territorial male segment in general is enhanced by a factor proportional to the relative number of males incorporated in the bachelor male segment. This reproductive gain seems to vary between 1.5 and 3 times, based on reported ratios of territorial to bachelor males. Individual males may enhance their access to receptive females still further by occupying territories in areas particularly favored by females during the main breeding period. For pronghorns, Kitchen (1974) demonstrated a positive correlation between forage quality in a territory and the mean numbers of females present. In Uganda kob, receptive females preferentially seek out the most central territories on the territorial grounds (Buechner and Schloeth, 1965; Floody and Arnold, 1975). Males holding such favorable territories can enhance their reproductive contribution by a factor of 5 times or more (see below). The selective consequences of such variations in reproductive success seem far in excess of those likely to result from variations in either individual survival rates or those of progeny.

It may be concluded that in ungulates territoriality has evolved primarily through processes of intrasexual selection apportioning mating opportunities among competing males. As Darwin (1871) originally pointed out, the products of sexual selection may be disadvantageous for individual survival, and even for the long-term viability of the species. Thus, widely adopted arguments emphasizing survival values in relation to ecological conditions cannot adequately account for the evolutionary origins of ungulate territorial systems. However, territoriality is only one possible form of mating system that can be adopted by males. Ecological factors come into play as they affect the selective advantages and disadvantages of territoriality in comparison with alternative mating strategies.

Male Mating Strategies

Previous authors have characterized mating systems by the relationship prevailing between males and females in terms of monogamy, polygyny, polyandry, and promiscuity (e.g. Orians, 1970). However, mating systems can also be differentiated in terms of the competitive strategies operating among males. Four basic forms of competitive relationship may be distinguished in ungulates, though further studies may reveal more. These are:

(i) a *spatially localized dominance* within a *territory* (the prevailing pattern among antelopes);
(ii) a *mobile dominance* associated with a particular female *harem* group (as in plains and mountain zebras; see Klingel, 1967; E. Joubert, 1972);
(iii) a relatively *stable ranking dominance* prevailing among a set of males simultaneously associated with a large female aggregation (the African buffalo is the best example; see Sinclair, 1974);
(iv) a more *temporary dominance* established in the precincts of individual estrous females, coupled with wide *roving* from female to female (as exhibited by most cervids and caprines; see, for example, Lent, 1965; Geist, 1971).

In particular species, the operating mating system can be a partial compromise between two of these basic types. For example, a roving dominance is usually coupled with varying degrees of stability in the relative rankings of males.

Genetic Gains and Costs

To estimate the potential genetic gain which could be conferred by a particular mating strategy, I will introduce a parameter called the "potential mating enhancement factor" (PMEF). This will be defined as the ratio of the mating success achieved by top males, in terms of number of females fertilized, to that of the average male in a random mating system, over a single breeding season. By "top male," I mean the individual at the top of the list if a cohort of competing males are ranked according to their mating success. This cohort would include all physiologically potent individuals capable of fertilizing a female in the absence of a superior competitor (even though some of these might be classed as subadult on morphological or behavioral grounds). It would encompass, for example, all the Uganda kob males associated with each territorial ground, or all the African buffalo males attached to a single female herd, and might number from 20 up to about 200 individuals.

On a seasonal basis

$$\text{PMEF} = \frac{\text{no. of females fertilized per top male}}{\text{no. of fertile females/no. of potent males}}$$

$$= \frac{\text{no. of females fertilized per top male}}{\text{adult sex ratio females/males}}$$

or, alternatively

$$= \frac{\text{\% of fertile matings performed by top males}}{\text{\% of available males comprised by top males}}$$

Usually potential top males are readily identifiable. They attract attention by holding an alpha position in dominance rankings, occupying particularly active territories, or being attached to unusually large harems. It is more difficult to determine the number of fertilizations achieved by these males. However, for ungulates it seems that only estrous females tolerate mounting and copulation (Fraser, 1968); and while some of the estruses could be "silent" (that is, unaccompanied by ovulation), this possibility probably does not influence male behavior. Thus, the relative number of copulations performed can be used as a reliable measure of fertilization success. Nevertheless, for many ungulates, copulations are surprisingly difficult to observe. In some cases circumstantial evidence can be used on a basis of knowledge of behavior patterns preceding matings, such as the formation of "tending" bonds or preliminary mounts. In others, a less satisfactory estimate may be made in terms of harem size or, where stable harems do not exist, simply the mean number of females a male associates with during the peak conception period.

