

## DYNAMICS OF THE PLAGUE TRANSMISSION CYCLE IN CENTRAL JAVA

(Ecology of mammalian hosts with special reference to *Rattus exulans*)

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*Penelitian mengenai ekologi penyakit pes yang dilakukan di Boyolali, Jawa Tengah dari tahun 1972 sampai dengan 1974 meliputi juga penelitian mengenai siklus penyakit serta hubungannya dengan tikus sebagai binatang perantaranya. Selama tahun pertama ditangkap 1113 ekor tikus beserta pinjalnya yang berasal baik dari dalam maupun diluar rumah sampai yang tinggal dihutan.*

*Berdasarkan atas data-data mengenai penyebaran, reproduksi, populasi dan resistensi terhadap basil pes ternyata bahwa *R. exulans* merupakan reservoir utama terhadap penyakit pes di Boyolali dan *R. tiomanicus* kemungkinan dapat memegang peranan sebagai reservoir kedua. *R. rattus* telah lama dikenal sebagai reservoir penyakit pes di Jawa.*

*Banyak jenis tikus-tikus lain yang juga ditemukan dalam penelitian namun demikian pada saat ini belum berperan dalam penyebaran penyakit pes Boyolali, karena kehidupannya jauh dari penduduk resisten terhadap basil pes dan jarang ditemukan.*

Rodents are the most widespread, most abundant (both in number of species and in number of individuals) and most readily adaptable of all known groups of mammals. They are worldwide in distribution and occupy virtually every subterranean, terrestrial and arboreal habitat capable of supporting mammalian life, some species even being semi-aquatic in habit. The role of wild and domestic rodents in the transmission of certain infectious diseases, such as plague, is well established. Within a zoonotic cycle, rodents may serve either as *primary* or *secondary* hosts for vectors of the pathogenic agent and, depending on their resistance-susceptibility status, may function either as *reservoirs* or *amplifying* agents for the pathogen. The distributions of zoonotic pathogens, and of potential vectors of these pathogens, are determined to a large extent by the respective distributions of suitable vertebrate hosts.

Some zoonoses involve man, domestic mammals and domestic vectors only accidentally (or incidentally) in terms of the normal life cycle of the pathogen. Plague is a classic arthropod-transmitted, rodent-borne zoonosis. In the enzootic phase (characterized by low-level, continuing infection) the plague bacterium, *Yersinia (Pasteurella) pestis*, normally circulates among populations of field and wild rodents in sylvatic (wild) environs, thereby maintaining "smouldering" plague foci during prolonged inter-epidemic periods, some of which endure from five to ten years.

During a biologically or environmentally induced epizootic phase (characterized by high-level, sporadic infection), the plague pathogen escapes its natural self-regulating sylvatic cycle, progresses through peridomestic flea and rodent populations, and eventually infects domestic fleas and rodents. Domestic rodents (*i.e.*, *Rattus rattus*) generally are highly susceptible to infection and readily succumb to the pathogen. Upon death of the domestic rodents, a residue of hungry, hostless fleas is left behind in the houses. These fleas in turn feed on man as an alternative

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host, and thereby may initiate an epidemic. It must be emphasized that, at least in Central Java, plague epizootics among domestic fleas and rodents, and subsequent plague epidemics among humans, are entirely dependent upon a prior series of events in the sylvatic and peridomestic environs (Fig. 1). Without continued maintenance

of sylvatic enzootics during inter-epidemic periods, without progression of the infection through sylvatic and peridomestic habitats, without the crucial contact between infectious field elements, and rodents and fleas in human habitations, domestic epizootics and resultant human epidemics probably would not occur.

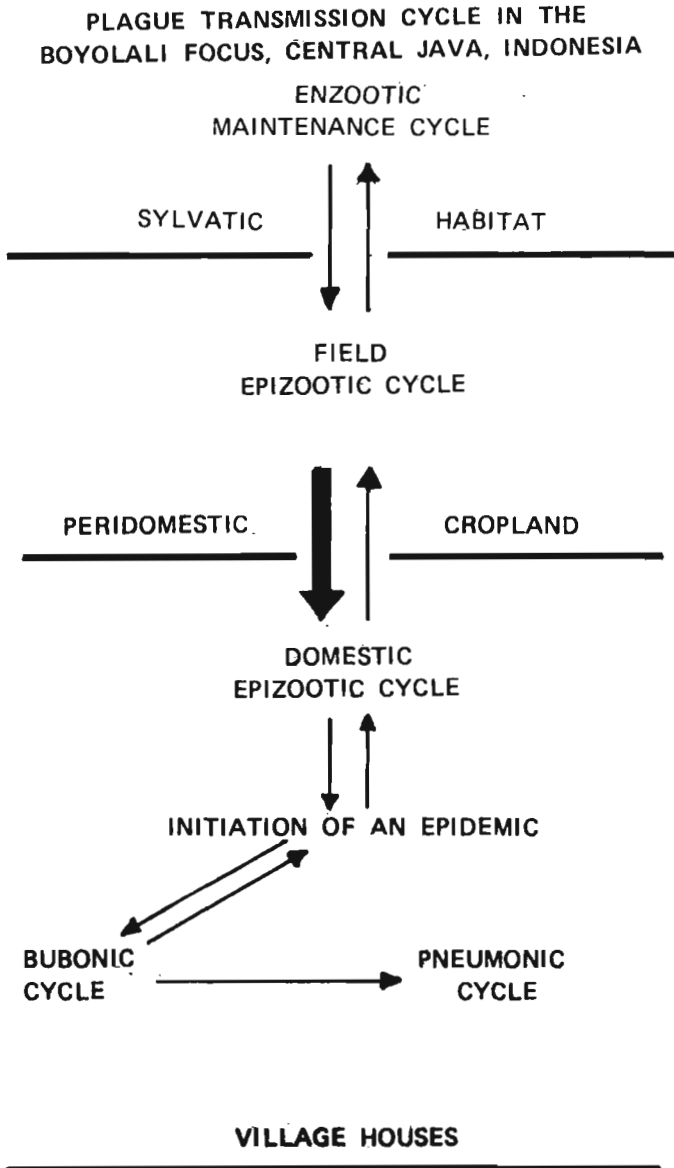


Fig. 1. The series of events that generally precedes the spread of infection to human habitations in the Boyolali plague zone. Note that the probability of transmission from the fields to the houses is greater than from the houses to the fields (also see Figures 12-A, B and A).

