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Social organization and communication of riverine hippopotami in southwestern Kenya

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Summary. — In 1982, the population of hippopotami within a 127 km stretch of the Mara River, southwestern Kenya, was in excess of 2800 animals. The average group size was 13.3 individuals ; 8 percent adult males, 36 percent adult females, 27 percent subadults, and 29 percent unweaned calves. Males were territorial but abandoned pools during low water conditions, exhibiting little attachment to specific sites. Nursery groups of females and offspring were unstable in composition and moved in response to changing water levels.

Responding to seasonal declines in water levels, animals were concentrated in fewer suitable pools. Levels of aggression increased during periods when changing water levels required redistribution of animals but few serious fights were observed. Although interactions between adult males were most striking, the most frequent recipients of aggressive actions were subadults which were commonly expelled from groups.

Communication was essential to the establishment and maintenance of dominant/subordinant ranking, both within groups and between individuals encountering each other outside of group situations. Gaping, posturing, and marking defecation were identified as important in the reinforcement of dominance and maintenance of breeding territories by dominant males.

There was no strong evidence that behavioural mechanisms played a role in limiting population growth. However, during the course of this investigation there were no identified environmental stresses, such as limited forage availability, imposed upon the population.

Résumé. — En 1982 la population d'hippopotames qui vivait sur une étendue de 127 km de la rivière Mara, au sud-ouest du Kenya, était supérieure à 2800 animaux. Les groupes, de 13,3 animaux en moyenne, étaient constitués de 8 % de mâles adultes, de 36 % de femelles adultes, de 27 % de subadultes et de 29 % de jeunes non sevrés. Les mâles étaient territoriaux mais ils ont abandonné le marais pendant les périodes de stress, tandis que les célibataires étaient en général solitaires et qu'ils ont montré peu d'attachement à des sites particuliers. Des groupes de femelles et de leurs jeunes en nurseries se sont montrés être de composition instable et se sont déplacés en fonction des modifications du niveau de l'eau.

En réponse à la baisse saisonnière du niveau de l'eau, les animaux se sont concentrés dans un nombre limité de mares accessibles. Le niveau d'agression s'est accru au cours des périodes où les variations du niveau de l'eau ont nécessité une redistribution des animaux, mais on a constaté peu de combats sérieux. Bien que les rencontres entre mâles soient les plus violentes, les subadultes, qui étaient habituellement chassés des groupes, ont été le plus fréquemment responsables des actions agressives.

Mammalia, t. 50, n° 2, 1986.

La communication s'est montrée essentielle pour établir et maintenir l'équilibre dominant/dominé, autant dans les groupes que parmi les individus qui se rencontraient à l'extérieur. Les mâles dominants renforçaient leur dominance et leur emprise sur les territoires de reproduction par des attitudes, par le marquage fécal, ou en bâillant.

Il n'est pas certain que des mécanismes comportementaux jouent un rôle dans la limitation de la croissance de la population. Au cours de ces recherches on n'a cependant pas identifié de contrainte de l'environnement qui se soit imposée à la population, comme par exemple une limitation de la nourriture disponible.

INTRODUCTION

The basic social unit within hippopotamus *(Hippopotamus amphibius)* populations is of mother and young. Groups are composed predominantly of adult females, their calves and subadults. Several adult males may be included in the group, although there is usually a single dominant male (Verheyen 1954 ; Olivier and Laurie 1974 ; Klingel 1979). Mating territories are held by these dominant individuals (Klingel 1979). However, spatial affiliations may be less strong in riverine than lacustrine habitats (Olivier and Laurie 1974). Bachelor males, generally evicted from parental groups at puberty, 7-8 yrs of age (Dittrich 1976 ; Skinner *et al.* 1975), may remain solitary or join groups predominated by males (Attwell 1963 ; Klingel 1979).

Social structures are maintained by poorly-documented systems of communication. Apart from overt combat, communication involves postural signals, ritualized dunging behaviour, and vocalization. The behaviour of dominant adult males has been described by Hediger (1951), Verheyen (1954), Olivier and Laurie (1974) and Klingel (1979). These authors identify two major social signals ; gaping (or yawning) and dung spraying, which are used in advertising and reinforcing dominance. Otherwise, as noted by Kingdon (1979) and Walther (1984), this species has not been well studied.