Few authors have presented the information needed to calculate PMEF's (Table 3). These estimates have in most cases been derived from rather incomplete data, and are to be regarded as provisional until more critical studies have been performed. Results suggest that for territorial systems PMEF's of from 4 to 8 times may be attained, whereas for other mating strategies PMEF's of from 6 to 12 times can result.

Let us provisionally accept that territoriality does indeed yield lower PMEF's than alternative mating strategies. Then it might at first seem surprising that territoriality should ever have evolved. However, it is not the temporary

TABLE 3

Mating enhancements achieved by top males by various mating strategies

SPECIES	MATING SYSTEM	MEASURE	PERIOD	% OF MATINGS	% OF MALES	MEAN NO. ♀s	RATIO ♀/♂†	PMEF ESTIM.*	REF.
Red deer	temp. harem	mean harem size	one season	—	—	10	0.84	12	Lincoln et al., 1970
Soay sheep	roving domin.	no. tending bonds	one season	16	1.6	—	—	10	Grubb, 1974
American elk	temp. harem	harem size & duration	one season	—	—	15	(1.5)	10	McCullough, 1969
Barasingha	rank domin.	% sexual activity	one season	48	6	—	—	8	Schaller, 1967
Pronghorn	terr.	no. of copulations	two seasons	14	1.7	—	—	8	Kitchen, 1974
Uganda kob	terr.	mating activity	—	90	12	—	—	7	Buechner, 1974
Uganda kob	terr.	% of mounts	one season	31	4½	—	—	7	Floody & Arnold, 1975
Vicuna	terr. harem	harem size	one season	—	—	9	(1.3)	7	Franklin, 1974
Plains zebra	harem	harem size	several seasons	—	—	6	(1.0)	6	Klingel, 1969
Grant's gazelle	terr.	mean harem size	two seasons	—	—	9.4	2.0	5	Walther, 1972
White rhinoceros	terr.	mean ♀s in terr.	three years	—	—	4.2	1.0	4	Owen-Smith, 1975

* These estimates have been calculated from authors' data and are to be regarded as preliminary and somewhat tentative.

† (bracketed), sex ratio assumed, not supplied by author.

$$\text{PMEF} = \frac{\text{\% of matings performed by top males}}{\text{\% of top males among all males}}$$

or, alternatively

$$\text{PMEF} = \frac{\text{mean no. of females fertilized by top male}}{\text{adult sex ratio } ♀/♂}$$

seasonal PMEF that is of evolutionary significance, but rather the lifetime mating enhancement achieved. Selection would favor territoriality if the alternative strategies reduced survival chances by a sufficient degree. What must be assessed, moreover, is not whether or not a particular male in fact lives out his full reproductive lifespan, but rather his likelihood of doing so should a particular strategy be adopted. Ultimately, selection is based on the average survival rates that have been achieved by various phenotypes. It is therefore necessary to introduce a second parameter called the "likely lifetime mating enhancement" (LLME). This is equal to the relative number of females likely to be fertilized by a male over his expected reproductive lifespan, divided by the number of litters likely to be produced during the average female lifespan. The latter term is introduced as a normalizing factor, so that the LLME of the average male surviving to puberty would be unity if male and female survival rates were identical.

$$\mathrm{LLME} = \frac{\sum_{x=x_p}^{x_m} m_x l_x \text{ (males)}}{\sum_{x=x_p}^{x_m} l_x \text{ (females)}}$$

where the units of x are the average breeding interval

x_p = age at puberty

x_m = maximum age of reproductive output

l_x = survival rate from puberty to age x

m_x = mating enhancement factor at age x.

Unfortunately, very few workers have provided data allowing the survivorship costs of alternative strategies to be assessed (Table 4). In the absence of mating competition, males might be expected to survive better than females, since they are free of the nutritional burdens imposed by pregnancy and lactation. However, there is suggestive information, from sex ratios at least (see Table 4), that male mortality rates generally exceed those of females. This evidence must be treated with caution, because authors might have accepted different age classes as adult in males and females, or only a small part of the total population range might have been sampled (males may predominate in peripheral areas). Furthermore, only some of the surplus male mortality need be a direct result of mating competition. In impala, the greatest male mortality is concentrated during the subadult period, following separation from the maternal group (Jarman and Jarman, 1973). However, in bighorn sheep an acceleration in male mortality is clearly associated with the attainment of dominant breeding age. Between two and seven years of age male mortality averaged 4 per cent per annum, whereas between eight and eleven years mortality increased to a mean of 16 per cent per annum (recalculated from Geist, 1972; unfortunately no reliable data on female mortality rates are available). Geist (1972) also noted that rutting injuries alone could account for an annual mortality of 10 per cent in Rocky Mountain goats and 4 per cent in moose.