Except for the excellent work of Bahmanyar (1958), a preliminary investigation by Chamsa (1970) and the as yet unpublished inter-epidemic studies of the U.S. Naval Medical Research Unir No. 2 (1968), most studies of plague in Indonesia have been initiated during epidemics and have stressed the treatment of human patients, containment of the infection, and control of domestic vectors. Sampling thus has been concentrated mainly in human habitations and very little information has been compiled applicable to the normal components of the transmission cycle in peridomestic and sylvatic environs. Epidemiological investigations should strongly emphasize the ecological study of all pertinent zoonotic components and should be multidisciplinary in approach, with participation of both medically trained professionals, and researchers trained in the basic natural sciences (Muul, 1970). A thorough understanding of the natural life cycles of the bacterial pathogen, siphonapteran vectors, and mammalian hosts is essential to the control and ultimate prevention of plague epidemics.

The public health importance of rodent-borne zoonoses in particular must be considered in relation to the general ecology of the respective potential host species. Fundamental biological data must be accumulated, analysed, and interpreted with a view toward eventual eradication of plague and other infectious rodent-borne zoonoses. These necessary data include: The accurate taxonomic identification of the hosts involved; an adequate knowledge of geographical, altitudinal, ecological, seasonal and temporal distributions of the hosts; a thorough understanding of host population dynamics (natality, mortality, mobility, density and rate of turnover); an evaluation of the reproductive capacity of each host species (sex ratio, age ratio, initial reproductive ages of both sexes, mating behavior, type of breeding cycle, pregnancy rate, length of gestation, average litter size, number of litters per year, and longevity of reproductive members of the population); a comprehension of host interaction with man and with the physical and biotic environment, and an insight into the disease resistance-susceptibility status of all po-

tential reservoirs.

With these points in mind, and with considerable foresight, the present study of the ecology of plague during an inter-epidemic period in Central Java was initiated jointly by the Directorate General of Communicable Disease Control (Zoonoses Division) and the National Institute of Health Research and Development, both of the Ministry of Health, Republic of Indonesia, and by the Southeast Asia Regional Office (New Delhi) of the World Health Organization. Intensive field work commenced in April, 1972, and will continue until December, 1974. Preliminary data from the first year of research are herein reported.

#### The research area

The Boyolali Regency lies about 7.5° South of the equator and is bounded on the west by two volcanoes, the still active Mount Merapi (2911 meters) and dormant Mount Merbabu (3142 meters). The research area (Fig. II) is comprised of the two westernmost subdistricts (Cepogo and Selo), which have a recent history of plague epidemics (in 1957, 1959, 1968 and 1970). Baltaxard and Bahmanyar (1960), Velimirovic (1972) and two other papers presented at the previous bulletin summarize the available knowledge concerning past epidemics in Java. Twenty-five villages, with approximately 65,500 inhabitants, are situated in an area of 85 square kilometers. Villages extend upslope to about 1600 meters, but mainly are concentrated on the intermediate slopes and in the high valley or "saddle" that intervenes between the summits of the two volcanoes. Based on the distribution of human cases in 1968 and 1970, the "plague zone" occurs mainly above 1000 meters in elevation (Fig. II).

Human dwellings in the study area generally consist of three to five rooms, with woven bamboo slat or wooden plank siding, tile or thatch roofing, and earthen floors (Croos *et al.*, 1970). For the most part, a few livestock (cattle, horses, sheep, goats or chickens) are sheltered within the houses.

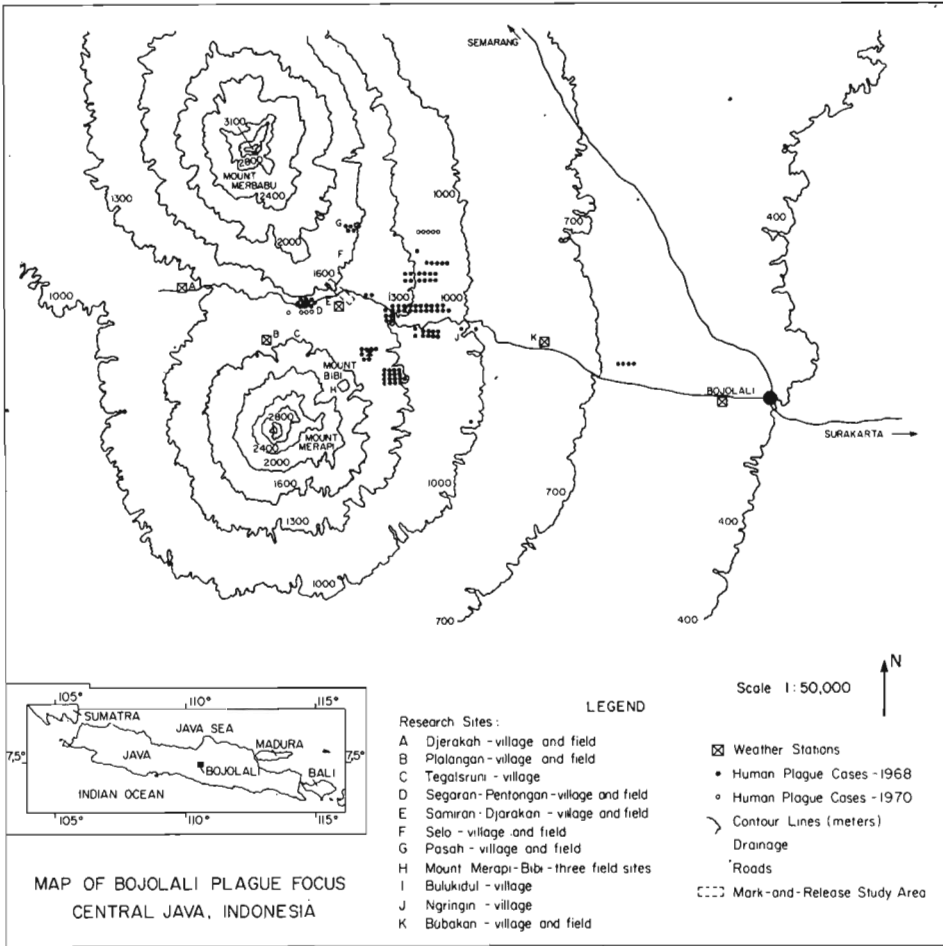


Fig. 11. Map of Boyolali plague focus Central Java.

