

Hoogerwerf 1970, Djasja et al. 1982]. No other dicotyledonous species in Ujung Kulon is known to carry large spines. Spines are probably effective in protecting the young shoots of the bamboo Bambusa blumeana and the tips of rattan palms from being eaten by rhinos.

Chemical defences

A large number of chemical substances in plants (so-called secondary compounds) have been shown to play a role in the defence against herbivores (e.g. Levin 1971, 1976, Rhoades and Cates 1976). Basically two groups of defensive substances can be distinguished depending upon how they act to damage the herbivore: Digestibility-reducing substances that act within the gut of the herbivore and prevent the absorption of nutrients through the wall of the gut. To this category belong tannins and phenolic resins that form complexes with protein in the diet. The second group are toxins which act negatively on the metabolic processes of the herbivore (Rhoades and Cates 1976). Best known among this group of secondary compounds are the alkaloids.

Defensive compounds are not distributed evenly throughout a plant, but are concentrated where they benefit the plant most against herbivores. Alkaloids are found in greater concentrations in immature than in older tissues (McKey 1974, Rhoades and Cates 1976). The location of digestibility-reducing substances (tannins, phenolic resins) is not so clear, however. It has been suggested by some authors (McKey 1974, Rhoades and Cates 1976) that, because of problems involved in storing these substances, they would be found in higher concentrations in older tissues. However, Coley (1983) found that young leaves of neotropical trees had two to three times the tannin content of mature leaves.

Different concentrations of secondary compounds are also found between species. Furthermore species differ in regard to the substances found in them (i.e. different species harbour different alkaloids or tannins, for example).

A broad correlation between the life-history patterns of plants and their chemical defence has been noted. Shade-tolerant species commit more resources to their defence than shade-intolerant species (Feeny 1976, Coley 1980, 1983). Shade-intolerant species apparently allocate more resources to growth and grow faster than shade-tolerant species; the former can afford to lose leaves to herbivores because of the relatively lower cost of producing them (Coley 1983). The same difference of resource allocation possibly also occurs between plants of the same species growing under different degrees of shading.

Nutritional quality

Plants may avoid being eaten by being of low nutritive value to herbivores (Moran and Hamilton 1980). This can be achieved through a low ratio of nutrient to fiber (especially lignin, which is indigestible) content. Coley (1983) found a negative correlation between nutrient content and toughness of leaves. Within a plant, older parts have higher fiber contents than younger, stems having the highest contents followed by mature foliage and young leaves. Persistent plant species have higher fiber contents than shade-intolerant species (Coley 1983). Most probably fiber content also varies within a species depending upon whether a plant grows in a shaded environment or not.

Discussion of the Javan rhino's adaptations

Javan rhinos eat mainly the youngest parts of plants. These are the parts with the highest nutritional value for rhinos (apart from fruit which, however, contribute only a small fraction to the rhino's diet in Ujung Kulon) since they are low in fiber content but rich in nutrients. However, young leaves contain high concentrations of alkaloids and possibly also of tannins; rhinos, therefore, have to be able to avoid the toxic effects of these secondary compounds. Unlike ruminants, caecal fermenters such as rhinos may be at a disadvantage with regard to plant poisons, because these may be absorbed into the animals body before they reach the sites of microbial degradation (Freeland and Janzen 1974). Since the effects of alkaloids are dosage dependent (Freeland and Janzen 1974) rhinos may be able to tolerate relatively large quantities of a certain plant toxin because of their large body size. By maintaining a highly diverse diet and by constantly switching from one food species to another when feeding (Schenke] et al 1978) rhinos can avoid ingesting a damaging amount of any one toxin. Some plants however may contain toxins which are too poisonous for rhinos even in small quantities. Such species will be avoided. This may be the case for some species that were not recorded to be eaten by rhinos, although they were not uncommon in the study area (e.g. Stelechocarpus burahol, Cynometra laxiflora or Purranjiva Roxburghii to name a few). The effect of tannins is dosage dependent as well but, compared to alkaloids, their action — the formation of indigestible complexes with leaf protein, thus reducing the nutrient value of the food — is much more generalized (Feeny 1976). This means that different tannins have the same effects in the rhino's gut, while different alkaloids act differently on the metabolic processes of the herbivore. Therefore, a rhino cannot avoid the effects of tannins by switching from one foodplant species to another. It is possible that rhinos can tolerate

high levels of tannins in the diet by passing them rapidly through the digestive system (Poore 1982; in Flynn 1983).

The different preferences shown by rhinos for different foodplant species can most probably be explained to a large extent by the nutritional value and the concentration of defensive secondary compounds. Presumably rhinos prefer those species with the highest nutritional values and lowest concentrations of secondary compounds.

4.1.4.2 Factors determining preferences for feeding habitat

Density of foodplants in different types of vegetation

Here I shall examine whether the preferences shown by rhinos for various types of vegetation were due to the average quantity of food available per hectare. For each type of vegetation I estimated the total quantity of potential food available per hectare. This was done by adding up the estimated quantity (QI_{ij}) separately for each vegetation type found in the sample plots and by dividing this through the total area covered by each vegetation type in all sample plots. In this estimate all potential (see 4.1.1) foodplants were included with the exception of gingers. Since nearly all species of climbers, bushes and saplings that were recorded in the sample plots have been found to be eaten by rhinos at one time or other (cf. lists of foodplants in Schenkel and Schenkel-Mulliger 1989a, Hoogerwerf 1970, Djaja et al. 1982) the inclusion of all species in the estimate of the quantity of available food seems permissible.

The quantity of food available per hectare is highest in forest and in shrubland (+ trees) (table 4.10) -- two types of vegetation which are not or negatively preferred. In shrubland without trees or that dominated by bushes, which,

Table 4.10 Average quantity of food available (QI_a) per hectare in different vegetation types

Vegetation type	QI_a /ha
Forest	2'355
Shrubland (+ trees)	2'115
Shrubland (+ bushes)	1'820
Shrubland (no trees)	1'714
Bamboo D	1'561
Acenga forest	1'521
Salak	650
Bamboo C	355

as well as the gaps of fallen trees, are preferred types of vegetation, the quantity of available food is lower. (The quantity available in gaps could not be estimated, because the gaps found in the sample plots were all very young and contained few rhino foodplants. With increasing age of the gap the number of rhino foodplants increases as well). In bamboo C and salak the quantity of available food is very small — less than one third of the quantity available in shrubland. While the quantity of available food probably plays no role in the rhino's preference for shrubland without trees or dominated by bushes, it may be the principal reason for their rejection of bamboo C and salak as feeding habitat.

The quantity of food available in Acenga forest is surprisingly large, although this type of vegetation has usually been described as unfavourable for rhinos because of the lack of food available there (Schenkel and Schenkel-Hulliger 1969a, Schenkel et al. 1978). The reason for this

was partially that sample plots contained not only one type of vegetation but often two or more and thus included the boundaries between them. Near the boundaries between Arenga forest and shrubland the density of saplings has been found to be high (Hommel 1983). This cannot be the only explanation, however. While locally Arenga forest may be practically devoid of undergrowth, this becomes abundant wherever the canopy of Arenga palms is less dense and light reaches the forest floor. Large number of saplings were in fact found in some plots containing Arenga forest as the only type of vegetation.

Average quality of foodplants in different types of vegetation

The average nutritional value, as well as the defence level of all plants in a community can vary between different types of vegetation. The causes for this may lie in the varying nutrient or water content of the soil or in the amount of light available to the plants.

For vegetation growing on nutrient poor soil the cost of replacing material eaten by herbivores is greater than in nutrient rich localities. Correspondingly the vegetation growing on nutrient poor soils contains higher concentrations of tannins and other phenolic compounds (McKey et al. 1978).

Plants growing in vegetation types which are not shaded by tall trees (this includes all shade-intolerant species) probably allocate more resources to rapid growth than to defence.

Availability of other resources

Some types of vegetation might be preferred as feeding habitat because they contain other resources besides food. These would be more attractive than vegetation types in which these resources are not available if rhinos would otherwise have to travel long distances to reach these resources and thus incur large energy expenditures. In Ujung Kulon this factor is probably not important. Most non-food resources are abundant and evenly distributed. Rhinos never have to travel very far to satisfy most of their requirements.

Discussion

Javan rhinos probably prefer to feed in forest gaps and shrubland without trees because plants growing there generally have a lower fiber content and lower concentrations of secondary compounds than plants growing under shaded conditions. This is because of the occurrence of shade-intolerant species which are generally less well defended than shade-tolerant species. Furthermore, shade-tolerant species probably invest less in chemical defence and are more palatable to herbivores when growing in unshaded locations.

4.1.4.3 Factors influencing the observed feeding pattern

The diet of the Javan rhino is characterized by the large number of species consumed. In this study 190 species of plants were found to be eaten by the Javan rhino. This list is by no means complete; when all species recorded in Ujung Kulon by other authors (Schenkel and Schenkel-Hulliger 1969a, Honninger 1970, Djaja et al. 1982) are considered the foodlist comprises around 250 species. Given a sufficiently

long observation time, the diet of the Javan rhino would probably be seen to include nearly all plant species of suitable size. One of the factors influencing a highly diverse diet, the necessity of avoiding damaging amounts of toxins, has been mentioned above. Because plant species differ from each other with regard to their nutrient contents, especially mineral concentrations, a diverse diet is necessary to obtain an optimal balance of nutrients (Westoby 1978). For non-ruminants a high dietary diversity may be essential for obtaining a wider variety of amino acids (Janis 1976, Laurie 1978).

Westoby (1978) suggested that variety in the diet could most likely be explained by a herbivore's need to sample all available foodplants in order to determine the nutritionally optimal diet. Sampling would be necessary (1) if the foodplant cannot be identified olfactorily before ingestion; (2) if the nutritional qualities of a species change over time or vary from place to place so that the rhino's previous experience with the species will be of no use. An example of such local variation — the salt content of Spondias pinnata leaves — will be given below (4.1.6). (3) when a rhino encounters a species unknown to it. This is most likely the case for young animals and for rhinos that move into areas that previously did not form part of their home range and where they encounter new species of foodplants.

4.1.5 Seasonal changes in food selection

Because seasons are very variable from year to year in their length and intensity, I have not tried to define them according to calendar months. Rather I have considered changes in the consumption and selection of food from month to month in relation to the amount of precipitation in each month. Since tracking of rhinos was not possible during the dry season, information for the dry months is lacking.

However, the variation of rainfall between those months in which tracking was possible was considered to be sufficient to cause observable changes in food selection.

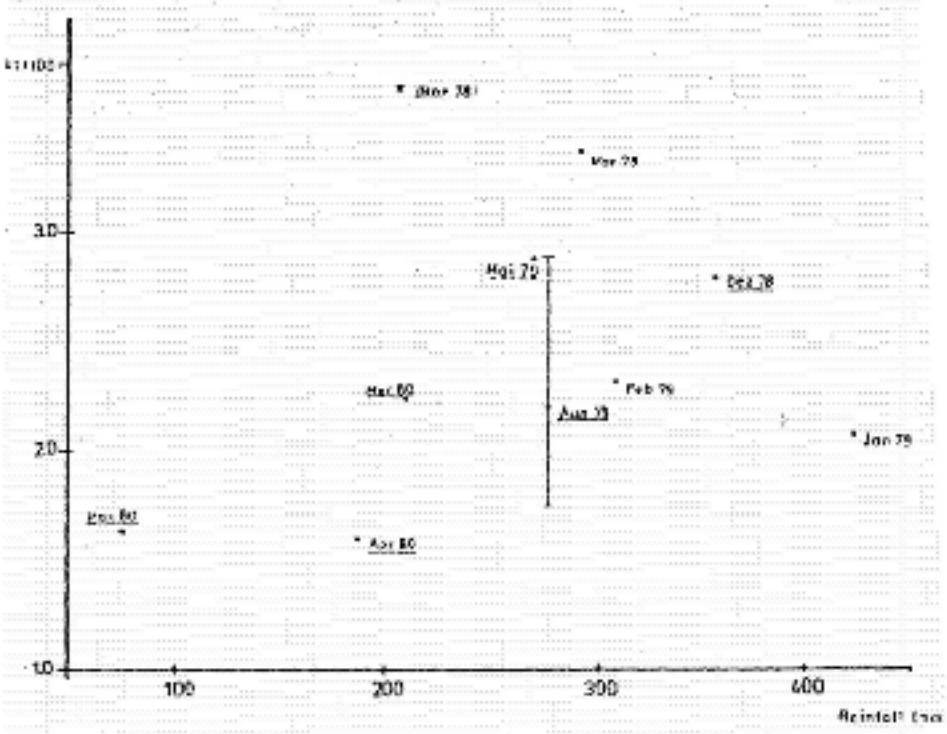
I gained the impression that growth rates of plants were higher during the wet season from the fact that it required more effort to keep the paths in the study area from being grown over in that season. Otherwise no overall seasonal changes of the vegetation could be observed.