Any form of mating competition must result in some reduction in life expectancy, on account of the time and energy expended and risks of injury incurred in interactions with other males. The limited data available (Table 4) allow no distinction to be drawn between male survival rates in territorial and non-territorial species. However, time and energy investments in the short rut by non-territorial male deer and sheep do seem far in excess of those occurring among most territorial antelopes, though again quantitative data are sparse. For example, Soay sheep rams devoted on an average only 47 per cent of the day to feeding throughout the two months spanning the rut, compared with 84 per cent on the part of females. During the penultimate week of the rut, the rams spent only 20 per cent of the day feeding (Grubb and Jewell, 1974). Red deer stags devoted only 4 to 6 per cent of their active time to feeding during the mid-rut and late rut, compared with 93 per cent during the pre-rut period (Bützler, 1974). In contrast, though territorial bontebok and impala males spent less time feeding than did females, the seasonal variations were relatively minor, and amounted to an additional reduction by less than 10 per cent of the day during the peak conception period (David, 1973; Jarman and Jarman, 1973). However, territorial male pronghorns fed for only about 2 per cent of observation time during the two-week rut, compared with 30 per cent during the pre-rut (Kitchen, 1974); and territorial wildebeest males reportedly engage in "frenzied activity" during their brief rut (Estes, 1969). Thus no clear dichotomy between

TABLE 4

Costs in terms of mortality and time associated with various mating strategies

SPECIES	LOCALITY	MATING SYSTEM	SURPLUS MORTALITY ♂-♀ (% per annum)	SEX RATIO adult ♀/♂	TIME		PERIOD OF YEAR	REF.
					t_0(♂)-t_0(♀) (% of day)	t_f(♂)-t_f(♀) (% of day)		
Soay sheep	Hirta	roving domin.	26	5.0	—	−37	2 mon. including rut peak	Grubb & Jewell, 1974
Caribou	Newfoundland	temp. harem	5	1.8	—	—	—	Bergerud, 1974
Chital	Kanhai	roving domin.	—	1.4	—	—	—	Schaller, 1967
Plains zebra	Kruger Park	harem domin.	—	1.3	—	—	—	Smuts, 1974
Bighorn sheep	Banff	roving domin.	—	1.1	—	—	—	Geist, 1971
African buffalo	Serengeti	rank domin.	0	—	—	—	—	Sinclair, 1974
Red deer	Rhum	temp. harem	−14	1.0	—	—	—	Lowe, 1969
Impala	Serengeti	terr.	—	2.0	14	−5	year-round;	Jarman & Jarman, 1973
					16	−14	conception peak	

Grant's gazelle	Serengeti	terr.	—	2.0	—	—	—	Walther, 1972
Uganda kob	Semliki	terr.	—	1.9	—	—	—	Buechner, 1974
Defassa waterbuck	Rwenzori	terr.	—	1.9	—	—	—	Spinage, 1974
Roe deer	Switzerland	terr.	—	1.5	—	—	—	Kurt, 1968
Thomson's gazelle	Serengeti	terr.	—	1.4	—	—	—	Hvidberg-Hansen & DeVos, 1971
Coke's hartebeest	Nairobi	terr.	—	1.4	—	—	—	Gosling, 1974
Pronghorn	Montana	terr.	—	1.0	4†	—	prerut	Kitchen, 1974
					18†	(−30)^{x}	rut	
White rhinoceros	Umfolozi	terr.	2	1.0	3	−0.4	year-round;	Owen-Smith, 1973
					6	+3.5	mating peak	
Wildebeest	Serengeti	terr.	—	0.9	—	—	—	Talbot & Talbot, 1963
Bontebok	Swellendam	terr.	—	0.9	8	7	year-round	David, 1973
					11	8	rut	

† Social interactions only.