Major dryfield crops between 1000 and 1600 meters in elevation are corn, carrots, cabbage, canna, tobacco, white potatoes, sweet potatoes, beans and peas. Below 1000 meters, extensive areas of upland dryfield rice, tobacco, cassava, soybeans, peanuts, and green manure crops, and groves of coconut are encountered. On the fertile basal plains, wet rice paddies and vast expanses of sugar cane predominate.

Very little remains of the original sylvatic vegetation in the Merapi-Merbabu complex, which presumably was dominated by a mixed-deciduous woodland in earlier times. For example, the slopes of Mount Merbabu were covered by a tall, dense forest in 1785, with agriculture being

confined to the lower volcanic slopes and surrounding fertile plains; however, by 1836, these slopes were entirely devoid of native forest (Dames 1955). Currently, the open woodlands on the upper mountainsides are dominated by *Acacia decurrens*, which originally was imported from Australia as a shade tree for large plantations of coffee, tea, indigo and quinine in the 1800's. The semi-wooded ravines and gullies are dominated by dense thickets of bamboo, "glonggong" (*Thysanolaena maxima*) and woody shrubs. Ferns and bryophytes also abound in moist shaded areas in ravines, and some exposed slopes are covered in "alang-alang" (*Imperata cylindrica*) grassland. These deep ravines form natural boundaries between many of the ne-

ighboring villages.

## MATERIALS AND METHODS

### TRAPPING MAMMALIAN HOSTS.

Populations of terrestrial small mammals are sampled with live-traps (21 x 12 x 10 centimeters) that are equipped with spring-loaded doors. A small ear of corn is used for bait, and the traps are examined for captures early each morning. Three systems of sampling are utilized: monthly trapping on a "mark-and-release" grid in the Samiran-Jarakan area; bimonthly trapping in houses and fields at 20 permanent research sites; and semiannual trapping in the houses of 60 subvillages in and near the Boyolali plague zone. Approximately 87,350 trap-nights (one trap set for one night) of sampling effort were accumulated during the first year of the project, 41,350 in houses and 46,000 in Fields.

Two types of studies are carried out simultaneously: removal studies, in which all trapped mammals are killed and processed in the laboratory; and mark-and-release studies, in which all trapped mammals are processed alive in the field, and then released at the original site of capture.

**Trapping in Houses** — Four traps are placed in each house that is sampled and are set for three consecutive nights. This results in three trapstation-nights (12 trap-nights) per house in each trapping session. Twenty houses are sampled in each of ten subvillages chosen as permanent research sites, but all of the houses are sampled in each of the 60 subvillages that are trapped on a semiannual basis.

**Trapping in Field Environs** — In peridomestic and sylvatic environs, two parallel lines of trapstations, each marked by a stake with a numbered tag, are established in selected habitats. Two live-traps are placed at each station and are checked for three consecutive nights. Approximate distances of 15 to 10 meters are maintained between trapstations and between lines of trapstations. Two longitudinal lines of 25 to 50 trapstations are used at the ten permanent

field research sites, resulting in 150 to 300 trapstation-nights (300 to 600 trap-nights) in each trapping session.

**Mark-and-Release Trapping** — In the mark-and-release studies, for (rather than two) longitudinal lines of trapstations were established as described above. These lines are approximately one kilometer in length and transect all major habitats in the area, including two subvillages. During the first three nights (*Precensus Period*), two traps are placed at each *odd-numbered* station. In order to interrupt patterns of trapvisitation by individual rodents, and expose the traps to more individuals in the population, all traps are moved to the *even-numbered* stations during the second three nights (*Census Period*). Thus, during each monthly trapping session, the traps are checked for six consecutive nights, resulting in 675 trapstation-nights (1350 trap-nights) in the fields and 126 trapstation-nights (504 trap-nights) in houses. Upon first capture, each individual animal is marked with its individual number by two amputation and ear puncture (Fig. III) and later is released at the exact site of capture.

### PROCESSING.

Each morning of sampling, traps containing captured animals are properly labeled, placed separately in tightly secured cloth bags to prevent loss of ectoparasites, and transported either to a field station at Gebyok (mark-and-release studies) or to the Boyolali Plague Laboratory (removal studies) for processing.

**Ectoparasites** — In sequence, each cloth bag containing the trap and captured mammal is placed in a deep enamel bucket containing a large piece of ether-soaked cotton. After sufficient time has elapsed to allow the host (and most of the fleas) to become anesthetized, the mammal is placed in a deep enamel pan and thoroughly examined for ectoparasites. Each individual is brushed along the grain of the fur, then against the grain, then once more