4.1.5.1 Seasonal changes in the amount of food consumed

The energy requirements of an adult animal can be seen, in a simplified way, as consisting of two components: the energy required for basic metabolism and the energy required for activity. Basic metabolic requirements are a function of time. That is, within each time period a constant amount of energy is required. The amount of energy required for activity within the same time period is variable and depends upon the extent of activity. When total energy requirements are measured per unit of time the result will be higher, corresponding to the higher amount of activity within that time unit. When total energy requirements per unit of activity are measured however then the result will be lower, the higher the amount of activity per time unit. This paradoxical result arises because the energy requirements for activity are constant per unit of activity, but the basic energy requirements within the time unit considered are distributed over more activity units, the higher the amount of activity is in that time.

For each month, in which I tracked rhinos and recorded the quantity of food eaten by them, the average quantity (Q1) consumed per 100 m travelled was calculated and plotted against the amount of rainfall for that month (figure 4.4).

Figure 4.4 Relationship between quantity of food consumed per 100 m travelled and rainfall



- Mar 79 data from male rhinos
- Apr 80 data from female rhinos
- Feb 79 data from male and female rhinos
- Nov 81 data from cow/calf pair

The steepness of the terrain was considered not to influence the results since the rhinos were tracked in the flat alluvial plain or the gentle slopes of the Tsaloo plateau.

Although the results appear very scattered when plotted against rainfall (figure 4.4), there is a distinct tendency towards higher values in wet months. This is however only a tendency and the association between energy requirements and amount of precipitation is not significant when tested by the Spearman rank correlation coefficient ($r_s = 0.417$ $p > 0.05$, Nov 78 not included). Especially the result for January 79, the month with the highest precipitation, was very low. In August 78 I had not recorded the quantity of food eaten. To obtain the result shown I calculated the average QI per feeding event (separately for sucklings and climbers) in each month and multiplied the number of feeding events in August 78 with the smallest, the largest and the mean value for all months.

I have argued above that the extent of activity within a certain time period (in this case the distance travelled per day) will influence the results. While it was not possible to estimate the daily speed for all tracking sequences, the results of those sequences, for which such an estimate could be made, show that the distances travelled per day were variable within each month, but did not appear to be correlated with the amount of precipitation (see 4.3.3). It is assumed that, although daily speed may vary from day to day, there are no seasonal fluctuations and that the average daily speeds are approximately the same in all months.

Different energy requirements or average distances travelled per day by males and females could also influence the results, if all observations in each month were from rhinos of one sex only and the observations of each sex were restricted to one of the seasons. While females were tracked

only in the wetter months, males were tracked both in dry and in wet months, and here the pattern of higher energy requirements per distance travelled in wet months can be observed clearly.

I conclude therefore that even if males and females differ in their energy requirements, this was not the cause for the observed seasonal differences in energy requirements. The two sexes did not appear to differ in their average daily speeds (see 4.3.2).

The seasonal differences of energy requirements per distance travelled were not due to seasonal differences of distances travelled per day nor to seasonally uneven distribution of observations of males and females. I conclude from this that rhinos had higher total energy requirements in the wet seasons than in the dry season. One possible explanation for this is that rhinos require more energy for travelling in the wet season, because of the muddy or swampy nature of the ground. Alternatively rhinos may be building up fat reserves in the wet season when suitable and better quality food is more abundant. (A fat layer up to 2.5 cm in thickness was found to underlie the skin of the white rhinoceros (Cave and Allbrook 1959).

A remark must be made on the extremely high result of the month November 70. The data for this month were all from a cow/calf pair. The high value reflects the higher energy requirements of the female, that was still nursing her young. The daily travel speed of this pair may also have been lower than that of solitary rhinos.

4.1.5.2 Seasonal changes in the selection of food species

In tropical forests many tree species show seasonal cycles of leaf change and associated with it the growth of young shoots

(Richards 1952, Whitmore 1975). There is evidence that, in some species at least, these may be correlated with changes in the water supply (Whitmore 1975). Rhinos prefer to feed on the young, non lignified shoots (4.1.2.2). They should show seasonal changes in the composition of their diet, if they fed more heavily on species with seasonal growth periods at times when the production of young shoots was high. No seasonal changes of diet composition would be found, if foodplants had no marked growth season.

Seasonal changes of food selection were investigated by calculating the proportions of the four principal food species (Amomum sp., Dillenia excelsa, Leea sambucina, Spondias pinnata) in the diet for each month and plotting them against rainfall (Figure 4.5). (The proportions of other species in the diet were very small and the observed monthly variations were thought to be too much influenced by chance). Three possible relationships between the growth of young shoots and rainfall were considered: the reaction of plants to rainfall might be fast, that is they might produce young shoots within a few days after the onset of rain and production might cease and the shoots lignify soon when no rain fell. Second, the reaction might be slow and several weeks might pass before shoots were available to rhinos: growth would continue for some time after no rain fell. Third, growth cycles might be adapted to long-term annual patterns of rainfall and governed by internal rhythms. Accordingly the values for each species were plotted against rainfall of the same month (fast reaction), rainfall of the previous month (slow reaction) and the long-term average amount of rainfall for that month (internal rhythm independent of actual rainfall). The closeness of association was tested by the Spearman rank correlation coefficient.

A significant positive correlation was found between the proportion of Dillenia excelsa in the total quantity of food

Figure 4.5 Relationship between proportion of four species in the diet and rainfall in different months

Ammodramus sp.:

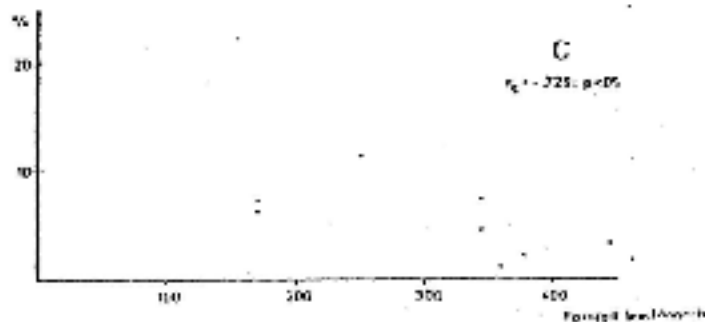
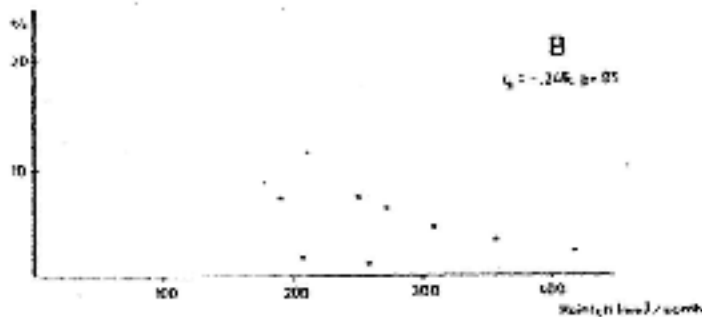
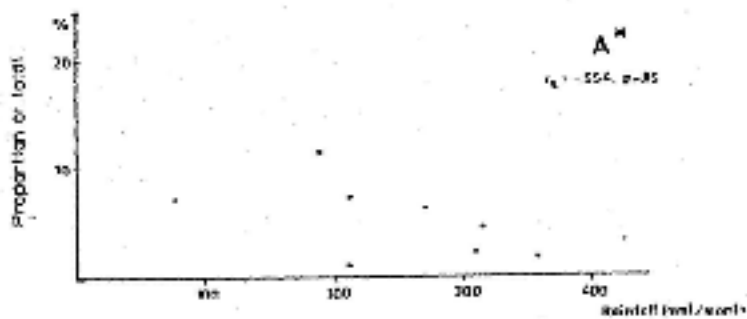


Figure 4.5 (cont.)

Dillena excelsa:

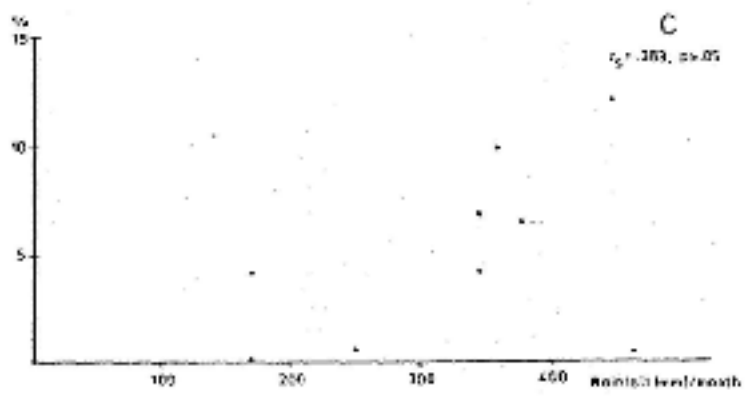
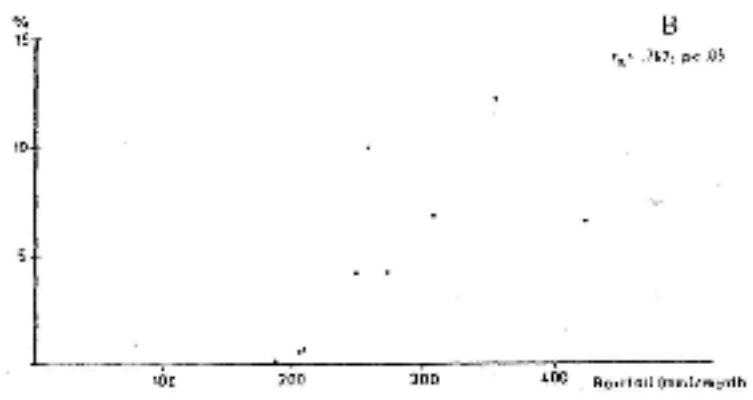
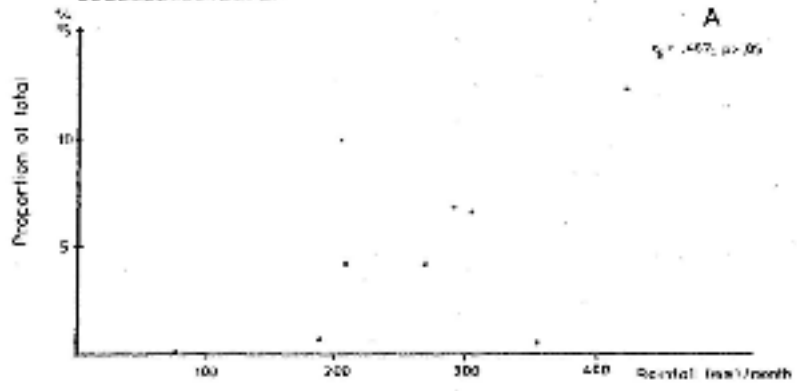
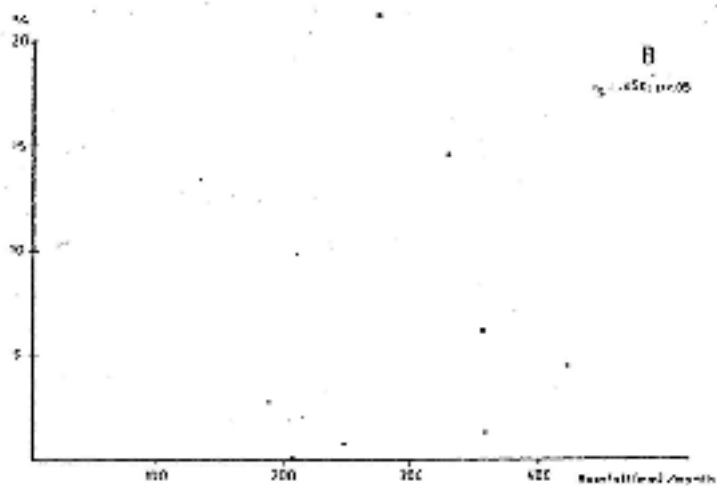
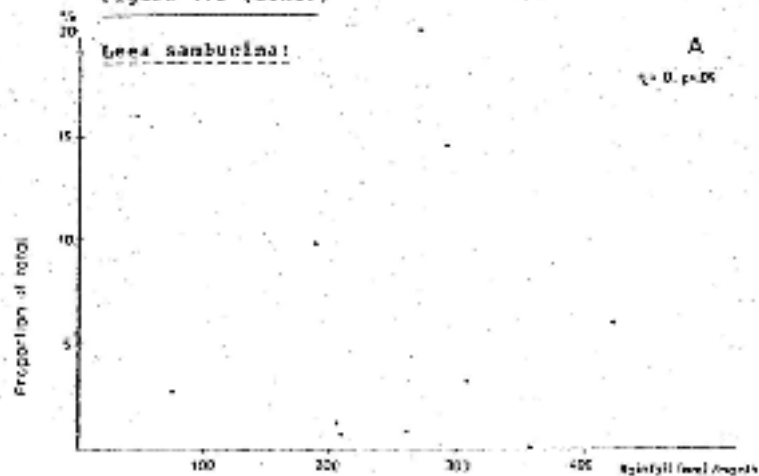
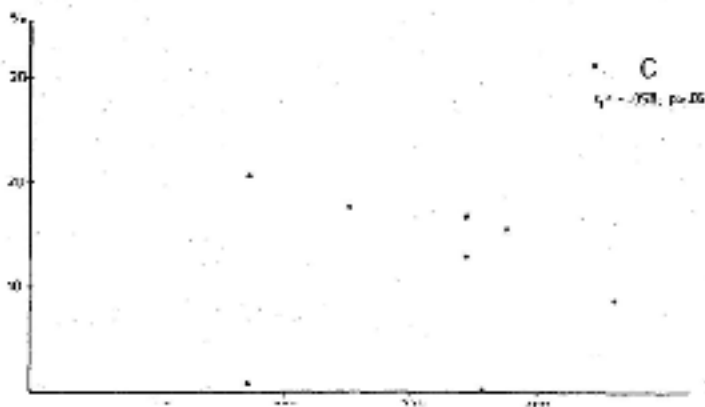
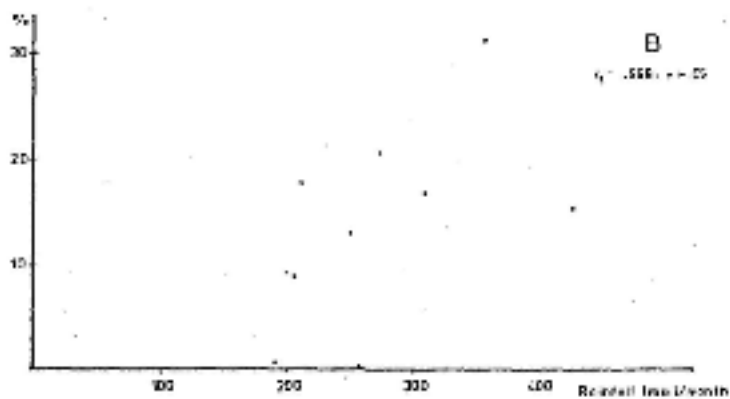
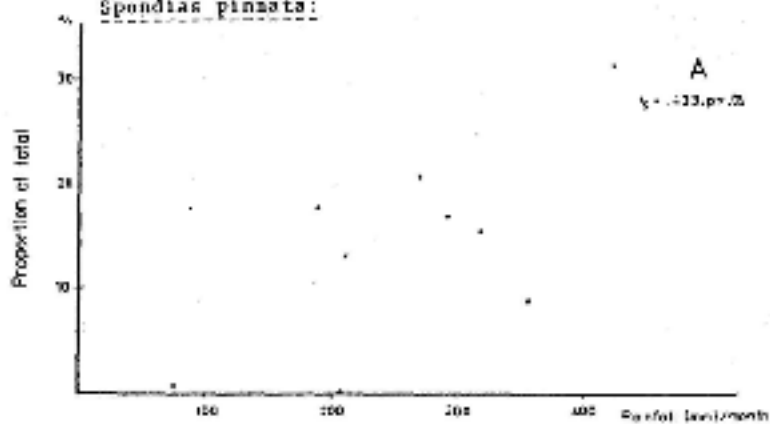