A role of aggression in population regulation has been suggested but not tested definitively. Attwell (1963) and Olivier and Laurie (1974) implicated increased aggression with higher mortality rates in all age classes during environmental stress, such as severe crowding within pools or poor nutritional regimes.

As part of an ecological investigation into the rapidly expanding population of hippopotami within the Mara River in southwest Kenya (Karstad 1984), we collected behavioural data from September 1981 to September 1982. The primary objective was to describe the social dynamics of riverine hippopotami and to reflect on the role of behaviour in determining population size.

STUDY POPULATION

The population under study has exhibited an average annual increase of 12 % per annum since 1960. Density redistributions in response to population expansion were noted between 1980 and 1982 (Karstad and Hudson 1984). Social pressures appeared to be the driving force, governed by pool availability. Densities of around 25 hippopotami per km of river were rarely exceeded locally. Since the main thrust of the redistribution was northward, toward the headwaters of the Mara River, the expansion cannot continue indefinitely and may revert to

local population growth focussed arou
might then be expected to play a mo
Behavioural studies described in this p
of the upper reaches of the Mara R
the Masai Mara Reserve.

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CLASSIFICATION

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Class 2 — Frontal slashing wit
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Class 3 — A protracted fight ;
vocalization.

local population growth focussed around specific pool locations. Social pressures might then be expected to play a more important role in population regulation. Behavioural studies described in this paper were conducted along a 10 km stretch of the upper reaches of the Mara River centering on Buffalo Camp north of the Masai Mara Reserve.

METHODS

Classification and identification

Adult males were identified by their large, more heavily muscled neck and head, particularly between the eye and the ear at the insertion of the masseter muscle. Thus, mature males appeared to have a less bulbous eye than females. Males also possessed thicker and longer lower canines that visibly distended the cheek pouches in which they were contained.

Comparison of head length (snout to ear) provided criteria for age classification. « Subadult » head lengths were 1/3 to 2/3 the length of the head of the largest member of the group, « young » head lengths were less than 1/3. « Adult » included all members with head lengths greater than 2/3 the length of the largest adult individual's head.

A photographic card index was constructed to aid individual identification, particularly of dominant males residing within the study area. A 600 mm Novoflex lense with high-speed 35 mm black and white film was used to record an image of the right head profile. From the photographs, an individual identification key was developed based primarily on eye-wrinkle patterns. Distinct markings such as scars and notched ears were noted.

Behavioural observations

A total of 112 hours of behavioural observations, made during two hour sessions between 16.30 and 18.30 h, was recorded between September 1981 and September 1982 (Tab. 1). An effort was made to concentrate observations during times of extreme river levels to compare behaviour at different levels of pool occupancy. The following social signals were recorded :

1. *Gapes :* All group members included.
2. *Vocalizations :* Recorded for both the number of sessions and the number of animals participating in each.
3. *Submissive defecations :* Cumulative for each 2-hr observation period.
4. *Mark defecations :* Cumulative for 2-hr observation period with special note made if involving an animal other than the dominant male of the group.
5. *Fights :* Aggressive interactions classified to three levels of severity ;

   Class 1 — Rush or jump, short, may be a slash from behind. Not always involving physical contact.

   Class 2 — Frontal slashing with contact or a persistent chase with or without contact. Usually included vocalization.

   Class 3 — A protracted fight ; physical contact with wounding. Always involved vocalization.

TABLE 1. — Agonistic encounters among age/sex classes (%) observed during 112 hours of observation (16.30 - 18.30 h).

	AM:AM	AM:AF	AM:SA	AM:Y	AF:AF	AF:SA	AF:Y	SA:SA	SA:Y	Y:Y	Nobs
C1 :	9.4	5.6	15.9	9.4	13.1	14.0	8.4	11.2	9.4	3.7	107
C2 :	47.4	.0	5.3	.0	10.5	21.1	5.3	10.5	.0	.0	19
C3 :	100.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	3

AM = adult male, AF = adult female, SA = subadult, Y = Young, CN = levels of aggression (classes 1 through 3), Nobs = number of observations.