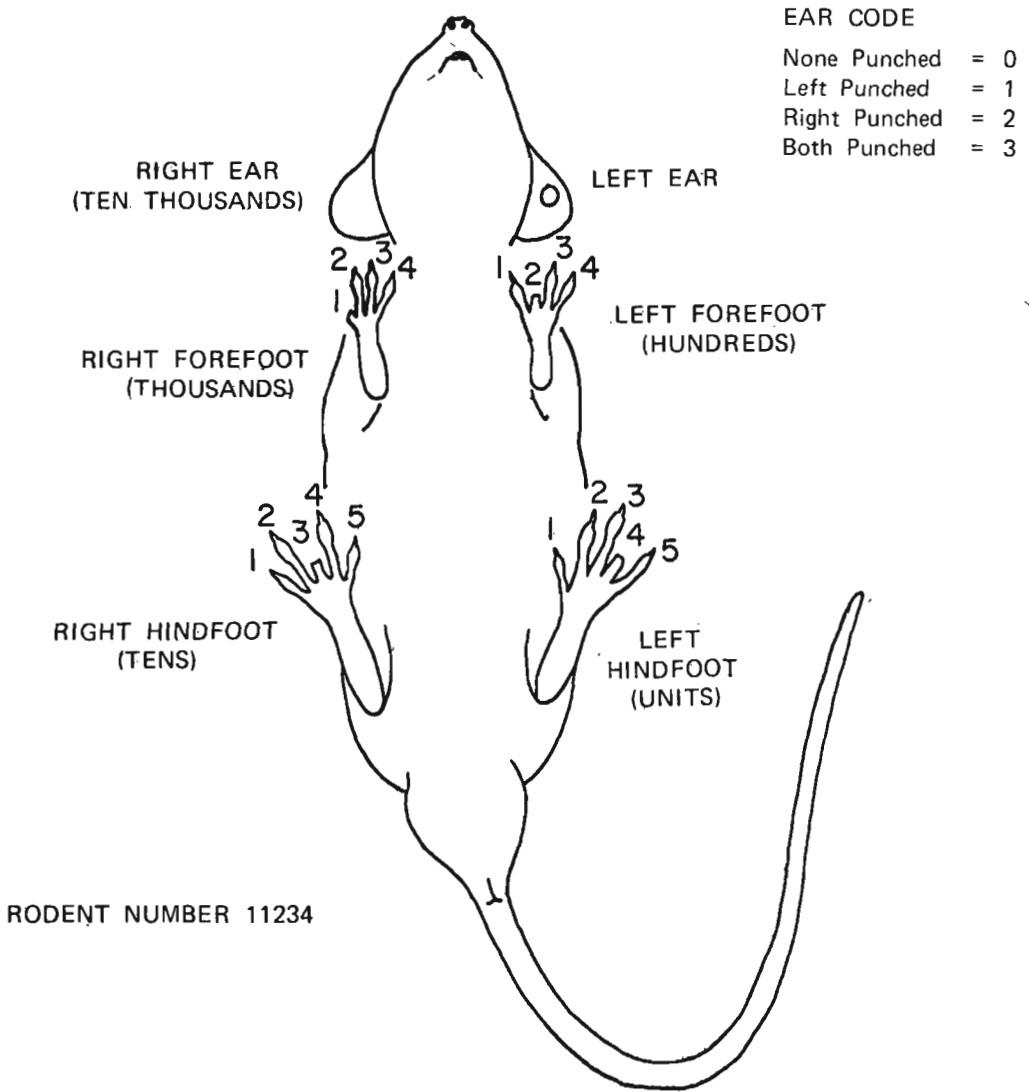


Fig. III. Numbering system for marked and released rodents.

along the grain in effort to dislodge ectoparasites from beneath the dense pelage. The anesthetizing bucket, trap and cloth bag (especially all seams) also are examined closely for extoparasites. Fleas obtained in this manner usually are placed in a properly labeled vial of two percent saline solution, but a reference sample also is preserved in 70 per cent alcohol and forwarded to a specialist (Dr. Robert Traub, University of Maryland) for confirmation of the identifications.

**Blood Samples** — After each mammal is examined for ectoparasites, the chest region is swabbed with 70 per cent alcohol and a blood sample (two to five cubic centimeters) is taken by cardiac puncture.

Blood samples are refrigerated overnight, then spun in a centrifuge. The formed elements are discarded and the sera are forwarded to the Yogyakarta Public Health Laboratory for serological examination (passive haemagglutination

test for the presence of plague antibodies).

**Pooling—test** — After being bled, the mammals are segregated by date and site of capture. The spleens of ten to twelve individuals of the same species are pooled together, macerated in sterile saline, and inoculated into two white laboratory mice. Fleas removed from those mammals included together in the same spleen-pool are separated by species, macerated in sterile saline, and inoculated into two more white laboratory mice.

Inoculated experimental animals are observed for morbidity or mortality twice daily for a two-week period. Symptomatic experimental animals are sacrificed and their spleens are subpassed into two more white mice.

Subpassed experimental animals are observed twice daily for three weeks.

If symptoms continue, the spleens of these animals are subpassed into two more white mice and a guinea pig. The organs (lungs, liver, spleen and anu buboes present) of these latter experimental animals are macerated in sterile saline and forwarded to the Yogyakarta Public Health Laboratory (in Cary-Blair transport media) for bacteriological examination. Approximately 2500 pools and subpasses, of which 1.5 per cent were plague-suspect, were completed during the first year.

**Mammalian host data** — All specimens captured alive in the monthly mark-and-release study are categorized as to sex (based on external genitalia) and age (based on the stage of molt and general body dimensions measured in millimeters: *total length* from the tip of the nose to the tip of the tail, excluding hairs; *length of the tail* from the base of the tail bent at a right angle from the body to the tip of the tail, excluding hairs; *length of the hindfoot* from the tip of the heel to the tip of the longest claw; *length of the ear* from the bottom of the notch, along the greatest distance, to the margin; and *weight* to the nearest 0.1 gram), and are examined for external reproductive data, prior to being released. Abdominal or scrotal position of the testes are recorded for males, and condition of the mammary glands (small, pendulous, or lactating) and vulva (perforate, closed with

spermatic plug, or closed with membrane) are observed in females, which also are examined for the presence of large embryos by palpation of the abdominal region.

Similar external reproductive data are recorded from specimens captured in removal studies. In addition, following preliminary processing (removal of ectoparasites, withdrawal of a cardiac blood sample, measurement of external body dimensions, completion of a general autopsy and splenectomy), the specimens are further dissected to obtain supplementary reproductive data. The testes of males are weighed (to the nearest 0.1 gram), the length and width are measured (to the nearest millimeter), and a smear of the caudal epididymus is examined microscopically for the presence or absence of sperm. The reproductive tract of females is examined for the number of pigmented uterine swellings (indicating recent implantation), number of embryos, and number of placental scars (in those females that already have given birth to young). The crown-rump length of all well-developed embryos (not undergoing tissue lysis and degeneration) is recorded, and "new placental scars" (dark pigmentation and plentiful blood supply at implantation site) are differentiated from "old placental scars" (fainter pigmentation and lack of blood supply at implantation site). Reproductive tracts of all pregnant females are weighed, and the respective body weights of these females are adjusted by subtraction of the tract weight.

**Environmental parameters.** — Five weather stations, each equipped with a humidity gauge, maximum-minimum thermometer and rain gauge, have been established at different elevations in the research area (Fig. II). Each week, a recording hydrothermograph is moved to the active site of trapping. Representative samples of soils and predominant plants are collected in each major habitat. In addition, the annual crop-cycle in cultivated areas also is carefully recorded.

**Data processing.** — All data are recorded on precoded data sheets, and later the data from these sheets are punched on IBM cards in

Jakarta. The IBM cards are forwarded to WHO Headquarters in Geneva, Switzerland for processing. In the final analysis, attempts will be made to utilize certain computer mapping and analytic programs developed by, or adapted by, the Vector Biology and Control Unit and Strengthening of Health Services Division of WHO.