Figure 4.5 (cont.) - 104



Spondias pinnata:



consumed in each month and the amount of rainfall in the previous month. The proportions of Loea saabucina and Spondias pinnata could not be correlated with rainfall. Presumably, these results extend to other foodplants and both patterns, both seasonal and random variation, are found among the species not investigated here. Probably the proportions of at least some, but not all, species in the diet vary seasonally. For Annonum sp. a significant negative correlation between its proportion in the diet and the long-term average amount of rainfall in each month was found. Annonum sp. is a fast growing, herbaceous species. Its growth rate did not appear to be higher in the dry season, and therefore its higher proportion in the rhino's diet in the dry season cannot be explained by the higher availability of young plant material. The increased preference for Annonum sp. in the dry season may reflect an overall decrease in the availability of young shoots and leaves (of all species) in the environment.

4.1.6 Salt requirements

Herbivores are confronted with the problem of how to satisfy their mineral requirements, especially their need of sodium, which is a rare element in most plants. Large herbivorous mammals often find salt at licks or sources rich in minerals. It is known from both the Indian (Laurie 1978) and the Sumatran rhino (Göthner 1979) that they visit salt licks. No licks have been found in Ujung Kulon (Schenkel and Schenkel-Bulliger 1969a). Certain areas along the south coast -- between Cibunar and Citadahan and west of Cibandowoh -- were highly attractive to rhinos; many tracks and feeding tracks showed that they were visited frequently. It was suspected that one reason for this was that plants growing near the coast contain higher amounts of sodium than plants growing farther inland.

To test this hypothesis leaf samples were taken from five Spondias pinnata saplings, all between 2 and 3 m high. Two of them grew on the forward slope of the beach ridge between Cibunac and Citadshan, about 200 m from the shore, in a location that was exposed to the strong southeast winds blowing in the dry season. The three other samples were collected in the study area between Trails A and B about 1 km from the shore. All samples were rinsed in sweet water to wash away any salt deposits from the leaf surfaces and dried in the sun. They were later analysed at the Institute of Inorganic Chemistry, University of Basel.

The leaves of Spondias pinnata plants growing near the shore contained six to seven times as much sodium than those growing farther inland (table 4.11). Presumably plants of other species growing near the shore contain higher amounts of sodium as well. Halophytes -- which are defined as any plant that tolerates higher than usual sodium chloride concentrations during any stage of its life -- take up more sodium from the environment, the higher the concentration of sodium in the environment is (Adriani 1958). In addition plants exposed to offshore winds may be covered with crystalline salt deposited on them by salt water spray.

Table 4.11 Salt content of Spondias pinnata leaves

Forest		Beach ridge	
Sample No.	Na	Sample No.	Na
1	0.08 %	3	0.50 %
3	0.07 %	5	0.50 %
4	0.07 %		

It is difficult to state whether rhinos may satisfy their sodium requirements just by feeding occasionally on vegetation growing near the shore. The high salt content and salt deposited on the surface of plants growing near the shore represent a previously unrecognized source of this element for rhinos. Franck (1935) and Schenkel and Schenkel-Bulliger (1969a) have suggested earlier that rhinos may drink sea water or brackish water from estuaries when visiting the coast.

4.2 Wallowing, bathing and resting

4.2.1 Wallowing

After describing the wallows of the Javan rhino I will explore which factors determine the location of wallows and which factors lead to their repeated use, or to abandonment.

4.2.1.1 Description of wallows

Two types of rhinoceros wallows were distinguished: "ad hoc" wallows and "permanent" wallows. The latter term is somewhat misleading, as will be seen below. The latter type of wallow consisted of one, occasionally several, well developed basins, to which usually much used animal trails led. Some permanent wallows showed signs of having been used repeatedly since a long time, but at irregular and infrequent intervals only. At some wallows which I controlled regularly, intervals of from four days up to two months lay between two visits. Many, even large and deep, wallows fell into disuse after some time. I was shown several pools that had been used by rhinos for wallowing some years previously but never since. "Ad hoc" wallows were simply shallow depressions formed where a rhino had rolled itself in muddy or loamy soil. Permanent

wallows were encountered more often, but "ad hoc" wallows were not rare. Of 56 wallows visited by rhinos which I was tracking 29 (= 51.8 %) were permanent and 20 (35.7 %) "ad hoc" wallows; the remaining 7 (12.5 %) wallows could not be classified.

4.2.1.2 Factors determining location of wallows

Undoubtedly the presence of loamy soil with a certain minimal water content is a necessary condition for a wallow to be made. All freshly used wallows were found to be filled with a loamy 'soup'. The importance of four other factors -- topography, type of vegetation, shading, concealedness -- is investigated below.

Topography: Because rhinos were mostly tracked in the plains more wallows were found there than in hilly areas. Forty-three (= 76.8 %) wallows were found in plains or on the Telsuca plateau, 8 (14.3 %) on ridges or hilltops and 5 (8.9 %) on slopes. In hilly areas wallows were mainly located on ridges, but some were found on terraces in hillsides and on gentle slopes. Steep slopes appeared to be unsuitable for wallows; none were ever found there. On some mountain spurs or broad ridges, groups of several wallows were found. In such cases the distance between individual wallows was 50 - 100 m. Natural basins such as rivulets (6 cases) or the holes excavated by the roots of fallen trees (8 cases) were sometimes used to wallow in.

Type of vegetation: The proportion of wallows found in the different vegetation types corresponds to the frequency of occurrence of those types in the study area, that is, rhinos neither preferred nor rejected certain types as environment for wallowing (figure 4.6). A strong preference was shown for Arenga forest, however, and on the other hand no wallows were

Figure 4.6 Use and availability of vegetation types as environment for wallowing

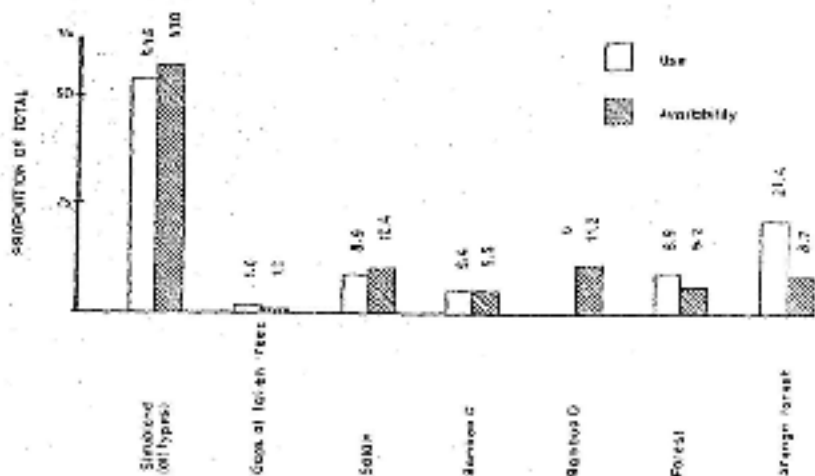


Figure 4.7 Shading of wallows

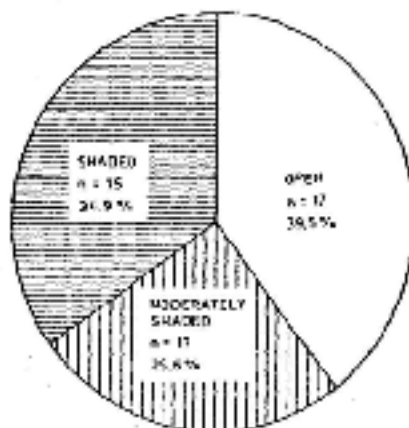
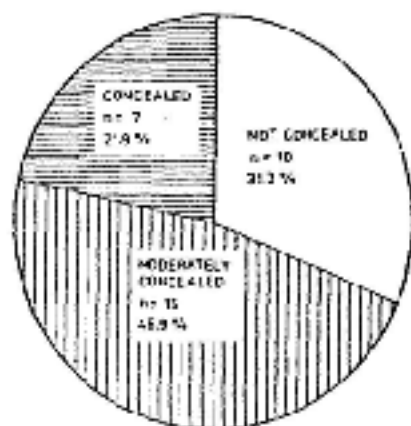


Figure 4.8 Concealedness of wallows



ever found in bamboo D. It should be remembered though, that the area in which the frequency of occurrence of vegetation types was estimated (the study area) was smaller than the area in which wallows of rhinos were found and their characteristics recorded. Areas outside the study area, especially towards the Telanca plateau, were estimated to contain larger percentages of Arenga forest. The rhinos' preference of visiting wallows in this type of vegetation may not be as pronounced as indicated here.

Shading: for 43 wallows the degree of shading was recorded (on a scale of 0 to 10, see 4.1.1.1). Shading influences the temperature of the water and the mud in the wallow. Three categories were distinguished: open (shading 0 - 2), moderately shaded (shading 3 - 7) and shaded (shading 8 - 10). Only about one third of the wallows belonged to the

letter category; almost 90 % were little shaded or not shaded at all (figure 4.7).

Concealedness: Some wallows were concealed in very dense vegetation and any rhino lying in them could only have been observed from a distance of less than 20 m. But many were located in Arenga forest or in grass-covered clearings where they could be seen from quite a distance. The largest distances from which wallows could be observed were about 50 m (2 cases). The maximum distance from which a wallow could be seen was recorded for 32 wallows. The results are shown in figure 4.8. Three categories were distinguished: concealed (maximum distance < 10 m), moderately concealed (maximum distance 10 - 30 m) and not concealed (maximum distance > 30 m).

It appears that very few factors limit the choice of a place for wallowing. Particularly shading and concealedness seem to have little influence in this respect. Accordingly wallows are found in a wide variety of different locations. Shading, however, influences the rate of evaporation from a wallow and consequently the length of time for which a wallow can be used. This point will be discussed below.

4.2.1.3 Factors influencing duration of use of wallows

Wallows that are not visited by rhinos gradually dry out and become filled with dead plant material. Thus they may become less attractive over time. Two factors have some influence on the length of time for which a wallow will be used -- shading and the number of rhinos present in a certain area.

As mentioned, the evaporation from wallows in shaded locations is lower than from wallows exposed directly to the sun. Such wallows can be used for a longer time and this

increases the likelihood that they are used repeatedly. Thus they develop into permanent wallows. In fact permanent wallows were found more often in shaded locations. Permanent wallows in open locations were often situated in natural basins, such as rivulets or at the base of fallen trees.