WATER LEVELS

River levels were recorded using a staff gauge firmly sunk in hard clay and attached at the top to the base of a large tree. Daily record patterns were categorized as increasing, decreasing, static high and static low conditions. 'Increasing' and 'decreasing' phases involved a constant change in river level of greater than five days duration, resulting in an overall change equal to or greater than 15 cm. Low and high 'static' conditions were less than 0.60 m in height for low, and greater than 0.60 m in height for high, as measured on the staff gauge.

STATISTICAL ANALYSIS

A Pearson correlation matrix was produced from pooled data. Data were also distributed among the four river dynamics categories. As sample sizes were reduced in this manner, non parametric analysis was adopted using Spearman's rank order correlations.

Agonistic encounters among sex and age classes were analysed using χ^2 tests. Neu *et al.'s* (1974) technique for analysis of availability/utilization data was used to determine category-specific confidence intervals. Class 3 aggression occurred very infrequently and was excluded. The hypothesis tested was that aggression initiated by each class was proportional to its numerical representation.

RESULTS AND DISCUSSION

SOCIO-SPATIAL ORGANIZATION

Adult males comprised 8 percent, adult females 36 percent, subadults (not sexed) 27 percent and young 29 percent of the study population. The low proportion of adult males may reflect either voluntary emigration or exclusion of rivals by dominant males. Very few 'bachelor groups' (Klingel 1979) were noted within the Mara River, as batchelors appeared to prefer a solitary existence. Individuals not associated with groups were noticably less attached to specific sites. Solitary subadults, assumed to be males, were commonly seen adjacent to groups and took the brunt of aggression from adult group members. These individuals quickly left sites when disturbed. Klingel's *(op. cit.)* observation that both bachelor and

female groups were rarely of a homoge
bers holds true for the Mara River

Territoriality.

Dominant males exhibited strong
and their offspring was more strongl
unsuitability of pools at particular ri
dominant male to join a small group
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Territories of dominant males we
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heaps (Hediger 1951). This has since
and Laurie (1974) and Klingel (1979
study since observations were limited
activity in the late afternoons.

Group dynamics.

Group sizes averaged 13 individ
occupancy varied widely with water le
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over at least nine peripheral pools

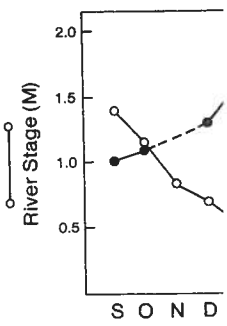

Fig. 1. — Water levels in the Mara Riv
within the 10 km study section.

s (%) observed during 112 hours of observa-

SA	AF:Y	SA:SA	SA:Y	Y:Y	Nobs
.0	8.4	11.2	9.4	3.7	107
.1	5.3	10.5	.0	.0	19
.0	.0	.0	.0	.0	3

lt, Y = Young, CN = levels of aggression
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female groups were rarely of a homogenous sex composition amongst adult members holds true for the Mara River population.

Territoriality.

Dominant males exhibited strong site attachment. The distribution of female and their offspring was more strongly influenced by river dynamics. However, unsuitability of pools at particular river levels occasionally caused the resident dominant male to join a small group in a nearby, more comfortable pool. On three occasions a dominant male was observed to follow a group of females to an adjacent pool and assume a subdominant position. Once water levels returned to suitable depths, males returned. Of course, this flexibility does not preclude territoriality, as concluded by Olivier and Laurie (1974).

The territorial behaviour of lacustrine hippopotami appears much more stable than riverine populations. Klingel (1979) records two dominant males in lake habitats holding the same territory for 8 years. For river habitats, his records indicate a higher rate of exchange which he attributed to the higher density. In the Mara River, most dominant males retained possession of territories (although they were temporarily vacated during unfavorable water levels) during the 12 month study ; only one dominant male was permanently displaced by a rival, and subsequently died from wounds inflicted in the altercation.

Territories of dominant males were once thought to include not only stretches of river or lake shore, but pear-shaped inland grazing areas delineated by dung heaps (Hediger 1951). This has since been discounted by Verheyen (1954), Olivier and Laurie (1974) and Klingel (1979). No further insight was provided by this study since observations were limited to the river during periods of peak social activity in the late afternoons.