()^{x} Reduction as percentage of observation time.

t_o, time devoted to "miscellaneous" activities (including social interactions).

t_f, time spent feeding.

territorial and non-territorial systems is evident, and additional factors such as the duration of the breeding season seem to exert an influence. Interactions among males seem much more frequent and vigorous during the rut in northern non-territorial species, from what few reports are available. An American elk stag associated with a harem engaged in 1.8 charges and 0.4 horn clashes per active hour (McCullough, 1969). In contrast, even the top male on a Uganda kob territorial ground engaged in only 0.5 agonistic encounters per observation hour (Floody and Arnold, 1975); while during the two peak rutting months, blesbok territory holders engaged in 0.9 challenge rituals or chases per observation hour (Novellie, 1975). Territorial wildebeest males engage in about six relatively ordered challenge rituals per day (Estes, 1969), and vicuna territorial males initiate about one to two encounters per day with neighbors (Franklin, 1974), while white rhinoceros territorial males encounter a neighbor only about once every four days (Owen-Smith, 1975); but these reflect year-round averages.

Northern deer and sheep males lose considerable body condition during the rut, which must reduce their survival chances during the subsequent winter (see Lincoln, Youngson, and Short, 1970; Geist, 1971; Grubb and Jewell, 1974). The high survival rates relative to females of male red deer on the island of Rhum (Lowe, 1969) thus seem remarkable. A significant factor confusing patterns here is perhaps the absence of large predators. Where these abound, as is still the case in most tropical habitats, even a small drop in physical fitness or injury could quickly prove fatal.

Model Simulation

The empirical data are inadequate to allow any reliable conclusions to be drawn regarding the relative gains and costs of alternative mating strategies based on cross-species comparisons. But the need is really not for a comparison of the economics of territoriality under one set of ecological conditions with those of other mating systems in rather different circumstances. The question is, what would happen, in evolutionary terms, were a male to adopt an alternative mating strategy under the same ecological conditions? This cannot be answered empirically, since it is to be expected that all males of a species are genetically programmed for the same mating strategy, that which has proved most successful in the past. The occurrence of bachelor males does not demonstrate an alternative strategy, but only a temporary alternation of tactics.

Some insight may be given through some calculations using the evolutionary model that has been developed above, involving the parameters PMEF and LLME. Let us provisionally accept that territoriality is indeed a "low benefit-low cost" system in comparison with rank or roving dominance strategies, and calculate the LLME's that could result. A constant survival rate through the reproductive life span will be assumed, potentially differing for territorial versus roving or rank dominance strategies. Maximum PMEF's of 6 and 10 will be allowed for territorial and rank/roving dominance systems, respectively. Life history parameters will be assumed that seem reasonable for a large ungulate the size of a red deer or waterbuck. The aim is to assess what reduction in chances of survival must be conferred by rank or roving dominance strategies in order to favor territoriality. Since it is unlikely that the maximum PMEF could be sustained by any individual throughout his reproductive lifespan, the effects of three different mating regimes will be considered:

(i) full PMEF attained for two consecutive seasons between the ages of 6 and 8 years, with reduced mating success during preceding and following seasons (perhaps through occupation of a less favorable territory, or subdominant ranking);
(ii) maximum PMEF retained for three consecutive seasons in territorial systems only (prior occupation of a territory might inhibit challengers);
(iii) mating contribution commencing a year earlier in rank/roving dominance systems (since young males seem to achieve a few matings in bighorn sheep, for example; see Geist, 1971).

The resultant LLME's calculated for top males under different mortality regimes are presented in Table 5. With the same mating regime (i) applying to both systems, territorial-

TABLE 5

Likely lifetime mating enhancements calculated for top males under different mating and survivorship regimes (see text)

		CALCULATED LLME (see text)				
		"territorial dominance"		"roving/rank dominance"		
	PMEF	6		10		
	additional ♂ mortality incurred (% per annum)	0	5	10	15	20
ASSUMED MATING REGIME	resultant adult sex ratio* (♀/♂)	1.0	1.2	1.4	1.6	1.9
i. $m_{(6-8yrs)}$ = PMEF; $m_{(5-6yrs)(8-9yrs)}$ = ½ PMEF; $m_{(9-10yrs)}$ = ¼ PMEF; $m_{(2-5yrs)}$ = 0		2.28	1.78	2.28	1.74	1.32
ii. $m_{(6-9yrs)}$ = PMEF; $m_{(5-6yrs)(9-10yrs)}$ = ½ PMEF; $m_{(2-5yrs)}$ = 0		2.77	2.13			
iii. $m_{(4-5yrs)}$ = ¼ PMEF; otherwise as in (i)				2.55	1.98	1.53

Assumes annual breeding season, reproductive maturity at 2 years, maximum reproductive longevity of 10 years, basic survival rate beyond 2 years constant at 0.95 per annum.