Some permanent wallows are used infrequently and irregularly over long time periods. Others on the other hand may be visited frequently by several rhinos over a relatively short time period and then fall into disuse again. Combinations between the two patterns are possible. The latter pattern is very common and must be seen in conjunction with the fluctuation of the number of rhinos in a certain area and the very high density of wallows in Ujung Kulon. Such fluctuations were shown to occur in the study area (see 2.2.1.2) and may be assumed to occur in other parts of Ujung Kulon as well. Rhinos may be attracted to freshly used wallows. Therefore, when there are many rhinos in an area wallowing activity may be concentrated on only a few wallows as the rhinos are attracted to those being used currently. When the rhinos move away again to other areas these wallows fall into disuse. Because of the many existing wallows and places where wallows can be made available to rhinos, wallowing activity will be concentrated on new wallows each time the number of rhinos in an area builds up again. Similar observations were made by Hoogerwerf (1970) at the wallows where his series of photographs of Javan rhinos was made.

In some cases wallows may fall into disuse when rhinos leave the area because of persistent disturbance through humans.

4.2.2 Bathing pools

Besides wallowing, rhinos are also known to bathe in streams and pools (Schenke) and Schenkel-Hulliger 1969a). In their lower courses most major streams are deep enough for rhinos to bathe in. Rhinos seem to bathe there even in the dry season when the water is brackish. Further upstream, pools deep enough for rhinos are frequently found. It is very likely that rhinos also bathe in pools of stagnant sweet water. It was not possible, when following rhinos tracks, to decide whether a rhino had just passed through a pool in a stream or had remained there for a longer time. Rhinos probably did not bathe each time they entered a pool.

4.2.3 Resting on solid ground

Occasionally rhinos lie down to rest outside wallows or pools. Such resting places were identified by the imprint of the rhino's skin on the ground. They were found much less frequently than wallows or bathing places in Ujung Kulon. On the one hand it is possible that not all places where rhinos lay down on the ground were recorded. Even on soft ground the imprint of the skin is inconspicuous, and no imprint can be seen at all where the ground is hard or covered with dead leaves. On the other hand it is possible that rhinos prefer to rest in wallows and pools. Because of the density of these facilities in the lower lying areas of Ujung Kulon, rhinos never have to walk far to find them. In mountainous areas, for example, such facilities may be less available and resting on solid ground more common. In addition, walking in mountainous areas may require rhinos to rest more often. Rhinos do not always lie down to rest, but may just stand still, apparently "dozing", with their head hanging low.

4.2.4 Functions of wallowing, bathing and resting on solid ground

The function common to wallowing, bathing and resting on solid ground is to satisfy a rhino's need for resting. Wallowing and bathing, however, have several additional functions (Schenkel and Schenkel-Hulliger 1969a).

Probably their most important function is to keep the skin moist. Sumatran rhinos that were prevented from wallowing developed ruptures and inflammations of the skin (Hubback 1939, Van Strien 1974). The coat of mud that rhinos acquire when wallowing may help to conserve moisture. In this respect the quality of the soil may be of some importance. On human skin some types of soil seem to draw out moisture when left to dry there, while for other soils this effect is not noticed. Rhinos seemed to wallow almost anywhere but showed a strong aversion to wallowing in barbeo D and a preference for Arenga forest. Possibly the quality of the soil played a role. In Arenga forest rhinos wallowed in loamy soil which occurred locally in small patches.

A further function may be the regulation of body temperature; rhinos probably get rid of excess body heat in this manner. In unshaded wallows, however, the cooling effect may be less pronounced, especially during the daytime. Rhinos might visit unshaded wallows more often at night, but one rhino was encountered in an unshaded wallow at 11 a. m. Wallowing and bathing may also serve to reduce the level of infestation by parasites. The mud with which rhinos get covered when wallowing probably protects them against ectoparasites (biting flies of the family Tabanidae). When bathing in streams rhinos do not acquire this protective mud coat. However, fish and crustaceans appear to clean ectoparasites off the bodies of bathing animals (Schenkel 1971). Rhinos usually urinate into wallows and impregnate the mud heavily

with their scent. When the rhino moves on, the mud clinging to its body is scraped off by the vegetation, through which the rhino passes, and forms a scent marker (see 5.1.2.1).

4.2.5 Frequency of wallowing and bathing

The average number of times a rhino had wallowed and/or bathed per 24 hours could be calculated for 16 tracking sequences for which time estimates were available (table 4.12) (see 4.3.1 for an explanation how time estimates were arrived at). Evidently it was possible to determine whether a rhino had wallowed, but not whether it had just waded through a pool or had been lying and resting in the water. Therefore all pools entered by a rhino are included in this analysis although rhinos probably did not bathe every time they entered a pool.

Cases 1, 3, 8 and 15 demonstrate that over short time periods (1 - 1 1/2 days) rhinos can do with bathing alone. (Although in two cases tracking covered a time span of less than 24 hours; the rhinos may have wallowed shortly before or afterwards). Over longer time periods rhinos were nearly always observed to wallow.

One female rhino that was tracked in the area of Cikendeng (in the northwest corner of the study area) did not visit a wallow for at least 72 hours, although it entered several pools in the Cikendeng. This was an exceptional observation, however.

On the other hand, cases 2, 5, 6, 9, 12 and 16 demonstrate that rhinos can go without bathing facilities for periods up to four days, although they always wallowed during this time. On the average rhinos wallow 0.7 - 0.8 times per 24 hours. If wallowing and bathing are considered, an average as high as 1.8 times per 24 hours is not impossible.

Table 4.12

Frequency of wallowing and bathing per 24 hours

Route ¹⁾ Nr.	Time (h)		wallowa visited	pools visited	Total	wallowing per 24 h	bathing per 24 h	w. + b. per 24 h
	min	max						
15	12:00	18:00	0	1	1	0	1.3 - 2.0	1.3 - 2.0
8	18:31		0	2	2	0	2.6	2.6
5	24:00		1	0	1	1.0	0	1
1	24:04		0	2	2	0	2.0	2.0
3	24:59	36:00	0	3	3	0	2.0 - 2.9	2.0 - 2.9
9	36:44	38:29	2	0	2	1.2 - 1.3	0	1.2 - 1.3
7	41:10		1	2	3	0.6	1.2	1.7
6	42:00		2	0	2	1.1	0	1.1
2	49:00		3	0	3	1.0	0	1.0
10	71:00	95:00	2	7	9	0.5 - 0.7	1.8 - 2.4	2.3 - 3.0
4	73:20	96:20	5	3	8	1.2 - 1.7	0.8 - 1.0	2.0 - 2.7
11	80:00		3	2	5	0.9	0.6	1.5
14	84:00	120:00	4	3	7	0.8 - 1.1	0.6 - 0.9	1.4 - 2.0
12	92:00		3	0	3	0.8	0	0.8
16	96:00		8	0	8	2.0	0	2.0
13	158:00		3	6	9	0.4	0.9	1.3

¹⁾ Route numbers correspond to those used in table 4.16

4.3 Movement

In this section some aspects of movement shall be treated. To obtain a better evaluation of the census results (see 2.2.1.1) information was required on the distances moved by rhinos within 24 hours, as well as whether there were any movement differences between the sexes or from one season to another. In addition I was interested in knowing whether any correlation between the distance wandered per 24 hours and the quantity of food consumed could be observed. I further tried to detect whether there were any regular patterns in the movements of individual rhinos.

4.3.1 Method

The length of the path travelled by a rhino was calculated from the number of paces taken by the observer following its track. The length of the observer's paces was determined by walking a known distance in suitable vegetation and by dividing that distance through the number of paces made. Paces varied between 0.65 and 0.70 m in length. From this a minimum and a maximum of the distance travelled by the rhino were calculated. The time it took a rhino or a "group" of rhinos to travel a certain distance could either be estimated from the age of the tracks or be accurately determined if the rhino was encountered. In some cases the quality of the tracks was too bad to permit a single estimate, e. g. because the footprints had been washed out by rain or because the ground was very dry. In such cases a minimum and a maximum time estimate had to be made. Minimum and maximum distances travelled per 24 hours were calculated by dividing the maximum distance through the minimum time and vice-versa. Time estimates could not be made every time a rhino was tracked because it was not always possible to estimate the age of the tracks. The 16 tracking sequences for which this

was possible represent only a limited sample of the total number of times a rhino was tracked.

I did not determine how far a rhino had displaced per 24 hours since it was impossible to determine a rhino's location regularly at a certain time.

4.1.2 Distance travelled per 24 hours

The results of sixteen tracking sequences for which time estimates could be made are shown in table 4.13. The length of the path covered by solitary rhinos per 24 hours lay between 1.4 and 3.0 km (mean: 2'248 - 2'586 m, n = 10, table 4.13a). The two special cases mentioned below are not included in the calculation of the average.

Twice solitary rhinos were observed to travel exceptionally long distances per 24 hours and special circumstances were noted in both cases (routes 5 and 15 in table 4.13a):

Route 5: In the home range of the male D two separate feeding areas could be distinguished joined by a narrow corridor along the coast (figure 4.11). At intervals of 1 to 3 weeks this rhino moved from one feeding area to the other. The movement was always made in less than 24 hours. The observed movement was such a change of feeding areas.

Route 15: The tracks of this male were only rarely encountered in the study area and then mainly on path E. Its home range was presumed to lie on the Telanca plateau and in the alluvial plain north of the study areas. It is assumed that this trip was either of an exploratory character or the rhino had wandered down to the coast to satisfy its salt requirements.

In both cases the rhinos were moving part of the distance outside their habitual feeding areas, and in the second case the rhino may have even been outside its home range on part of the way.

Table 4.13

Average distance travelled per 24 hours

a) solitary rhinos

Rhino Nr.	Individual	Sex	Distance (n)		Time (h)		Dist./24 h (n)	
			min	max	min	max	min	max
1	G	♂	1'456	1'568	24:00		1'452	1'564
12	J	♀	5'893	6'346	92:00		1'537	1'636
8	J	♀	1'680	1'809	18:31		2'177	2'344
4	G	♂	8'756	9'629	72:20	96:20	2'131	1'129
9	J	♀	3'501	3'709	36:44	38:29	2'133	1'423
13	J	♀	15'032	16'619	168:00		2'205	2'374
10	J	♀	8'913	9'596	71:00	95:00	2'252	3'244
16	G	♂	9'818	10'574	96:00		2'455	2'643
7	I	♀	4'286	4'614	61:00		2'510	2'702
11	J	♀	11'762	12'539	80:00		3'511	3'777
5*	D	♂	2'249	7'783	24:00		7'249	7'783
15*	K	♂	6'689	6'018	12:00	18:00	7'432	12'036

* special cases, see text

Table 4.13 (cont.) Average distance travelled per 24 hours

b) groups of rhinos

Round No.	Individual	Sex	Distance (m)		Time (h)		Dist./24 h (m)	
			min	max	min	max	min	max
6	H	♀ + calf	3'183	3'392	42:00		1'802	1'912
3	G/?	♂ + ♀	905	975	24:59	36:00	605	936
2	G/?	♂ + ♀	2'226	2'398	96:03		773	832
14	G/K,L	♂ + ♀♀	9'529	10'369	84:00	130	1'926	2'963

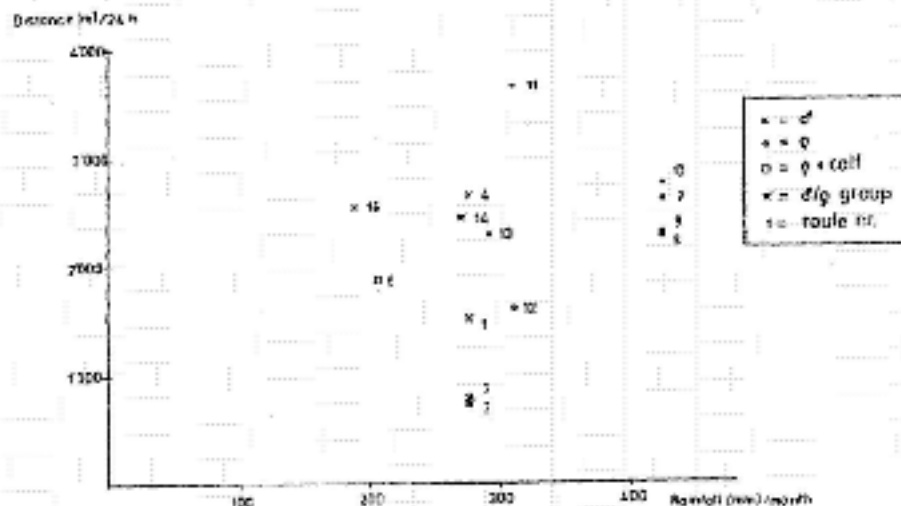
The higher movement rates when travelling between separate feeding areas do not imply that the rhinos walked at a faster speed. Rather it seemed that they spent less time on other activities, although they occasionally fed or even wallowed. Most of the feeding, however, occurred after they had reached their habitual feeding areas.