Group dynamics.

Group sizes averaged 13 individuals (Karstad and Hudson 1984), but pool occupancy varied widely with water levels. The fluctuation in numbers of hippopotami at Main Pool was the result of contraction and dispersal of individuals over at least nine peripheral pools within the 10 km stretch of river embraced

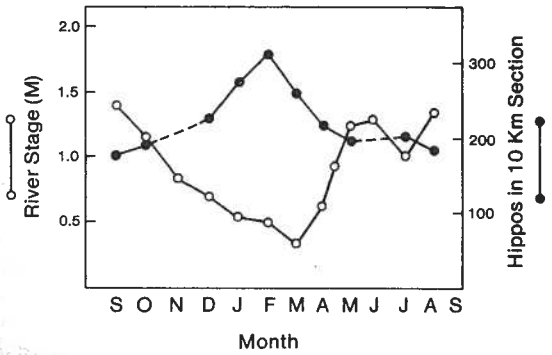

Fig. 1. — Water levels in the Mara River and the corresponding number of hippopotami within the 10 km study section.

by this study. However, redistribution occurred over long stretches of river as well. Fig. 1 illustrates the number of animals within a 10 km section of river. Suitable pools were encountered both up and downstream of the study section during the dry months. Low water levels in the river were the most apparent cause of the influx, but the possibility of movement dictated by forage availability and/or adjacent human activity cannot be excluded. Although only some individuals were easily recognizable, groups appeared unstable in composition. No temporal or spatial alliances were detected.

Klingel (pers. comm.) notes that solitary males inhabiting stretches of river may not be as unsuccessful in attracting females as casual observation would suggest. Changes in water levels result in group movements, particularly on a seasonal basis. Territories occupied by solitary males during low water levels may contain a group of females and their offspring during high water levels.

Overt aggression

Analysis of observed/expected aggression initiated by each age class showed significant differences ($P < .05$) between adult males and calves. Adult males initiated a disproportionately high number of agonistic encounters ; calves a disproportionately low number (Fig. 2). The agonistic behaviour of adult group

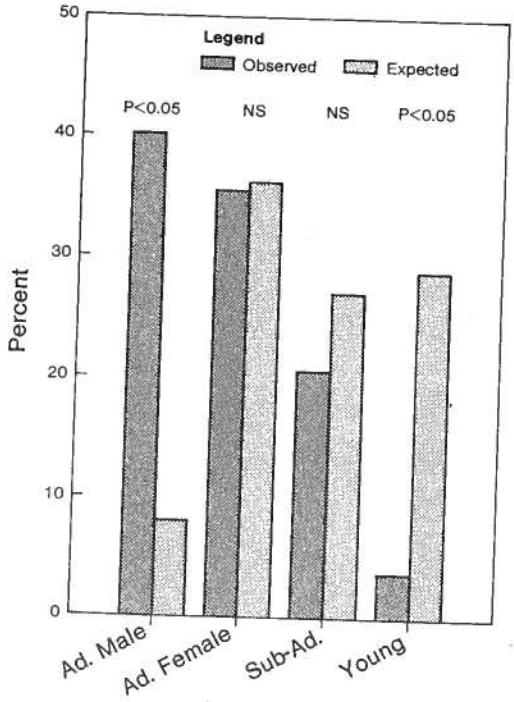

Fig. 2. — Percentage of aggressive encounters initiated by specific sex/age classes of hippopotami. Observed frequencies are compared with those expected on the basis of age/sex structure.

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Postural communication.

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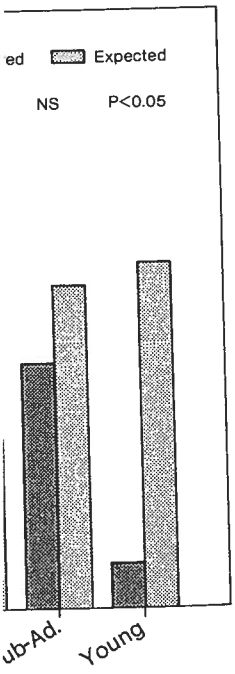

rs initiated by specific sex/age classes of
ɔmpared with those expected on the basis

males and females was implicated with the expulsion of subadult males. Aggression of adults towards subadults made up 32 % of all agonistic encounters. This corroborates Dittrich (1976) and Skinner *et al.'s* (1975) analysis of age at expulsion from groups. Class 3 fights (the most severe) were infrequent and limited to contests among adult males. The reverse-parallel stance reported by Leuthold (1977) and Klingel (1979) was not assumed during serious fights observed between rival males.