## ECOLOGY OF MAMMALIAN HOSTS.

### Ecological Distribution

Ten species of mammals (Table 1) that may serve as potential reservoirs or amplifying agents for plague were collected during the first year of study in the Boyolali Regency. The ecological and altitudinal distributions of these mammals are depicted in Fig. II and 5. There species, *R. argentiventer*, *Chiropodomys gliroides*, and *Bandicota indica* are quite rare in the Boyolali plague zone, and do not merit further comment at this time.

*Field Species*: those mammals that usually do not live within the confines of human domiciles, although they may take up temporary residence from time to time :

*Peridomestic Species*: those mammals that live near man, in cultivated fields and adjacent habitats that have been modified by the activities of man. These species consume agricultural produce and may enter houses, but generally do not remain and nest therein (e.g. *R. exulans*, *R. argentiventer*, *R. tiomanicus*, *M. cervicolor*, and *C. notatus*).

*Sylvatic Species*: those mammals that live quite distant from human habitations, consuming native plant products, nesting in natural environs, and having little contact with man (e.g., *R. niviventer*, *R. tiomanicus*, *R. exulans* and *C. notatus*).

Table 1. Taxonomic names applicable to mammalian hosts in Central Java and corresponding designations used by past plague workers. Quotation marks indicate misidentifications.

Common Name	Taxonomic Name	Obsolete Taxonomic Names
House Rat	<i>Rattus rattus diardii</i>	<i>Mus rattus griseiventer</i> <i>Mus rattus diardii</i>
Polynesian Rat	<i>Rattus exulans</i>	<i>Mus concolor</i> , <i>Rattus concolor</i>
Malayan Wood Rat	<i>Rattus tiomanicus</i>	<i>Mus rattus refuscens</i> , <i>Rattus rattus roquei</i>
White-bellied Mountain Rat	<i>Rattus niviventer</i>	<i>Rattus rattus niviventer</i>
Ricefield	<i>Rattus argentiventer</i>	" <i>Mus rattus diardii</i> ," <i>Rattus rattus brevicaudatus</i> , <i>Rattus rattus argentiventer</i>
Greater Bandicoot	<i>Bandicota indica</i>	<i>Necokia setifera</i>
Fawn-colored Mouse	<i>Mus cervicolor</i>	" <i>Mus musculus</i> "
House Mouse	<i>Mus musculus</i>	-----
Pencil-tailed Tree Mouse	<i>Chiropodomys gliroides</i>	-----
Plantain Squirrel	<i>Callosciurus notatus</i>	-----
House Shrew	<i>Suncus murinus</i>	<i>Pachyura murina</i> , <i>Suncus indicus</i>

The ecological distribution of small mammals in the research area can be classified according to their relationship to man:

*Domestic Species*: those mammals that live with man in houses, nesting there and consuming human food supplies (e.g., *R.r. diardii*, and *S. murinus*).

Some authors argue against using the term "sylvatic" because, in the most restricted sense, it means "belonging to forests." However, Caius Plinius Secundus (Pliny, the Elder) used this term to designate "wild animals" in his *Naturalis Historia*, published in the First Century A.D. (Baltazard, 1966). Thus, the term has a long



history of common use in epidemiological and ecological literature, and creates difficulty only for those purists who favor semantic arguments.

It must be borne in mind that small mammals do not always adhere to man-made systems of classification. Although domestic species rarely are encountered in peridomestic and sylvatic habitats in Central Java, peridomestic species often frequent domestic and sylvatic environs, and sylvatic species frequently occur in peridomestic habitats and occasionally invade houses. Thus, the above described ecological categories are not mutually exclusive.

**Domestic Species:** — Two kinds of small mammals in Central Java can be classified as being domestic in habit. All of the 23 specimens of *S. murinus* (which is an insectivore rather than a rodent) obtained in the first 12 months of study were trapped within human habitations, at elevations up to 1500 meters. However, this species is much more common at elevations

below 1000 meters, explaining its rarity in our collections. Approximately 99.2 per cent of 2614 *R. r. diardii* also were captured in human domiciles. The latter species occasionally is encountered in field environs (0.7 per cent in cropland, 0.1 per cent in ravines, and less than 0.1 per cent in woodlands), but these occurrences probably represent transient movement through these areas rather than actual habitation.

**Peridomestic Species:** — Fairly high population densities of *R. exulans* occur in the cultivated fields surrounding human habitations, however, this rodent also appears to range through all other available habitats in the region (Fig. IV). Of 1113 Polynesian Rats captured in the first year of investigation, 46.4 per cent were from cropland, 22.0 per cent from houses, 16.1 per cent from woodland, 5.3 per cent from bamboo and "glonggong" thickets, 4.3 per cent from Shurbland, 3.4 per cent from grass and herbland, and 2.5 per cent from ravines.