Two cases in which a male and a female travelled together are notable because of the very short distance covered in 24 hours (table 4.13h). In both cases this was considerably less than the smallest distance observed in a solitary animal. In a third case where a male was travelling together with two females the distance covered in 24 hours lay within the range of those covered by solitary rhinos. Presumably in all three cases the male was following the female(s) in order to mate with her (or with one of the two) (see 5.6.4). Practically nothing is known of the courtship behaviour of the Javan rhino, except that the male/female pair stays together for several days. Possibly during most of the time the male just follows the female and the movement rate corresponds to that of solitary rhinos. The rate of movement may be lower at the culmination of oestrus.

The movement rate per 24 hours calculated for a cow/calf pair lay somewhat below the average but still within the range of movement rates of solitary rhinos. The age of the calf was estimated to be 4 to 5 months. The average distance travelled per day by cow/calf pairs may be shorter when the calf is still very young. However, it was observed once that a female accompanied by a three month old calf moved from Kalejetan to the area of Karangranjang, a distance of 6 - 8 km. in the time of 12 to 24 hours. Even younger calves are therefore capable of moving long distances in a short time. Presumably such high rates of movement can only be sustained for short time periods.

Figure 4.9

Relationship between average distance travelled per 24 hours and monthly rainfall



4.3.3 Seasonal variation of distance travelled per 24 hours

To determine whether the distances travelled per 24 hours could be correlated with the seasons, these distances were plotted against the amount of rainfall of the month in which they were recorded (figure 4.9). The plot shows that the distances travelled per 24 hours were independent of the season.

4.3.4 Food consumption in relation to distance travelled
per 24 hours.

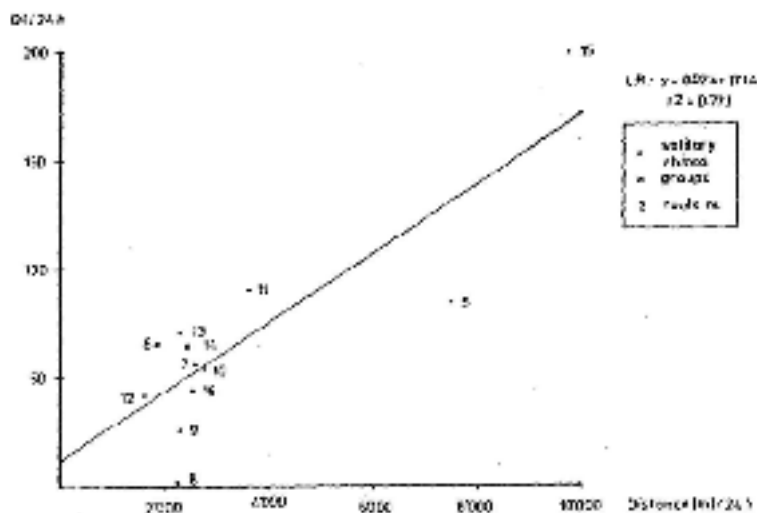
The farther a rhino travels within a certain time, the higher is its energy consumption. Its higher demands for energy can be satisfied either immediately by increasing the rate of food consumption, or by using up energy reserves stored in the body which are replaced later during phases of lower movement activity. It may therefore be asked whether any correlation between the average distance travelled per 24 hours and the average amount of food consumed in the same time period can be detected. Furthermore, if rhinos do travel longer distances without or with very little feeding: how long are these distances and how much time does a rhino go without feeding? Are there certain "dispositions" which supersede and reduce a rhino's motivation to feed?

In order to obtain clear answers to these questions, it would have been desirable if the following conditions could have been met:

1. All data should be from the same individual. This would eliminate any influence of body size or sex. Only if data from a large number of tracking sequences were available, these might be from different individuals.
2. It should be possible to record all feeding events and estimate the quantity of food consumed with reasonable accuracy.

The first condition could not be met because time estimates and estimates of the quantity of food consumed were made only for 12 tracking sequences involving different individuals. The second condition could not be met in the case of "groups" of rhinos. "Groups" or pairs of rhinos do not always move

Figure 4-10 Relationship between quantity of food eaten and distances travelled per 24 hours



close together, but frequently separate up to 50 m from one another. I usually did not follow every track in the group, but only one of them, and some feeding events may have gone unrecorded. Nevertheless, some answers can be given to the above questions on the base of the limited observations made.

The average quantity of food consumed per 24 hours was plotted against the average length of path travelled in the

same time period (figure 4.10). In general it can be said that rhinos that travel farther per 24 hours also have higher rates of food consumption. The data of 9 routes on which solitary rhinos were tracked (excluding routes 6, 8 and 14, see below) fit a regression line reasonably well ($r^2 = 0.77$). Routes 6 and 14 were not included because they involved a cow/calf pair (6) and a group of three rhinos (14). For the reasons mentioned above the results for groups cannot be compared with those of solitary rhinos. Route 8 was not included, although the rhino was travelling alone, because it took the rhino only 10 1/2 hours to cover the distance of about 1.7 km. It had practically not fed during this time and consequently the quantity of food calculated to have been consumed per 24 hours was extremely low as well. However, it is most likely that the rhino fed just before or after it was tracked, and that the feeding rate was higher. Nevertheless, this result indicates that rhinos do travel longer distances and can go for periods up to at least 10 1/2 hours with practically no food.

The result for the cow/calf pair (route 6) lies above the regression line. To judge from its dung, this calf was still almost completely dependent on its mother's milk for food. Lactating females have higher energy requirements and therefore higher rates of food consumption than solitary rhinos.

The result for the group of three adult rhinos lies above the regression line as well. However, in this case a much higher result was expected, since three rhinos consume more food than a single rhino. One possible reason, namely that I did not record all feeding events from a group of rhinos, has been given above. Another reason may be that the male was probably following the two females in order to mate with one of them. Possibly rhinos engaged in courtship are less motivated to feed than solitary rhinos.

4.3.5 Movement patterns and the use of trails

Food is not distributed homogeneously throughout the rhino's environment, but is more abundant in some areas than in others. As a result of this uneven distribution of food resources rhinos do not visit all parts of their home range (see 4.5) with equal frequency. They appear to spend most of their time in those areas with the highest abundance of food. Whenever a home range encloses several separate areas with high food density rhinos remain for periods of a few days up to three weeks in an area with high food density and then shift to another. Rhinos may sometimes remain several days in a small part of their home range. On one occasion a rhino was observed to stay within 1 km² over a period of eight days. Examples for movements from one part of the home range to another are route 5 and the movement of the cow/calf pair from Kalejatan to Karangranjang described in 4.3.2.

For the black rhino Schenkel distinguished between two types of movement (Schenkel and Schenkel-Bulliger 1969b, Schenkel and Lang 1969).

- Movement in a feeding area: characterized by low movement rates, frequent and pronounced changes of direction and frequent feeding.
- Movement from one ecologically relevant place (i.e. feeding area, wallow, salt lick etc.) to another: characterized by high movement rates, few and not very pronounced changes of direction and little feeding or other activities aside from movement.

Intermediate forms between these two types occur, so that often it is not possible to make a clear distinction. Schenkel implicitly suggested the existence of these two types of movement in the Javan rhino (Schenkel et al. 1978). The observations made during this study confirm this. Both types as well as intermediate forms were recorded.

In the black rhino the types of movement are reflected in the different types of trails used by them. In feeding areas a network of slightly used trails is found. Different feeding areas and other ecologically relevant places are connected by intensively used trails (main trails). These latter appear to be the result of a compromise between the most direct route and the route requiring the smallest effort (Schenkel and Schenkel-Hulliger 1969b). In Ujung Kulon a continuous network of trails is absent (Schenkel and Schenkel-Hulliger 1969a, Schenkel et al. 1978), however, the type of movement is reflected in the choice of the route. When moving from one part of the study area to another without feeding, Javan rhinos generally choose the most direct route. Whenever major obstacles, such as steep terrain or extremely dense vegetation, lie across this route then detours are made

One female whose track was being followed was observed to alter her route so as to go around the swampy area at the foot of the Telanca plateau in the study area. Movement through the swamp is seriously impeded by the muddy soil and the dense vegetation. The change of direction was made before the rhino had reached the edge of the swamp.

Movement between ecologically relevant places usually appears to follow the route representing a compromise between the most direct and the easiest route. On the other hand, on feeding trips in areas of high food density this economy of energy expenditure is not apparent. Javan rhinos may frequently be observed to traverse extremely difficult terrain while feeding.

In spite of their preference for easy routes Javan rhinos have not developed a continuous network of trails in Ujung Kulon. The reason for this was supposed to be the low population density (Schenkel and Schenkel-Hulliger 1969a). In fact, where the local topography canalizes the movement of rhinos, trails are generally found, thus suggesting that the low population density has been responsible for the absence

of a network of trails. However, it was found that the Javan rhinos show a low tendency to follow a trail whether animal or man-made. This was observed to be the case both when rhinos moved around a feeding area or when they displaced between feeding areas. In most cases they stayed on a trail for less than 200 m, although the trail could have been followed over a longer distance. The longest distance recorded was 1.4 km along one of the man-made patrol paths. This was an exceptional case however. Furthermore it is possible that in a tropical forest environment animal trails, that are not intensively used, remain visible to the human eye for a shorter time than in the African savanna.

4.4 Diurnal activity pattern

In the course of an animal's day (a "day" here denotes a 24 hour period) not all activities are pursued at any hour. Some activities occur only at certain times of the day. Thus a certain activity pattern results. In the case of the Javan rhino I wanted to determine whether such activity patterns exist and which activities are predominant during which periods of the day.

4.4.1 Method

For answering these questions the initially recorded activity in direct encounters with rhinos was considered. Information from tracks was in most cases too unreliable for this purpose, because the age of a track could not be estimated with sufficient accuracy. Only when I was sure that the age of a track could be estimated with an error of less than one hour was this information included. Such cases were rare however.

Only two levels of activity were distinguished, namely whether rhinos were active or resting. Active rhinos were moving or feeding; resting rhinos were lying on the ground, in a pool or in a wallow. Because rhinos were only encountered during the daytime, only their diurnal activities are considered here. The time of day was divided into three periods: morning (6 to 10 a.m.), noon (10 a.m. to 2 p.m.) and afternoon (2 p.m. to 6 p.m.). The observations in each period were totalled.

4.4.2 Results

In 23 encounters rhinos could be observed directly or they could be heard nearby. In three more cases the time at which a certain activity had taken place could be determined accurately from the age of the track.

Table 4.14 Diurnal activity

Period	6 - 10 h	10 - 14 h	14 - 18 h	Total
active	5 (4.4)	9 (11.0)	5 (3.7)	19
resting	1 (1.6)	6 (4.0)	0 (1.3)	7
Total	6	15	5	26

figures in brackets are expected number of observations

$$\chi^2 = 1.41, p > 0.1, df = 2$$

Rhinos were active during all periods of the day (table 4.14), and in all periods more active than resting rhinos were recorded. Altogether nearly three times as many active than resting rhinos were encountered. But resting rhinos were found more often in the noon period, than was expected on the base of the overall ratio of the two levels of activity, and less frequently than expected in the morning and afternoon periods. This indicates a tendency for rhinos to rest preferably during the noon period. However, the deviation of the ratios in each period from the overall ratio is statistically not significant. The tendency has already been reported by Schenkel and Schenkel-Hulliger (1969a).

The tendency to rest over noon, both in wallows and outside, can probably be explained by the rhinos' need to regulate their body temperature (see 4.2.4). In the forest on P. Peucang the maximum air temperatures reach 34° C, but outside the forest temperatures can be in excess of 40° C at noontime (Halder 1975). Such high temperatures may pose a problem for rhinos if they are exposed to them for a long time, and therefore they will tend to reduce both the extent of their activity and the time spent exposed to direct sunlight during the hottest period of the day. In fact, all but one of the resting rhinos that were encountered in this period were lying in the shade.

The tendency to rest over noon has been reported from the black and the Indian rhino (Schenkel and Schenkel-Hulliger 1969a, Laurie 1978).

4.4 Home ranges

In many terrestrial mammals it has been observed that individuals do not wander freely over the whole area accessible to them but most of the time restrict their

movements to a part of it. This observation has led to the concept of an animal's "home range". Burt (1943) defined the home range as "...that area traversed by the individual in its normal activities of food gathering, mating and caring for young". This definition leaves the possibility of occasional movement out of the home range open. Animals may leave their home range either spontaneously, e.g. to explore unknown areas, or in reaction to unusual, very strong stimuli.

When defining an animal's home range it should be stated for which time period. Home ranges are not permanent over the whole lifetime of an animal. Their size and location may change seasonally because of seasonal fluctuations of the environment, or more slowly because of long-term environmental changes. Animals may also be forced to leave their home ranges permanently due to external pressure, e.g. by conspecifics or humans. In many species individuals are not always attached to a home range but may be nomadic during certain life stages. The home ranges shown below are those that were occupied by the individuals during the time of this study.

In practice it has proven difficult to determine the exact size of a home range. The reason for this is that no distinct boundary line exists which separates home range from non-home range. This boundary should rather be viewed as a zone surrounding the home range in which the animal's familiarity with the area and the probability of its being there decrease rapidly with increasing distance from the centre of the home range. Any figure given for an animal's home range must therefore always be considered an approximation.