Correlations between aggression, water levels and the number of individuals within groups for the four river dynamic states were generally non-significant ($P < .05$). However, one trend was suggested. Decreasing river levels resulted in the highest non-parametric correlations between Class 1 fights and water level ($P = .07$, $rs = .39$) and between Class 1 fights and group size ($P = .02$, $rs = .52$). The highest levels of aggression occurred as groups coalesced while water levels were actively dropping. Weak correlations during static low levels suggests that once a social equilibrium was attained, aggression decreased in spite of high occupancy.

Fights resulting in serious injury were uncommon. Lone subadults as well as a proportion of those in groups exhibited fresh scars during all seasons. Very few hippopotami were not extensively covered with scars, though subadults generally exhibited a greater proportion of fresh shallow cuts. Severe wounds were noted on many adult animals but comparably few on subadult and young. The apparent lack of environmental stress (e.g. drought) may account for the generally harmonious existence observed within even the largest pools. Attwell's (1963) correlation between density and high levels of aggression-related mortality were based on observations made during an extended dry season.

Communication

Communication may be important in maintaining low levels of overt aggression. Rarely was aggressive physical contact not preceded by a clear exchange of signals. The most obvious forms of communication involved threats, both postural and vocal.

Postural communication.

Several specific postures in addition to gapes were associated with exerting dominance or conveying a willingness to fight. Confrontations between adult males utilized most postures described below, although all other sex/age classes occasionally adopted similar behaviours.

Dominant males were the only group members consistently seen with ears in a cocked-forward position. Females, and all other subdominants normally angled their ears back along the neck. Klingel (pers. comm.) pointed this out to us and we found it reliable as an indicator of status.

The most commonly observed dominance posture was an arched neck. The arch exaggerated the size of the neck and shoulders and lifted the eyes clear of the water. The nostrils usually remained submerged. This attitude was commonly used to elicit tail-wagging or defecation displays from subdominants. The head was held in the same manner during most charges and, therefore, may be a threat as well as dominance display.

Humped postures often followed this display. The head was lowered so that only the arched back was visible above the water. This posture gives the impression of massiveness and often preceeded submerged charges. It appeared to be a more intense signal than the neck arch and more clearly associated with threat as opposed to dominance.

All group members were aware of the dominant male's disposition, the simple act of turning his head to look directly at an animal would stimulate a subdominant to deliver a defecation display. Totally relaxed positions were assumed with the neck extended, and often individuals entering groups were halted by the dominant male leaving the relaxed position and turning to look directly at the intruder. It is not necessary, due to the eye placement, for hippopotami to focus binocularly on objects, hence this 'staring' behaviour appeared to be a form of intimidation.

Although submissive gestures are considered rare in swine and hippos (Frädrich 1967), they were evident in this study ; the head, neck and back were maintained in the same plain. This allowed the ears, eyes and nostrils to clear the water. Ears were angled back or down.

Gape.

Gaping or yawning was common to all age and sex classes. The specific social implications are not completely clear, though the action normally attracted attention. Of the several ritualized aggressive encounters observed between adult males, gapes were frequent and prolonged (up to 8 seconds). Dominant males exhibited the most energetic gapes and assumed a specific stance with the neck extended and the head thrown back, so that the top of the head (ear to snout) was almost perpendicular to the back. Young, probably emulating the dominant male, were the only other age group which exhibited this particular posture while gaping. This position exposed the vulnerable underside of the neck, seemingly an expression of confidence.

Gape breadth, the distance between upper and lower lips, was constantly compared between animals within the young and subadult age classes and appeared to be a major play activity. The process involved carefully matching lips, then gaping and pushing, an activity that could be repeated for hours. Usually the larger participant 'won' by pushing the opponent up and back. Adult females were observed to 'lip wrestle' on several occasions, and twice the activity preceeded mating by the dominant male.