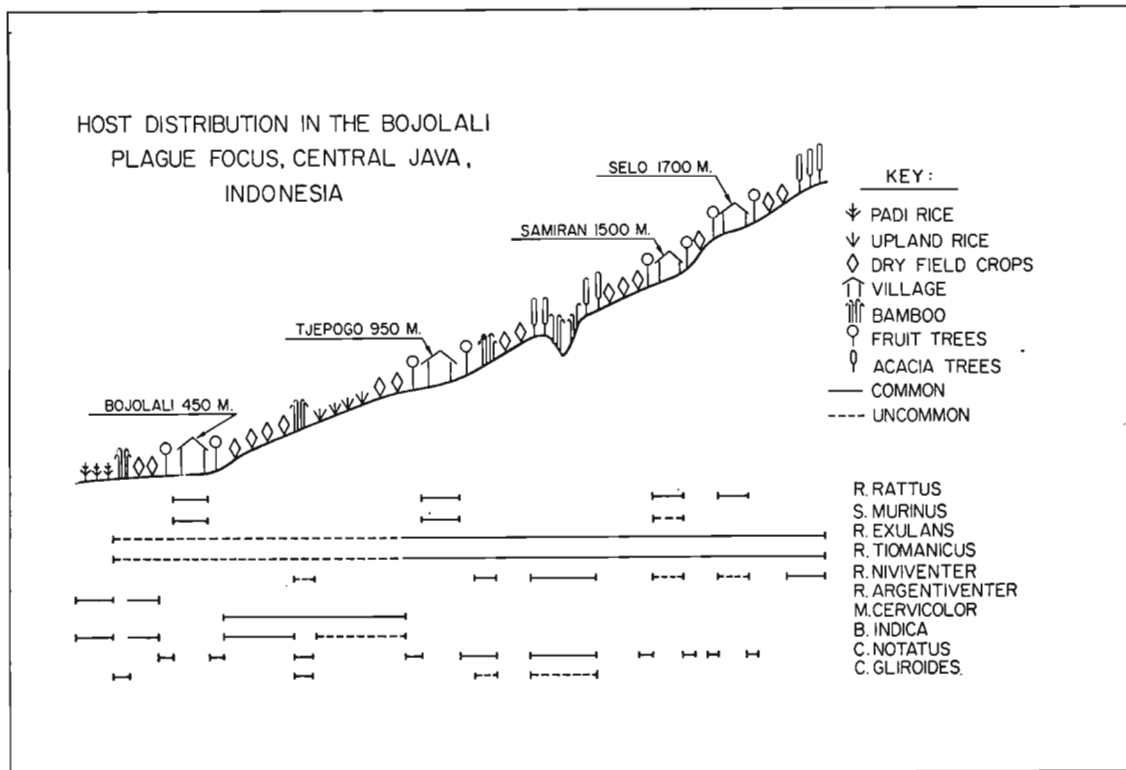


Fig. IV. Host distribution in the Boyolali plague focus, Central Java.

HOST DISTRIBUTION

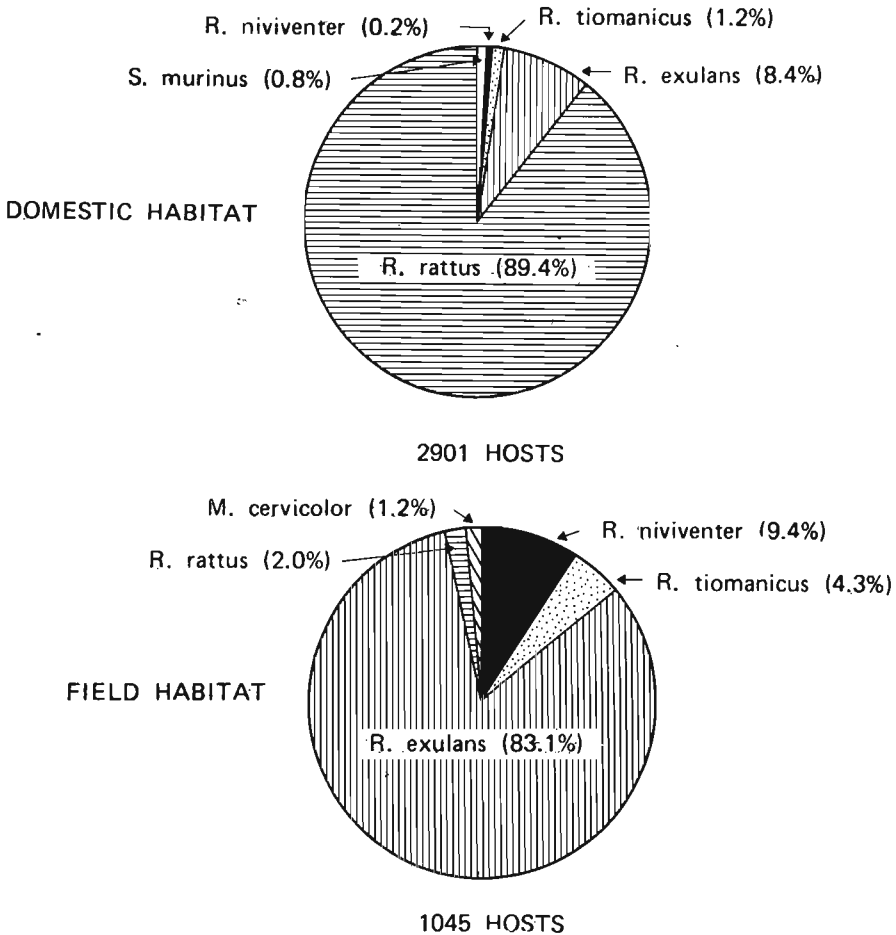


Fig. V Habitat distribution of mammalian hosts.

This species is less common at elevation below 1000 meters and comparatively rare in wet rice paddies and sugarcane fields. Although generally considered to be sylvatic in distribution, *R. tiomanicus* appears to be a peridomestic species in Central Java, with 43.8 per cent of 80 specimens being from human domiciles, 17.5 per cent from bamboo thickets bordering cropland. In more remote areas, 23.8 per cent of the total specimens were from ravines, 6.2 per cent from acacia woodlands, and 1.2 per cent from shrubland on upper volcanic slopes. Another rather uncommon peridomestic species *M. cervicolor*, has been captured in dryfield croplands below 1000 meters. Of the 13 specimens collect-

ed, none were from houses. *C. notatus* occurs in great numbers among coconut and other fruit trees in villages, but also inhabits bamboo thickets and semi-wooden ravines in sylvatic environments. It should be noted that members of the squirrel family (Sciuridae) serve as primary reservoirs of plague in the southwestern United States. The potential role of the Plantain Squirrel in the plague infectious cycle in Central Java has not been investigated previously. Only one of 40 specimens has been collected within a house thus far.

**Sylvatic Species.** — The White-bellied Mountain Rat may be considered as sylvatic in distribution. This species resides mainly in deep

gullies and steep ravines (58.2 per cent of 103 specimens) that dissect the area, but occasionally is captured in sylvatic shrubland (15.5 per cent), cropland (7.8 per cent), bamboo-bordered terraces (7.8 per cent) and in open disturbed woodlands (5.8 per cent) on the upper volcanic slopes. Only 4.9 per cent of the *R. niviventer* captured were from houses. Populations of *R. exulans* and *R. tiomanicus* also occur in sylvatic environs.

#### Reproduction of *Rattus exulans* :

Adult mammals exposed to plague either resist initial infection, resist the disease once infected (perhaps becoming immune to future infection or serving as reservoirs), or succumb to the affliction. Because the transmission cycle requires a source of susceptible individuals, the rates of recruitment and overall population turnover of potential host and reservoir species is of crucial importance to propagation of rodent-borne zoonoses. Temperate zone species usually have fairly predictable breeding periods, with subsequent seasonal increases in population density and dispersal of young. In equatorial zones, some mammals may breed throughout the year, resulting in rather stable population, whereas other species may have seasonal peaks in reproduction, with consequential population fluctuations and seasonal variability in the production of young susceptible animals available for infection by the plague bacillus. It is possible that the enzootic phase could become epizootic at such times. In addition, little is known concerning the comparative reproductive cycles and life histories of different host species in Indonesia.