* This assumes an equal sex ratio at 2 years.

ity would be favored evolutionarily only if the additional male mortality resulting from a rank/roving dominance strategy exceeded 10 per cent per annum. However, if territoriality conferred an extra season at maximum PMEF [i.e., mating regime (ii)], it would be selected for even if the surplus mortality associated with alternative strategies were only about 6 to 7 per cent per annum. On the other hand, if males in compensation had mating opportunities at an earlier age under rank/roving dominance systems, the balance is shifted back again almost to that prevailing under (i).

This analysis is instructive in demonstrating the sensitivity of the ultimate genetic success of males to three factors:

(i) maximum mating enhancement attainable;
(ii) duration of lifespan over which a mating contribution is made; and
(iii) mortality costs resulting from energy expenditures and risks incurred.

Clearly, more empirical data are needed on these aspects, not only on the prevailing patterns in different species, but also on the circumstances influencing their variability, to enable modelling to be extrapolated between differing sets of ecological conditions.

Conditions Favoring Territoriality

If the assumption that territoriality is basically a "low benefit-low cost" system is accepted, then territoriality should be favored under conditions (ecological, sociological, or morphological) where the costs associated with alternative mating strategies are likely to be particularly high. The observed incidence of territoriality seems in accordance with this prediction.

(i) *Habitat seasonality.* As explained by Geist (1974), there is a vast seasonal superabundance of forage production during the summer in temperate habitats, allowing males to store extensive energy reserves in the form of fat. This fat can be utilized later to sustain them through the intense but brief rut. In tropical savanna regions, in contrast, population levels remain closer to carrying capacity year round, and breeding seasons are commonly extended. As a result, the potential for fat buildup is more limited, and a male engaging in very vigorous interactions would more quickly bankrupt himself energetically. This difference accounts for the general prevalence of territoriality among tropical ungulates, but does not explain the non-territorial exceptions.

(ii) *Local population size.* The greater the number of males coming into competition, the less easy individual recognition becomes, and the more difficult it becomes to maintain dominance rankings without frequent contesting. In general, tropical zone ungulates maintain higher local population densities than temperate zone species of similar body size (see Tables 1 and 2).

(iii) *Predation pressure.* As suggested earlier, wherever large predators abound even a relatively minor combat injury or loss of physical fitness could prove fatal. Spotted hyenas, in particular, prey selectively on weak or injured individuals (Kruuk, 1972). This circumstance would favor the reduction in combat frequency that is likely to result from territoriality. Large predators are particularly abundant in tropical savanna habitats.

(iv) *Size, cohesion, and mobility of female groups.* Where females are wide-ranging, so that their location during the breeding season is unpredictable, territorial localization will be disadvantageous. If females move in small but intrinsically cohesive groups, a male can move with such a group and dominate its precincts without excess expenditure. This situation results in harem dominance, as in plains zebras. If females aggregate in large herds, several females are likely to be in estrus simultaneously. It then becomes advantageous for subdominant males to attach themselves and accept secondary mating opportunities, while the constant association among such males facilitates the maintenance of stable dominance rankings. This is the situation in African buffalo. The mobility and size of female groupings are determined independently by feeding and anti-predator strategies, as explained by Jarman (1974).

(v) *Weapons morphology.* Dangerously pointed horns or antlers increase the risks of injuries in combat (see Geist, 1966). This condition could account for the occurrence of territoriality in such northern forms as roe deer, pronghorn, and possibly chamois. Morphologically complex horns or antlers, on the other hand, could aid stability in rank dominance systems either by clearly differentiating sub-prime males (as seems to occur in bighorn sheep, see Geist, 1971), or by facilitating individual recognition (as demonstrated for red deer by Lincoln, Youngson, and Short, 1970). This relationship could help account for the absence of territoriality among tropical Asian deer, such as chital and barasingha.