Weapon size in many species is a component in establishing dominance through intimidation (Leuthold 1977). The gape display of hippopotami exposes tusks for evaluation, and the gape breadth may be an additional rank-indicator. Herring (1975) described the morphologic adaptations among suiforms that allow this wide gape.

Non-parametric correlations between gapes and all other recorded behaviours generally were not significant ($P < .05$). However, the frequency of gapes by dominant males during static high water levels was correlated with group size ($P = .02$, $rs = .46$). This appeared due to groups being scattered and numerous during high water levels, with a corresponding high number of territorial males dominant over groups. All social signals correlated strongly with group number at this time, indicating a pronounced degree of territorial possesseveness by the dominant male within large groups.

The frequency of gape displays incr prepared to leave the river to graze (Tab increase in excitement of the group.

TABLE 2. — Frequencies of signals p

Time period (h)	Gapes by dominant males
16.30 - 17.00	0.15
17.00 - 17.30	0.25
17.30 - 18.00	0.55
18.00 - 18.30	1.70

Vocalization.

Vocalizations were common and like and intense in the late afternoon and ear the first time period (30 min) may be gi of the observer. Vocalization is a star does not force the animals to submer

Within groups, vocalizations were c tion of one to nearly the entire group. V zing inhalation followed by several reve nostrils.

Groups and individuals separated or As the sound may carry well over or hear a chain of vocalizations from on the river. The full function of vocalizat contact call, is not known.

Vocalizations during serious aggres similar to a lion's roar to high pitche accompanied by clashing jaws during

Non-vocal auditory signals may be during most agonistic confrontations. produced a noise that, while not loud, message.

Submissive defecation.

Submissive displays were often exp necessarily defecation. The subdominar the water and splashed water with its t The animal's head was held low and This signal was not offered exclusivel as all age classes with the exception of ve No dominant male was observed to ac males submitted in this manner to the a dominant male 'make the rounds' ar within the group, most commonly star water and the head angled down from

The frequency of gape displays increased towards nightfall as hippopotami prepared to leave the river to graze (Tabl. 2). It may, therefore, reflect a general increase in excitement of the group.

TABLE 2. — Frequencies of signals per 30 min. period from 16.30 - 18.30 h.

Time period (h)	Gapes by dominant males	Gapes by all individuals	Vocalizations
16.30 - 17.00	0.15	6.5	9.0
17.00 - 17.30	0.25	9.0	8.0
17.30 - 18.00	0.55	15.2	14.0
18.00 - 18.30	1.70	34.0	37.0

Vocalization.

Vocalizations were common and like gape displays were particularly frequent and intense in the late afternoon and early evening (Tabl. 2). Vocalization during the first time period (30 min) may be greater than the second due to the arrival of the observer. Vocalization is a standard response to any disturbance that does not force the animals to submerge.

Within groups, vocalizations were conducted in sessions, with the participation of one to nearly the entire group. Vocalizations usually consisted of a wheezing inhalation followed by several reverberating honks emitted through dialated nostrils.

Groups and individuals separated on land at night often answered each other. As the sound may carry well over one kilometer, it was not uncommon to hear a chain of vocalizations from one group or individual to another along the river. The full function of vocalizations, other than as a warning or general contact call, is not known.

Vocalizations during serious aggressive encounters ranged from sounds very similar to a lion's roar to high pitched squeals. A steady grunting is usually accompanied by clashing jaws during aggression.

Non-vocal auditory signals may be a component in the energetic splashing during most agonistic confrontations. Jaw champing conducted at these times produced a noise that, while not loud, probably acts as an additional auditory message.

Submissive defecation.

Submissive displays were often expressed by tail wagging and often but not necessarily defecation. The subdominant animal lifted its hindquarters clear of the water and splashed water with its tail in the face of a dominant individual. The animal's head was held low and extended, with ears normally laid back. This signal was not offered exclusively to the dominant male of the group, as all age classes with the exception of very young animals exhibited this behaviour. No dominant male was observed to adopt this behaviour. Non-dominant adult males submitted in this manner to the dominant, and it was common to observe a dominant male 'make the rounds' and elicit defecations from several animals within the group, most commonly standing with back and shoulders above the water and the head angled down from an arched neck. Hissing inhalations and

short explosive exhalations often accompanied prodding of the subdominant animal's anal region.