In order to obtain information concerning the seasonal aspects of host reproduction in the Boyolali plague zone, population of the respective species are sampled throughout the year. Unfortunately, the copious reproductive data accumulated thus far for *R. r. diardii*, *R. tiomanicus*, and *R. niviventer* have not been analysed as yet, and the following discourse will be limited to *R. exulans*.

**Reproductive characteristics.** — Various reproductive parameters have been described for wild-captured *R. exulans* from Malaysia (Harrison, 1951, 1955, and 1956), Hawaii (Ta-

marin and Malecha, 1971, 1972; Wirtz, 1973), and Ponape Island (Jackson, 1962; Jackson and Barbehenn, 1962), and Egoscue (1970) and Wirtz (1973) observed breeding of captive *R. exulans* in the laboratory. Female Polynesian Rats are polyestrous (capable of breeding many times each year), promiscuous (will breed with any available male, and often with several males), have a gestation period (time that the developing embryo is carried within the body of the female) of 19 to 23 days (Egoscue, 1970; Wirtz, 1973), and a breeding cycle that includes a post-partum estrous (females will mate again immediately after giving birth to young). Presence of nursing young may or may not have an effect on the length of the next following gestation period. Wirtz (1973) recorded a captive female that gave birth to a second litter 24 days after the first litter, whereas Egoscue (1970) noted that gestation in lactating females generally was prolonged from three to seven days. In the laboratory, females have an average lifetime reproductive potential of 12 months or less. However, a few individuals may reproduce for more than 24 months, with a maximum production of 18 litters (Egoscue, 1970).

**Sex ratio.** — The over-all sex ratio (annex) of *R. exulans* captured in the Boyolali Regency during the first year was approximately equal, with 102 males captured for every 100 females. However, an apparent excess of males was encountered from November through February during a general period of reduced reproductivity (Fig. VI and Table 2). Apparent excesses of females were encountered in August, October and March, but no obvious pattern was suggested. It should be noted that very few *R. exulans* were captured in October, and the resulting small sample size may have biased the representative data for that month.

Differential growth, mortality, or catchability may influence the observed sex ratios. Greater captures of males generally is attributed to larger home ranges and greater trap exposure, as compared to females. More information on this phenomenon will be available at a later date when the accumulated movement data obtained

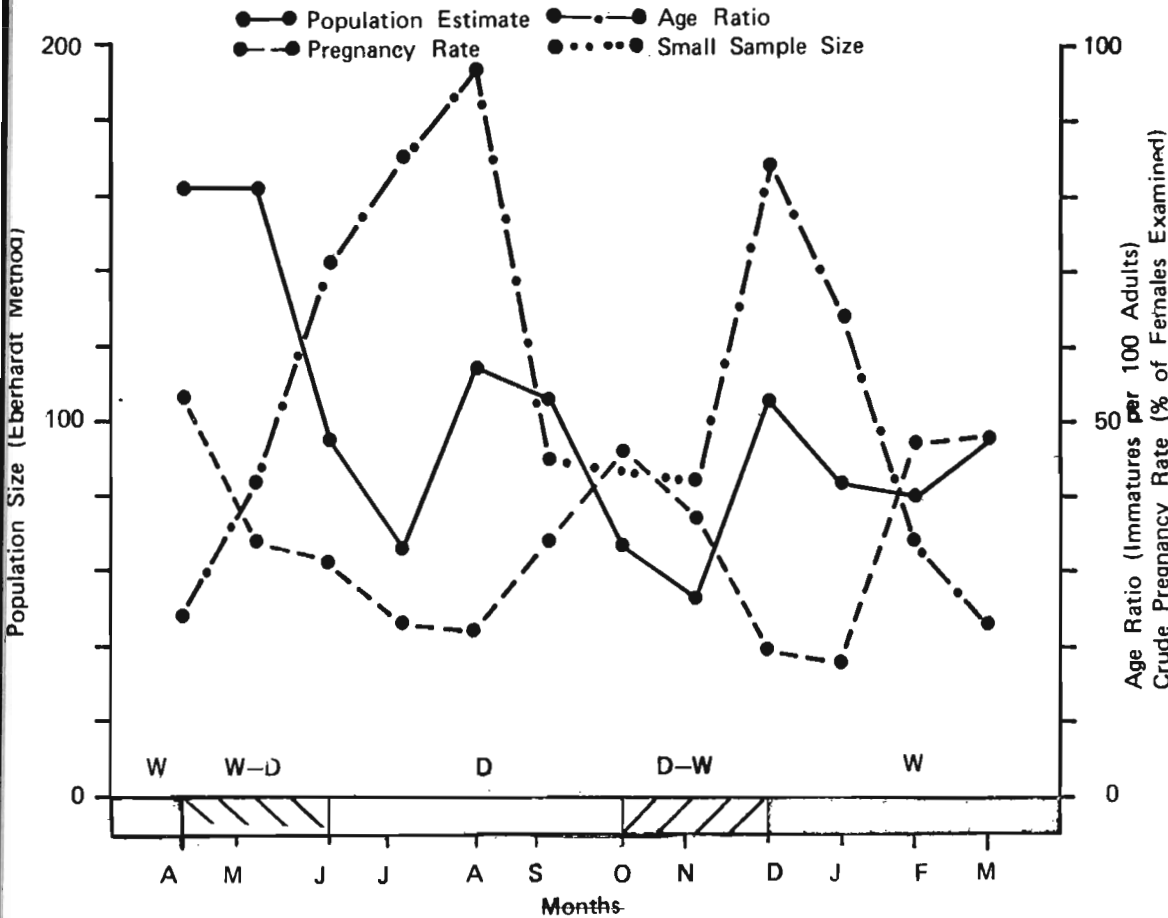


Fig. VI. Seasonal variation in population paramaters of *R. exulans* in Central Java (1972-1973).

in the ongoing mark-and-release studies are analysed.