(vi) *Food selection.* For species feeding selectively on food morsels in limited but relatively predictable (in time and space) supply, exclusion of other conspecifics from a territory could significantly enhance the food available there for the occupants. The major selective results of this circumstance would arise when this food supply is shared by a mated pair and their offspring, as in dikdik. In effect, emphasis is shifted from mating to progeny-rearing strategies, since with a monogamous bond the mating enhancement factor is close to unity.

However, there remain several as yet poorly known species in which the absence of territoriality is not so readily explained. These include the lesser kudu and other tragelaphine antelopes, giraffes, and Asian rhinoceroses. Perhaps to be added are the macropod marsupials (Kaufmann, 1974) and ungulimorph South American rodents (Eisenberg and Mackay, 1974), both of which share ecological similarities with the ungulates. More information is also needed on the social systems of tropical Asian and South American deer, and also on various wild pigs, in order to elucidate the relative importance of ecological and phylogenetic factors in the evolution of mating systems.

COMPARISONS AND CONCLUSIONS

Evidence has been presented that in most ungulates territoriality is exclusively a male mating strategy which has evolved through processes of intrasexual selection. This conclusion arises from the circumstance that male ungulates generally exert little influence on the survival of their offspring, so that differential genetic success arises primarily from differences in their mating contributions. Rather than being unusual, such a situation seems to be the prevalent one in the animal kingdom. Territoriality apparently functions primarily to enhance mate acquisition also in pinnipeds (Bartholomew, 1970), grouse and other birds with precocial young (Wiley, 1974; Hogan-Warburg, 1966), lizards (Milstead, 1967), crocodiles (Modha, 1967), and dragonflies and other terrestrial invertebrates (Johnson, 1964; Brown and Orians, 1970). In fact, it is the situation in small passerine birds with altricial young, upon which previous reviews of territoriality have largely been based, that seems the special case. For them, opportunity to breed is dependent on the acquisition of a nesting site, which is necessarily fixed in space. This limitation favors spatial localization by males seeking opportunities to mate successfully. The successful rearing of offspring is critically dependent upon provisioning, to which both parents can contribute. Food for this purpose is most efficiently obtained from the immediate surroundings of the nest, and as a consequence the exclusion of conspecifics from this area is advantageous. This in turn favors a monogamous mating system, with differential genetic success based mainly on the occupation of optimum nesting sites and subsequent success in raising progeny there. Territorial exclusion arises largely as a consequence of the localization of nest sites. Correspondingly, among fishes, territoriality is most prevalent wherever breeding opportunities are dependent on limited nest sites, for example in cichlids (Baerends and Baerends-van Roon, 1950) and reef-inhabiting pomacentrids (Clarke, 1970). Territories of rodents and lagomorphs are also usually based on a fixed nest or burrow site (see King, 1955; Archer, 1970; Armitage, 1974; Lockley, 1961; Mykytowycz and Gambale, 1965). Territoriality based exclusively on food for individual survival is the most unusual case. It has been documented for the squirrels *Tamiasciurus hudsonicus* and *T. douglasi*, which rely on stored pine cones for their winter food supply (C. C. Smith, 1968). Notably, in these species males and females maintain separate territories. The winter feeding territories claimed for several bird species seem less clearly substantiated, except in the case of red-headed woodpeckers, which store acorns within their territories (Kilham, 1958). Feeding territories described for hummingbirds, localized on individual flowers (Wolf, 1969), are rather trivial cases.

Among primates the situation is more complex (Bates, 1970). Exclusive territories are occupied by male-female pairs among gibbons (Ellefson, 1968) and titi monkeys (Mason, 1968), and by single-male, multi-female units in several forest-dwelling cercopithecines and colobines (Aldrich-Blake, 1970; Yoshiba, 1968; Marler, 1969). The multi-male units formed by red colobus monkeys (Struhsaker, 1974), grey langurs in arid habitats (Yoshiba, 1968), macaques (Simonds, 1965; Lindburg, 1971), and savanna baboons (DeVore and Hall, 1965; Altmann and Altmann, 1970) inhabit overlapping home ranges. Males do not occupy territories independently of females in any of the higher primates. It seems that the primary spacing out of the female units is based on selective feeding habits. Superimposed on this system is male-male reproductive competition, operating to sharpen the boundaries between the areas occupied by different single-male groups, so that these become exclusive territories. In the absence of such competition, the situation would perhaps resemble that in the coati *Nasua narica*, in which males are not permanent members of groups. Here female group home ranges have exclusive core areas but overlap marginally, and neighboring groups show little antagonism upon meeting (Kaufmann, 1962). The mating system of species forming single-male groups is thus basically a harem dominance, rather than territoriality. In multi-male groups, rank dominance controls mating success, and spatial exclusion is accordingly relaxed.