Adults, both male and female, normally submitted in this manner to territorial males when entering a group or territory. During times of general activity amongst pool members, sub-adults would frequently defecate in the face of the dominant male without any apparent prompting perhaps to reconfirm their recognition of his status.

The common denominator between receiver and submittor was body size for all interactions not involving the dominant male. The proportion of submissive defecations offered to the group dominant male was recorded for 58 hours of observation. The average number was 5.2 gestures per hour, 33 % of which were directed to the dominant male.

The results of a Pearson correlation test for all data, regardless of river dynamics, indicated that the rates of submissive defecations per individual correlated negatively with the number of animals within groups ($P = .02$, $r = -.84$), and positively with the rate of Class 1 aggression ($P = .04$, $r = .75$). The former indicates that group members were more active in social status reinforcements within small groups, the latter may indicate the function of the submissive gesture in terminating or avoiding agonistic encounters. There were no significant relationships with rates of Class 2 aggression, nor between river dynamic state and submissive defecation.

Marking defecation.

Marking defecations were performed both in the water and along the bank. Only once did an animal other than a territorial male exhibit this behaviour ; a lone female with a neonate expressed her agitation at being disturbed by an observer in this manner. During 112 hours of observation, 65 displays were noted. The action usually involved the territorial male backing up to a bank or the shore and copiously defecating, scattering dung up to 2 m in radius by flapping its tail vigorously. Often the male was accompanied by several young and subadults showing great interest by sniffing and eating the dung. Dung scattering was also an important component in the ritualised aggression between rival males.

CONCLUSIONS

The intermittant occupation and defense of specific sites by dominant hippopotamus males, determined primarily through river levels, can be considered to constitute territoriality. Other territorial ungulates also possess dynamic territories whose flexibility in size and location depends on several factors such as the distribution of females and resources such as forage and water. Particularly in river habitats, hippopotami differ from many other territorial species in the relatively solitary behaviour of batchelor males. Since mating apparently occurs in water and animals are widely dispersed while feeding at night, social interactions are most intense in pools used for resting during daylight hours.

A seasonal trend in numbers and intensities of aggressive behaviour (mediated through water levels) was apparent although statistical analysis did not strongly

associate aggression with crowding within
as extremely low water levels and/or lack
this study, these results do not preclude
a component in population regulation vi

Calves were the objects of aggression
recorded. If aggression were to intensify
of stress, then calf mortalities might be exp
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adults, because of their mass, are much

ACKNOWLED

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associate aggression with crowding within pools. As environmental stress, such as extremely low water levels and/or lack of forage, was not evidenced during this study, these results do not preclude the possibility that crowding may be a component in population regulation via aggression.

Calves were the objects of aggression by adults, though no mortalities were recorded. If aggression were to intensify, as would be expected during times of stress, then calf mortalities might be expected. Adult mortalities were recorded, and would also be expected to increase if the population were stressed, though adults, because of their mass, are much less prone to serious injury.

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Rodent movements

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Summary. — Nocturnal movements of the
the greater bandicoot rat *(B. indica),* and t
in Bangladesh using radio tracking technique
is the most important pest in wheat fields. T
while the greater bandicoot rat moves betwe
the lesser bandicoot rat averaged only 18 squ
harvest. Findings indicated that in field app
control will be increased if baits are placed
burrow systems.

Résumé. — L'étude présentée ici porte s
bengalensis observée par radio-tracking dan
L'enregistrement des déplacements noctu
des domaines vitaux instantanés, le degré d'
de la prédation, ainsi que sur la stabilité
Il apparaît que ceux-ci ont une faible s
disponibilités alimentaires et des densités. I
que la moisson ou l'inondation, provoquent d
vital instantané : des déplacements de 175 à 2
de cours d'eau de 15 m de largeur. Des conc
lutte efficace dans les champs de blé.

INTROD

An important component in develo
control involves the study of various as
range » (Burt 1943), or area an animal m