How can the size of a home range be determined? This would be possible if one could infer from the animal's behaviour, pattern of movement or activity whether it is inside its home range or not. However, in many species, including the Javan

rhino, it is not possible to determine whether an individual is moving around "normally" inside its home range or engaged in "exceptional" activity outside, especially since animals also engage in routine activities (e.g. feeding) when they are outside their home range. Another possibility — used in this study — is to determine, through long-term observation, the area in which an individual is found most of the time. This also permits a recognition of "unusual" movement outside the home range.

Home ranges have been determined for three of the other four rhino species: black (Goddard 1967), white (Owen-Smith 1975) and Indian rhino (Laurie 1978; 1982). Eotner (1979) supposed that Sumatran rhinos occupied home ranges as well, but did not determine their size. In the case of the Javan rhino it was suspected, before this study was undertaken, that individual rhinos occupied home ranges. Schenkell and Schenkell-Holliger (pers. comm.) had noticed during previous visits to Ujung Kulon that tracks with the same measurements could be found repeatedly in the same area. The same impressions were gained from an evaluation of track sightings reported in the station books at the guard posts. I made similar observations during the first months of this study. The frequent and regular occurrence of tracks with the same measurements in certain parts of Ujung Kulon led to the assumption that individual rhinos do not wander over the whole Area of Ujung Kulon, but restrict their movements to a certain part of it — their home range. As will be shown below, this assumption could be confirmed.

4.5.1 Methods

The forms and sizes of home ranges were basically determined by the method of the smallest convex polygon (e.g. Southwood 1978); all locations where a rhino or its track had been

found were determined and a line drawn around them in a manner that enclosed the smallest possible area, but so that all inside angles were smaller than 180°. However, I excluded larger areas from the polygon when I was certain that they had not been visited by the rhino in question. Therefore not all home range polygons are convex. Small areas inside the home ranges that were never visited by rhinos were not specifically excluded, as they only formed a small percentage of the total area. Examples of such enclaves are the lighthouse compound at Tg. Laya and possibly the swamp in the northwest corner of the study area (see figure 1.7).

The geographical locations of rhinos were determined in one of the following three manners:

- (1) by recording where their track crossed a patrol path of the study area.
- (2) By trigonometrical calculation of their route from a point where they had crossed a patrol path. This method was used mainly to determine locations outside the study area, but occasionally it was used for locations in the study area as well.
- (3) By estimating their position relative to some known point on the coast. This was done only in the case of the two males D and F whose home ranges lay outside the study area. There were no surveyed paths in these two home ranges, nor did I record the number of paces or the compass direction when following their tracks.

All locations were drawn in on a map of the study area to the scale 1 : 5'000 etc. in the case of the males D and F, on a map of Ujung Kulon to the scale 1 : 50'000.

These methods of calculating or estimating the locations of rhinos were not very accurate and the locations obtained in this manner differed from the true ones to a certain extent. The maximum possible deviation from the true location depends

upon the method by which the location was determined. When surveying the paths of the study area the locations of the points where two paths met were surveyed twice (once for each path). The two calculated locations of each crossing point never differed more than 20 m from each other. The maximum error of method (1) above was therefore estimated to be 20 m. The accuracy of method (2) could be checked when a rhino track, I had been following, crossed a patrol path in the study area. The difference between the location obtained by trigonometrical calculation of the rhinos track and the location obtained from the survey of the path was 150 m at most. The larger error of method (2) was due to the less accurate method of recording the direction and distance travelled by a rhino compared to the method of surveying the paths. If such errors are made when calculating the outermost locations — i.e. the corners of the home range polygon — they will have an effect on the calculated size of the home range. I calculated the maximum variation of home range size caused by the inaccuracy of method (2) by moving the locations of rhinos obtained by this method 150 m closer to or away from the centre of the home range on the map and computing the resulting smaller and larger areas. The variation of the calculated size of all home ranges that lay partly or completely inside the study area was between 3 and 5 %. Because of the even less accurate method (3) of estimating the geographical locations of the males D and F and also because the locations were plotted on a scale 1 : 50'000 map the size of the home range was estimated to be as much as 10 % smaller or larger than the size given here.

The advantage of the polygon method lies in its ease of application. It is, however, sensitive to the size of the sample. The larger the number of locations obtained for an animal, the closer the calculated size of the home range will approach the size of the area regularly visited by it (Jennrich and Turner 1969); when the number of locations is

small. The size of the home range will be underestimated. Overestimates may result when areas that are not visited by the animal are included in the home range. This may be the case where the outline of the actual home range is concave, but the size estimate was made for a convex polygon.

In the case of some rhinos whose home range lay partially in the study area, but whose tracks were not followed or encountered outside the study area, the size of the home range was estimated as follows: It was assumed that the proportion of a rhino's home range lying in the study area corresponded to the proportion of the time that the rhino spent in that part of its home range. The size of the part of the home range lying in the study area was determined by the convex polygon method described above. The percentage of time spent in that part of the home range was determined from the number of times the rhino was found there during the 18 times the study area was patrolled (see 2.1.1.2). From this percentage the total size of the home range ($= 100 \%$) was calculated. Obviously, this can only be considered a very crude method, since the time a rhino spends in a part of its home range does not depend on the size of that part but on the quality of the resources there and the time the rhino spends to exploit them.

4.5.2 Results

The smallest home range of a male Javan rhino was about the same size as the largest female home range; on the average male home ranges were larger than those of females, the largest male being about ten times the size of the smallest female home range (table 4.15, figures 4.11, 4.12). The size of the home range varied considerably among individuals of the same sex: the largest home range of a male was about twice the size of the smallest and the largest home range of a female rhino about three times the size of the smallest female home range.

Table 4.15 Home range size

Individual	Size (km ²)	Error margin (km ²) of polygon method	Percentage of time present in the study area*	Estimated size of home range *	Isolated observations	Tracking (days)
Males						
D	22.5	11.2 - 33.7			75	10
F	26.4	23.7 - 29.0			13	-
G	21.0	20.3 - 22.1			42	22
Females						
H	1.6	3.4 - 3.8	83 %	4.3	41	0
I	2.6	2.4 - 2.7			25	0
J	8.4	7.9 - 8.8			21	29
K/L	8.2	7.8 - 8.6	61 %	13.6	28	5

* Estimates only made when part of the home range lay in the study area and tracks of the rhino were rarely followed or encountered outside the study area.

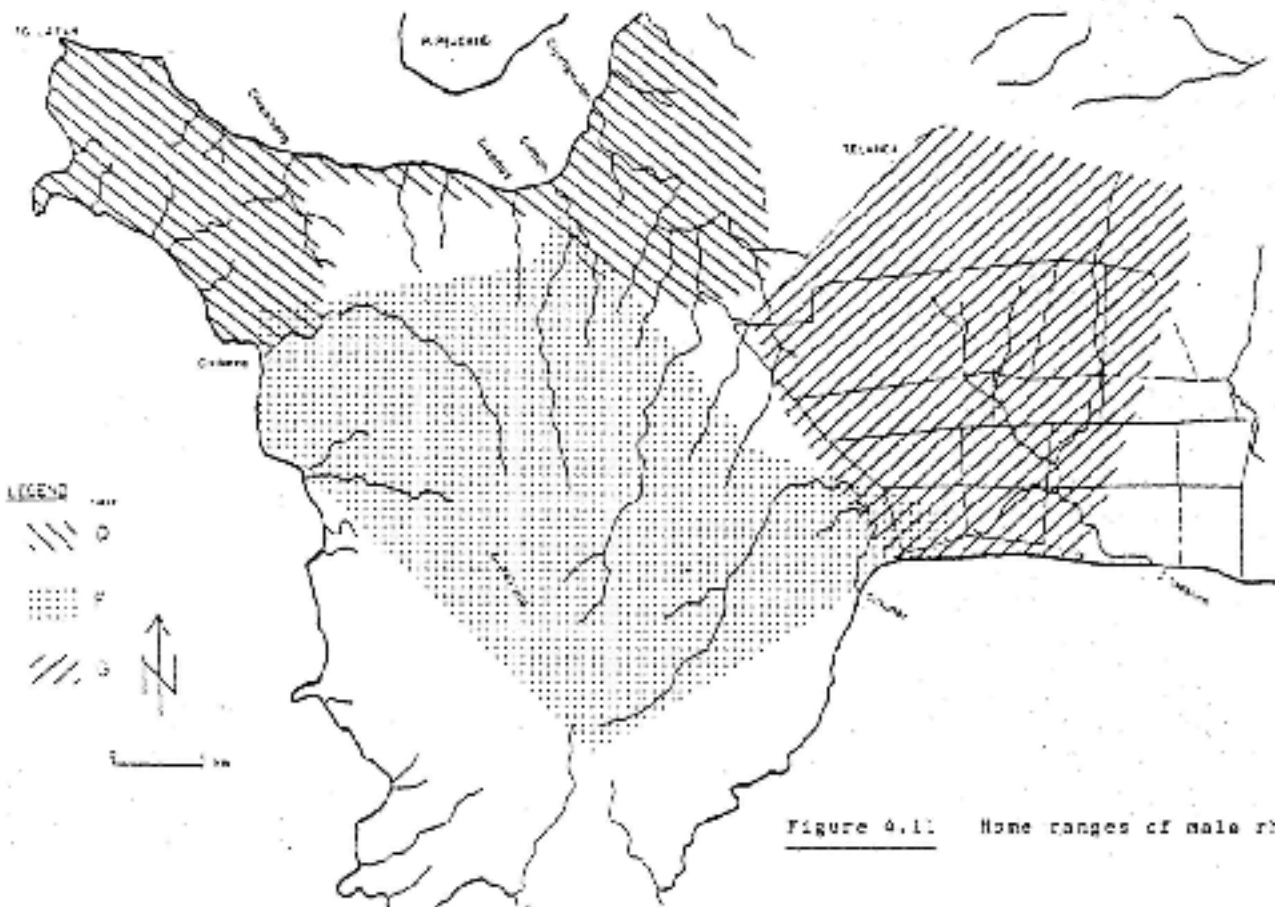


Figure 4.11 Home ranges of male rhinos

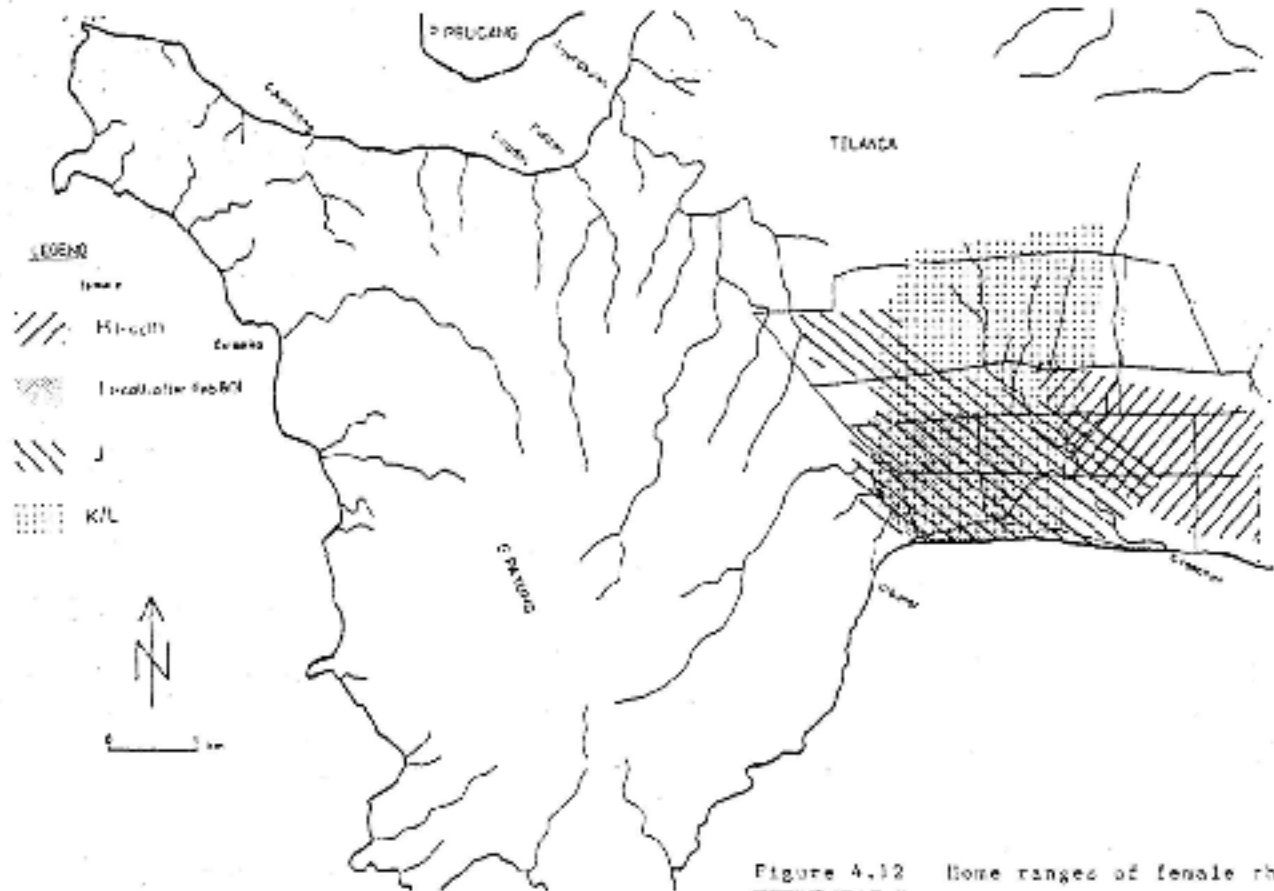


Figure 4.12 Home ranges of female rhinos

The home ranges of the males D and F were probably larger than the sizes given in table 4.15. Male D possibly visited the area on the north slope of G. Payung between the streams Cicadas and Cikenbang (i.e. south of the narrow corridor along the north coast) as well. The rhino's tracks were never followed into that area, nor was the area patrolled regularly. Extensive patches of shrubland combined with gentle slopes suggest its suitability for rhinos. The calculated home range size of male F is based on only a few sightings of its tracks. In view of this small number of observations it is most likely that its home range was considerably larger and extended over the southern part of G. Payung as well. In this case the size of its home range would be in excess of 30 km².