Territoriality is simply one possible way of socially organizing dominance relationships. Under different conditions it may function primarily to enhance food supply, or mate access, or the acquisition of breeding sites. As demonstrated by the ungulates, dominance may be localized within a spatial territory even when the significant resource, in this case females, is not. Rather than trying to decide whether a particular species should be classified as territorial or not, we should consider the detailed strategies used by individuals to secure a disproportionate share of each resource of potential significance to genetic success. The question is not why does territoriality exist, but rather, why has territorial dominance been favored, rather than some alternative system of dominance organization? This conclusion must lead to a careful comparison of the likely costs and benefits that would result from different alternatives under the prevailing ecological, social, and morphological conditions. Actions may be modified in accordance with varying environmental circumstances, retaining similar selective advantages but producing seemingly drastic alterations in social structure. Such flexibility tends to confuse a classificatory approach.

As in the case of all evolutionary arguments, the experiment has already been performed and we merely observe the outcome, that is, the behavioral phenotypes that have proved most successful under the conditions that have prevailed in the past. Our aim is simply to explain this result by unravelling the factors that have influenced it. To test our understanding, we need to construct evolutionary models, and then investigate how variations in key factors might have influenced the outcome. Currently, this exercise is hampered by the paucity of empirical facts. It is one of the aims of this review to point out the kinds of data needed in order to do this, in the hope that future field research will remedy this deficit before opportunities disappear. For ungulates, detailed information is required on natural population densities, interaction frequencies, frequency of escalation of contests and injuries sustained, time and energy expenditures, age/sex specific mortality rates, seasonal mating successes achieved, and age variations in mating performance.

SUMMARY

The characteristics of territoriality, as exhibited by ungulates, are examined. The following features emerge:

(i) the term *territory* is required to refer to geographically fixed spaces influencing social relationships;
(ii) each territory is occupied by one territorial male who moves beyond its limits only in special circumstances;
(iii) within their own territories, territorial males challenge intruding males and advertise their presence by visual, auditory, or olfactory displays;
(iv) ritualized confrontations with neighboring territorial males take place usually at mutual borders;
(v) outside their territories, territorial males behave submissively;
(vi) bachelor males generally move more widely and respond submissively to all territorial males;
(vii) in most species, females range widely in overlapping home ranges; and
(viii) in a few species only, females may share individual male territories, whereas in others a weaker spacing between female home ranges may exist.

Each territorial male in effect exerts a spatially localized dominance over all other individuals. Mutual spatial exclusion follows from this relationship, and the resulting form of population organization constitutes territoriality. This spatial dominance confers enhanced access to mates. The consequences in respect to access to food or viability of progeny seem insignificant in most ungulates. Through territorial dominance, top males may achieve a seasonal mating enhancement of four to eight times. This figure is lower than what can be achieved under alternative mating systems, which include rank dominance, roving dominance, harem dominance, or combinations of these. However, the costs, in time and energy expenditures and injury risks leading to reduced life expectancy, are probably lower in territorial systems. According to an evolutionary model that is presented, selection could favor territoriality if the adoption of an alternative strategy resulted in an excess male mortality greater than 10 per cent per annum. Territoriality is favored in tropical regions on account of reduced seasonal forage surpluses favoring less intense interactions and extended breeding seasons, high local population densities, and numerous predators, except where female groups are wide-ranging and cohesive, or very large. Morphologically dangerous weapons may further favor territoriality. Territoriality is simply one form of dominance relationship, and in other animal groups it might serve different evolutionary functions. More empirical data are needed to test theoretical models.

ACKNOWLEDGMENTS

This paper has benefited from the critical comments of J. D. Skinner, V. Geist, J. A. J. Nel and E. Bursell, and upon an earlier version by J. T. Emlen, P. Marler, J. Kaufmann, W. Leuthold, G. Stephenson, M. Demment, and A. Bleed.

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