I recorded movement of one of the rhinos listed in table 4.15 outside its home range only once. This was the female H and her calf. The calf was about two years old at that time.

4.5.3 Discussion

The results indicate that the sizes of home ranges are very variable. Variation is found at two levels: a difference between the home range sizes of the sexes and differences between individuals of the same sex. I shall first turn to the latter, and propose some explanations for the observed differences between individuals. It must be assumed that some of the variation can be explained by individual differences alone and was not caused by external factors. Nevertheless, I will suggest some factors which may have played a role in some cases.

The minimum size of a home range is determined by the density of resources. A home range must be at least large enough to contain a sufficient amount or number of those resources

which are necessary for the survival of the individual. In areas where resources are less abundant, home ranges are expected to be larger. This was probably the cause for the very large home range of the male F on G. Payung. On the upper slopes of G. Payung no shrubland vegetation is found. Many areas in the Payung region are unsuitable for rhinos because of the steep terrain.

The home range of male D was less than half the size of the home ranges of the two other males and about the same size as the largest female home range. This was a very old male that died in 1979. Can the small size of its home range be attributed to a high density of resources, especially feed resources, or to the rhino's advanced age? The density of feed resources in the areas along the north and west coasts and on the mountain spur leading down to Tq. Leyer did not appear to be higher than in the study area. The quality of the environment is therefore considered to have been of less importance than the rhino's age in this case. It is possible that old males do not have the strength to travel over large areas and restrict their movements to a smaller home range whose size is closer to the size of female home ranges.

The smallest home ranges of females were those of females which were accompanied by a calf. In these cases it is possible that the females restricted their movements to a small area because calves are not capable of travelling the same distances as adults over long time periods. An alternative explanation might be that the females reduce the amount of energy they expend for movement in order to compensate for the higher energy demands imposed on them by the production of milk for their calves.

The largest female home range was the one occupied by two adult females (K/L). The question remains open in this case whether permanently associated adult rhinos generally occupy

larger home ranges and whether the cause for this is the larger energy demand of the "group".

The average home ranges of male adult Javan rhinos were found to be larger than those of females. This was not so because the home ranges determined here lay in areas that differed in their topography and vegetation. This is demonstrated by the home ranges of the male G and the females H and J which all lay partly or completely in the alluvial plain. Nor can the different home range sizes have been caused by differing energy requirements of the sexes, since males and females are of approximately equal body size (see 5.2).

As mentioned above, animals may show seasonal variations in the use of their home ranges, as a reaction to seasonal changes in the quality and availability of resources. Where seasonal differences are very pronounced the members of some species may even occupy entirely different ranges in each season. Although the movements and locations of Javan rhinos could not be determined in dry months, such seasonal variations were considered unlikely except during long drought periods. No marked seasonal changes of the vegetation were observed in Ujung Kulon. It is possible that the nutritional quality of many foodplants declines during the dry months, but the decline is thought to affect all vegetation types uniformly. The Javan rhinos in Ujung Kulon react to seasonal changes of food quality by changing the composition of their diet (see 4.1.5) rather than by changing the pattern of home range use. In extremely long drought periods, however, when many streams dry out and water becomes scarce rhinos may be forced to leave their home ranges or to extend their regular movements, and thus their home ranges, to include places where water can still be found.

In which manner and at what age do rhinos become attached to a home range? During the first years of its life a calf

becomes acquainted with the home range of its mother. It is not known whether, after separation from the mother, subadults remain in or near the mother's home range or move away and settle in another area. Since males have larger home ranges than females, this implies that they have at least expanded the range they occupied as young animals. Most likely males explore new areas while they are still subadults or young adults. It is not known whether females have the same tendency to explore new areas. I suggest that exploratory activity is less pronounced in females and that they tend to establish their home ranges in or close to the home ranges of their mothers. Such a difference of behaviour -- if in fact it does exist -- might be explained by the different reproductive strategies of males and females. Males probably expand their home ranges in order to gain access to a large number of females. Females, on the other hand, probably try to establish themselves in an area which offers suitable conditions for raising their offspring. The nearest suitable area is obviously the home range of their mother, the suitability of which was demonstrated by the fact that they themselves were raised there successfully.

Undoubtedly olfactory traces of conspecifics and of the individual itself contribute to its attachment to a home range.

The advantage for a rhino to remain in a home range lies in the greater familiarity with that area. The rhino has a better knowledge of the location and condition of resources, which in turn enables it to exploit these resources more efficiently, e.g. to forage more efficiently or to travel by the shortest and easiest routes.

4.6 Interactions with other species

Interactions between different species may be of various types, e.g. competition, predation, parasitism, symbiosis etc. Some of these types of interaction that were observed to occur between rhinos and other species are discussed below. Interactions with man are treated separately.

4.6.1 Ecological competition for food resources

Large overlap of the diets of two species indicates strong ecological competition, if the respective populations are limited mainly by food resources; little or no overlap indicates no competition. Here I shall consider the diet overlap between the Javan rhino and the other ungulate species occurring in Ujung Kulon. The ecological competition between rhinos and invertebrates will not be discussed here because of the lack of information on the impact of invertebrate species on the food supply of rhinos.

Besides the Javan rhino five other ungulate species are found in Ujung Kulon: Bos javanicus (banteng), Cervus tigrionensis (rosa deer), Muntiacus muntjak (barking deer or muncak), Sus scrofa (wild pig) and Traquius javanicus (mouse deer or kancil). The last species cannot be considered a food competitor since its diet is completely different from the rhino's, consisting mainly of grasses and fruit (Lekagul and McNeely 1977). The diet of pigs is mainly fruit, but also small animals and carrion (Pauwels, in prep.) is also quite different from that of the rhino. Pigs, however, compete with rhinos for the same plant species in another way: female pigs construct large nests of plant material, mainly in the second half of the rainy season, in which they give birth. For the construction of the nests they preferably use small saplings. In this manner many rhino foodplants are

broken off. However, pigs construct their nests in the forest, i.e. in that type of vegetation where rhinos rarely search for food. In addition it was observed that the majority of saplings bitten off by pigs did not die but regenerated later (Pauwels, in prep.). The impact of the pigs' nest building activity on the food supply of rhinos is therefore probably insignificant.

The two species of cervids are unlikely to be of any importance as food competitors, even though their diet is not well known and there may be some overlap with the rhino's diet. The population of rusa deer on the peninsula is at present very small and apparently limited to the coastal plain along the north and east coasts. Muntjak, on the other hand, are numerous and widely distributed. However, their population density is low and their biomass comparatively small. They occur mainly in the forest (Schenkel and Schenkel-Hulliger 1969a) and feed only occasionally in glades or in shrub vegetation (Hoogerwerf 1970). In addition muntjak are not exclusive browsers but eat fruit as well.

A list of banteng foodplants compiled by Halder (1975) includes several species also eaten by rhinos. The large banteng population in Ujung Kulon (the banteng population has not been surveyed in recent years, but appears to have grown considerably since 1971 when its size was estimated to have been about 200 individuals (Halder 1975, Schenkel pers. comm.)) might be reducing the amount of food available to rhinos.

About one third of the species on Halder's list are monocotyledones: their percentage in the diet being about seven times as large as in the rhino's (table 4.16). When only the 24 species most frequently consumed by banteng are considered, the percentage of monocotyledones is even larger: 16 species or 67 %. Only one of these 16 species is regularly

Table 4.16 Taxonomical comparison of rhino and banteng diets

	Monocoty- ledones	Dicoty- ledones
rhino	11 (5.8 %)	179 (94.2 %)
banteng	24 (35.8 %)	43 (64.2 %)

eaten by rhinos (*Anomun* sp.). Among the monocotyledones there are many plant types that are hardly ever eaten by rhinos: palms, pandanus, bamboos and grasses. On the other hand, the rhino's diet includes many species of climbers, a plant type that does not figure on Halder's list. Twenty-three plant species were common to both diets; this represents 12.1 % of the species in the rhino's or 31.3 % of the species in the banteng diet. Halder did not investigate the quantity of each food species eaten by banteng nor their proportion in the banteng diet.

An animal's diet forms part of its ecological niche. Therefore, when the diets of two species overlap, their niches overlap as well. Niche overlap has often been equated with competition (e.g. Odum 1959). But in spite of niche overlap, there may be no competition if the relevant resource -- in this case food -- is not in short supply (Milley 1982). Whether a resource is in short supply depends upon how large the demand for that resource is: resources can be abundant but still in short supply if the demand for them is large and, conversely, they may be rare but not in short supply because there is no demand for them. Competition for a resource is expected to occur between two species if the demand by both competitors is large relative to the abundance

of the resource. The preferability index (RPI, see 4.1.2.4) of a food species relates demand to abundance and thus can be regarded as a measure of whether that food species is in short supply. RPIs are available only for rhino foodplants: Halder (1975) classified banteng foodplants into three categories according to frequency of consumption (regularly, occasionally and rarely eaten) but it cannot be inferred from these categories whether the food species are preferred by banteng or not. However, if a foodplant is highly preferred by rhinos (and therefore in relatively short supply) and regularly eaten by banteng it may be considered to be in short supply for banteng as well. In table 4.17 foodplants eaten both by rhino and banteng are listed according to Halder's categories. For each species the rhino RPI is given.

Of 26 species regularly eaten by banteng, 8 are eaten by rhinos as well. Only two of these, however, are highly preferred by rhinos (Hibiscus tiliaceus, Spondias pinnata). The RPI of the former species could not be calculated because it was not found in any of the sample plots in the study area. Its proportion in the rhino's diet was large (> 1 %) and its RPI was estimated to be very high (> 20). Of the 21 plant species occasionally eaten by banteng, 7 are consumed by rhinos as well. One species (Melastoma polyanthum) is moderately preferred by rhinos and another species (Gnelina elliptica) was estimated to be moderately to highly preferred (its RPI could not be calculated for the same reason as for H. tiliaceus). Of the 22 rarely eaten banteng foodplants 8 species figure in the rhino's diet. All of these species have a low RPI.

Discussion

The feeding ecology of the banteng in Ujung Kulon is still little known. It is quite possible that the diet of banteng includes more species than those listed by Halder and that

Table 4.17 Foodplant species eaten both by rhino and banteng

Species*	RPI (rhino)**
a) Species eaten frequently or regularly by banteng (Halder: +++):	
<i>Hibiscus tiliaceus</i>	(very high, > 20)
<i>Spondias pinnata</i>	15.20
<i>Lagerstroemia flos-reginae</i>	0.55
<i>Leca xambucina</i>	0.55
<i>Syzygium polyanthum</i>	0.22
<i>Annonum</i> sp.	(low, < 1)
<i>Cardia myxa</i>	(low, < 1)
<i>Dunax cannaeformis</i>	(very low, < 0.1)
b) Species eaten occasionally by banteng (Halder: ++):	
<i>Gaellina elliptica</i>	(moderate to high, > 1, < 5)
<i>Melastoma polyanthum</i>	1.54
<i>Dillenia excelsa</i>	0.52
<i>Baccaurea javanica</i>	(low, < 1)
<i>Vitex quinata</i>	(low, < 1)
<i>Vitex trifolia</i>	(low, < 1)
<i>Harringtonia macrocarpa</i>	0.09
c) Species eaten rarely by banteng (Halder: +):	
<i>Kleinhevila hospita</i>	270.04
<i>Mallotus dispar</i>	42.68
<i>Planchonia valida</i>	19.56
<i>Buchanania arborescens</i>	2.79
<i>Embelia ribes</i>	2.03
<i>Diospyros pedula</i>	(low to moderate, ca 1)
<i>Lantana camara</i>	(low, < 1)

* For some of the species listed here the scientific name given by Halder (1975) does not coincide with the name given here. Because the local names were the same and these plants were well known and identified without difficulties by the guides, they were considered to be the same species.

** The RPI values are taken from table 4.8 or calculated from appendices I & II. Whenever the RPI value could not be calculated it was roughly estimated (estimates are given in brackets).

the overlap between the two diets is more extensive than shown here. It is further possible that, because of the large increase of the banteng population mentioned above, there has been increasing intraspecific food competition among banteng and that in recent years they have expanded their diet and increased the overlap with the rhino's diet. As mentioned previously, nothing is known about the food species as regards the quantity eaten, their proportion in the banteng diet and how much they are preferred. Little is known as well about which vegetation types banteng prefer for feeding. Grassy plant communities (e.g. the grazing grounds) which are unfavourable for rhinos because the lack of food plants, are intensively used. The total area of grasslands in Ujung Kulon is, however, insignificant. Only a small part of the banteng population makes intensive use of the grazing grounds; most banteng feed mainly in the other plant communities found in Ujung Kulon (Halder 1975). According to Hoogerwerf (1970) banteng seem to prefer areas of secondary growth to forest-like vegetation types.

Changes in the diet of one of the competitors indicate that ecological competition for food is or has been occurring and that the ecologically weaker competitor is evading the stronger by shifting to food species that were not or rarely consumed previously. Such a shift has been suggested by Schenkel and Schenkel (1982) in view that presently rhinos seem to consume more climbers than formerly. But the shift could have been caused by changes in the vegetation rather than competition with banteng. As mentioned above, however, it is more likely that there never has been a diet shift but that the higher observed proportion of climbers in the rhino's diet is a result of the methods and study areas chosen (see 4.1.2.1).

The food niches of rhino and banteng overlap less than the overlap of diets alone suggests. Rhinos can reach food

growing higher up and break down larger saplings than banteng; saplings browsed upon by banteng are probably often smaller than those browsed upon by rhinos. Beside the competitive aspect of interaction one should not forget the possibility that banteng through their browsing activity retard the growth of foodplants in a similar manner as has been suggested for rhinos (Schenkel and Schenkel-Hulliger 1969a), thus preventing the plants from growing out of their reach. In the case of foodplants eaten by both species the benefits would extend to both species as well.

On the base of the present information there seems to be little ecological competition for food between rhino and banteng. Banteng tend to eat monocotyledonous plants such as palms, bamboos and grasses, while the rhino's diet comprises mainly dicotyledonous species. There is some overlap between the two diets, but only few of the plants eaten by both species appear to be in short supply. Nevertheless, in view of the present limited knowledge of the banteng's feeding ecology, the size of the population in Ujung Kulon and the impact of banteng on the food supply of the rhinos studies in this direction are highly necessary.

4.5.2 Common use of wallows

Rhino wallows are often used by wild pigs and by male rusa deer during the mating season. They are also visited by monitor lizards. Pigs show an aversion towards wallowing in the water of a rhino wallow; rather they rub their bodies in the muddy edges of large wallows (Fauvels, in prep.). Through their wallowing activity they soften up the mud of the rim and push it down into the wallow with the result that the wallow is enlarged. If visited only by pigs, wallows would become progressively wider and shallower, and dry out fast in the dry season. Visits by rhinos, however, result in the

wallow being deepened. Larger and deeper wallows dry out more slowly and remain usable for a longer time into the dry season. Rhinos also frequently open up wallowing facilities for pigs. It was observed several times that "ad hoc" rhino wallows continued to be used by pigs for some time before they dried out.

4.6.3 Parasites

Javan rhinos accommodate a large number of invertebrate parasites from the classes Cestode, (Fam. Aspilocephalidae), Trematoda (Paramphistomidae) and rematodes (Euposporinae, Gesophagostominae, Trichostrongyloidea, Strongyloidea) Palmieri et al. 1980). Eggs were found in all dung samples examined. Fluorocaccia gigantea has been described for Javan rhinos from the Sunderbans (Garrod 1877).

Three ticks (Amblyomma sp.) were found next to fresh rhino tracks where no banteng tracks were found nearby and the ticks had just fallen off a host -- most probably a rhino. Amblyomma crepitarum has been described as a parasite of the Javan rhino (Sequest 1933, Krauseveld and Keidel 1956). Rhinos are also pestered by ectoparasitic biting flies (Tabanidae among others). In the vicinity of rhinos I was frequently attacked by them (cf. Schenkel and Schenkel-Hulliger 1969a). In one wallow leeches were observed.

It seems that certain characteristics of the Javan rhino's behaviour serve to reduce the level of infestation by parasites:

- Crustaceans and fishes clean off ectoparasites from rhinos bathing in streams (see 4.2.4).
- The layer of mud acquired when wallowing probably protects rhinos from ectoparasitic insects (see 4.2.4).

- The limited time during which many wallows are in use and the usually long time periods between rhino visits at other wallows (see 4.2.1.1) probably also result in reducing the risk of parasitic infection.
- Rhinos do not defecate into wallows. This reduces the risk of infection by endoparasites as well. (However, rhinos urinate into wallows. Parasites of the urinary tract — should they exist in Javan rhinos — might be transmitted via wallows.)

4.6.4 Reactions to man

The behaviour of rhinos in encounters with man has been described in detail by Schenkel and Schenkel-Hulliger (1969a) and Hoogewerf (1970). Here I present some observations concerning the movements of rhinos after encounters with man as well as their reaction to human scent.

Upon encountering man or fresh human scent not older than a few hours rhinos flee a short distance at high speed. After that they continue to move away at normal walking speed. Having moved a distance of 500 m at most they continue their normal activities such as wallowing, feeding, resting which indicates that they are not alarmed any more and feel safe. After repeated contact with human scent within short time periods (a few hours), they usually leave the area and wander several kilometers away.

Human scent older than six hours does not cause a flight reaction any more. It was observed several times that rhinos used trails in the night after people, sometimes large groups, had travelled over them the day before, even when no rain had washed away the scent. On two occasions rhinos had made an "ad hoc" wallow on a man made path. One was on the permanent patrol path leading from Cigenter to Tg. Along-alang, the other was made on trail E of the study area. In both cases the paths had not been used by humans for a period of two weeks before the wallows were made there.

In the vicinity of buildings that are inhabited or frequently used by man, human scent does not cause any flight reaction:

- At least two different rhinos passed several times directly in front of the lighthouse compound at Pt. Lajar. This usually happened at night -- when a diesel generator was running in the compound -- and on a few occasions at dusk.
- Once a rhino fed less than 50 m away from the guard post at Kalejatan at night.
- Rhino tracks were seen several times near the observation tower at the Cidson grazing field.

The regular presence of humans in the study area did not appear to disturb the rhinos there. Even after several months of regular patrolling of the study area up to 14 rhinos could be found inside it.

Obviously the reaction of rhinos to human scent is variable. The type and intensity of the reaction depends primarily upon the age of the scent trace -- the fresher the trace, the more intense the reaction of the rhino. Obviously each rhino's individual experience with humans, which may have led to increased timidity or habituation to human scent, influences its reaction as well. Rhinos may become accustomed to human scent in certain localities. The tradition of a reaction norm from mother to calf also plays a role.

It is very likely that the intensity of reaction to human scent has receded in recent years because of the cessation of hunting pressure.

4.7 Discussion

4.7.1 Habitat requirements of the Javan rhinoceros and suitability of Ujung Kulon as rhino habitat

Several factors have contributed to the survival of the Javan rhinoceros in Ujung Kulon. The eruption of Krakatau destroyed the previously existing settlements there and rendered the area unsuitable for cultivation. Later legal protection stopped resettlement of the area. The rhino population also benefited from the remoteness and inaccessibility of the peninsula (Schenkel and Schenkel-Hulliger 1969a).

The layer of volcanic ash deposited by the eruption prevented the successional development of the former climax vegetation on the formerly cultivated areas. A dense tangle of shrubs and rattans with few tall trees developed instead (see 1.3.4.2). Does the environment in Ujung Kulon suit the Javan rhino's ecological requirements or did the population survive there in a sub-optimal environment because of the favourable circumstances described above? The answer to this depends upon whether the original habitat of the Javan rhino can be defined. Unfortunately, little information in this respect can be found in the literature (see 1.2.2). One must draw conclusions from the preferences observed in Ujung Kulon and hypothesize on the qualities which characterize the optimal habitat of the Javan rhino. Such a procedure seems valid in view of the broad range of vegetation and habitat types available to rhinos in Ujung Kulon.

Javan rhinos prefer to feed in gaps in the mature forest and in shrubland where mature trees are absent. In Ujung Kulon the main concentrations and the highest population densities are found where shrubland is abundant. The factors underlying

these preferences have been discussed above (see 4.1.4). The information available in the literature supports these observations. Javan rhinos always seem to have been attracted by the vegetation growing on plantations and man-made jungle clearings (ladang) (see 1.2.2). It would seem, therefore, that the rhinos' optimal habitat is characterized by vegetation types in which a canopy of tall trees is lacking.

Would a population find suitable conditions in primary forest in which large areas of shrubland and human influence are lacking? The canopy layer of primary rainforest is not continuous; wherever trees die and fall down, gaps are created which are rapidly colonized again (Whitmore 1975). Poore (1968) found that 9.9 % of a survey area in lowland dipterocarp forest in Malaya was in the gap phase. This percentage is much lower than the percentage of shrubland and forest gaps in the study area. The extent of the gap phase may vary from forest to forest, however, depending upon the factors which cause the deaths of the trees (Whitmore 1975). It would seem therefore that in primary forest good quality forage is less abundant. However, fast growing and therefore less well defended plants may be more abundant in the newly created and rapidly overgrown gaps than in the shrubland of Ujung Kulon. Much of the vegetation in shrubland consists of monocotyledones and bushes (e. g. Lantana camara) which are little preferred by rhinos. In Ujung Kulon rhinos showed a much higher preference for gaps than for shrubland (see 4.1.3.2). Most probably the area of a forest which is in the gap phase is in most cases sufficiently large to support a population of Javan rhinos in primary forest. In fact if this were not the case, it is difficult to imagine how populations of Javan rhinos survived in the vast areas of rainforest throughout their range at a time when man was not yet altering the forest through shifting cultivation.

A further question is whether large areas of shrubland without any trees would be suitable for Javan rhinos. Trees are probably necessary to provide shading against heat (Schenkel and Schenkel-Hulliger 1969a); willows that are shaded dry out more slowly. In general it can be said that in forest the seasonal fluctuations of water availability are probably not as extreme as in non-forested areas. Furthermore, because many of the rhino's foodplants are saplings of species that grow into tall trees (see Appendix 1), the presence of mature trees may be necessary as a source of saplings. In conclusion it appears that forest, or patches of forest, form a necessary element of the rhino's habitat.

What should therefore be considered the optimal habitat of the Javan rhino? Most probably this would be a mixture of treeless vegetation types in which food of high quality is abundant, and forest-like types of vegetation which are necessary to satisfy other of the rhino's ecological requirements.

The vegetation in Ujung Kulon includes large areas of shrubland vegetation, especially towards the south of the peninsula, in which rhinos find abundant forage of high quality. Moreover, these open areas together with patches of forest, clumps of trees and other types of vegetation form a fine mosaiclike pattern. Such a mixture of vegetation types was suggested above to be the optimal habitat for Javan rhinos. In this mosaic of vegetation types a rhino will never have to travel far to find the type of vegetation that suits its actual requirements. In addition water is abundant and never far away in Ujung Kulon, except during long drought periods. Salt is available as well although rhinos living in the interior of the peninsula will have to travel to the coast to obtain this resource. In view of the density and abundance of resources, as well as the fine mosaic of different vegetation types, I conclude that in many areas of Ujung Kulon Javan rhinos find a suitable habitat.

4.7.2 Ecological separation between the Javan and Sumatran

rhino

Groves (1967) pointed out that although the former ranges of the Javan and Sumatran rhino overlapped extensively, they appeared to avoid competition by occupying different habitats. Information in the older literature indicates that where both species occurred sympatrically a tendency for Javan rhinos to prefer lowlands and for Sumatran rhinos to prefer mountainous areas could be observed. Wherever one species was found alone it could occupy both habitats (e. g. on Java R. sondaicus could be found in the lowlands as well as on the highest volcanoes (Sody 1953), while on Borneo Sumatran rhinos were found to inhabit swamp forests in the lowlands (Groves 1967)).

There is some further evidence for the Javan rhino's preference for lowlands:

- In Ujung Kulon the population density on the mountain G. Payung is lower than in the south of the peninsula (see figures 2.4 & 2.5).
- Information in the literature indicates that Javan rhinos had disappeared from the volcanoes on Java at a time when there were still local populations in the lowlands in the south of the island. The population density on these volcanoes was probably always low because of the sub-optimal quality of the environment. In fact the volcanoes may have been population sinks into which surplus rhinos from the lowlands moved. Because of the sub-optimal habitat on mountains the subpopulations there had low reproduction rates and were dependent upon the influx from the lowlands for their survival. Once the populations on the volcanoes were isolated from the surrounding lowlands by cultivated land, and the movement of rhinos from the lowlands was stopped, they were not able to sustain themselves anymore.