**Age of sexual maturity.** — The overall age ratio of *R. exulans* in the plague zone in the first year averaged 51 immatures (juveniles and subadults) per 100 adults captured. Above average age ratios were encountered from June

through August, in October (perhaps due to small sample size) and in December and January. The time lapse between birth and effective entry of young into the trapable population was one to two months after peaks in reproduction (Fig. VI). The young generally are weaned (leave the nest) in the third or fourth week of life and

Table 2. Reproductive condition of 398 female *Rattus exulans*.

Reproductive Condition of Females	Percentage of females examined												
	1972												1973
	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Average
Single litter	63	30	48	32	33	48	59	50	35	23	44	53	43.2
Multiple litters	15	40	38	22	23	32	12	29	25	17	20	33	25.5
Reproductive	78	70	86	54	56	80	71	79	60	40	64	86	68.7
Non-reproductive	22	30	14	46	44	20	29	21	40	60	36	14	31.3
Sample Size	27	46	21	50	18	54	17	28	20	43	25	49	33.2

complete the postjuvenile molt (become subadults) at 60 to 66 days of age (Wirtz, 1973). However, due to small size, young that have recently abandoned the nest may still elude capture by escaping through the mesh of the trap.

The weight or body length (excluding the tail) at which 50 per cent of the animals examined possess a given characteristic is a common technique used to estimate onset of sexual maturity. This parameter has been estimated variously for parous (reproducing) female *R. exulans* at 22.9 grams (Harrison, 1951), 39.2 grams (Tamarin and Malecha, 1972) and 43 grams and 116 millimeters (Jackson and Barbehenn, 1962). In the present study, the mean weight and mean body length of 167 primiparous females (those with their first litter) were 40 grams and 122 millimeters, respectively.

Based on these morphological criteria, 71.4 per cent of all females captured were classified as sexually mature. It should be noted that functional maturity may precede morphological maturity. For example, 19.1 per cent of the reproductive female *R. exulans* (i.e., pregnant or evincing new placental scars) trapped in the Boyolali Regency were below average in weight and body length, and the smallest pregnant female encountered weighed only 26 grams and was only 102 millimeters in body length. In the laboratory, females of this species (Ponape colony) conceived at 49 days of age and gave birth at 72 days, whereas the oldest female to produce a litter was 782 days or 2.2 years old (Egoscue, 1970). In contrast, Wirtz (1973) noted that captive females (Kure Atoll, Hawaii colony) gave birth to their first litters between the 17 and 30th weeks (85 to 210 days).

Sexual maturity for male *R. exulans*, based on the presence of sperm in the caudal epididymus, has been estimated at 22.2 grams (Harrison, 1951), 36.6 grams (Tamarin and Melecha, 1972), 43 grams and 115 millimeters in body length (Jackson and Barbehenn, 1962) and 63 to 90 days of age (Wirtz, 1973). Because the examination of epididymal smears was initiated only recently in the present study, estimati-

on of sexual maturity of male Polynesian Rats in Central Java has not been attempted as yet.

**Seasonality.** — *R. exulans* in the Boyolali Regency breed throughout the year, but seasonal peaks in reproductive activity are attained from February through April and from September through November (Fig. VI and Table 2). May through August, and December and January are characterized by reduced reproductivity. In general, reproduction seems to follow a variable two to four month cycle. Although reproductive peaks occur in both the wet season and the dry season, that in the former period is of greater magnitude due to the higher population densities and greater availability of parous females for production of young. Of 398 females examined in the first year, 43.2 per cent had given birth to a single litter, 25.5 per cent had given birth to multiple litters, and 31.3 per cent showed no signs of reproductive activity.

**Rates of Reproduction 15.** — The reproductive potential can be estimated as the number of young produced: per 100 females of greater than nestling age (i.e., those that have been weaned and abandoned the nest, hence are exposed to traps), per 100 adult females, or per 100 rats (i.e., of both sexes and of greater than nestling age) in the population sampled. Because the transmission of a rodent-borne zoonoses is a population phenomenon, the latter estimate is of greatest importance in epidemiological studies. In order to calculate the overall rates of reproduction, several kinds of information and a series of computations are necessary (see Table 3).

In examining the results of other authors (Table 4), estimates ranging from 29 to 60 young produced per 100 rats in a population are noted. It is apparent that such estimations may vastly understate potential rates of recruitment of young into the adult population. If a population is to remain stable (neither increase nor decrease), then every 100 rats would have to produce 100 young in order to replace themselves. A reproduction rate of 29 young per 100 rats (Ponape Island) would mean that the population is

Table 3. Definition and calculation of reproductive parameters.

- Sex Ratio: The number of males per female (number of males, divided by number of females).
- Combined Sex Ratio: The sex ratio, plus 1.00 (for example, 97 males per 100 females, expresses as 1.97).
- Embryo Number: The average number of embryos per litter (total number of embryos, divided by either the number of pregnant females, or the number of litters produced by these pregnant females).
- Rate of Pregnancy: The proportion of females in the population that are pregnant:
- Crude Pregnancy Rate: Number of pregnant females, divided by the total number of females captured (i.e., of greater than nestling age).
- Adjusted Pregnancy Rate: Number of pregnant females, divided by the number of sexually mature (i.e., adult) females.
- Corrected Pregnancy Rate: Because in rodents of the genus *Rattus*, implantation of the new embryo does not occur until the sixth or seventh day of pregnancy (thus, pregnancy is not visible to the observer until this time), the actual number of pregnancies is underestimated. In order to allow for invisible pregnancies in *R. exulans*, the observed pregnancy rate is multiplied by a correction factor of 1.3. This factor is derived by dividing 23 days (average length of the gestation period), by 17 days (average length of visible pregnancy).
- Embryo Rate: Average number of embryos produced by 100 females:
- Crude Embryo Rate: Per 100 females of greater than nestling age (Embryo Number, multiplied by Crude Pregnancy Rate).
- Adjusted Embryo Rate: Per 100 sexually mature females (Embryo Number, multiplied by Adjusted Pregnancy Rate).
- Rate of Reproduction: Average number of embryos produced by 100 rats (of both sexes) in a population:
- Crude Rate of Reproduction: Per 100 rats of greater than nestling age (Crude Embryo Rate, divided by Combined Sex Ratio).
- Adjusted Rate of Reproduction: Per 100 sexually mature rats (Adjusted Embryo Rate, divided by Combined Sex Ratio).
- Incidence of Pregnancy: Estimated number of litters (i.e., of pregnancies per parous female each year (Pregnancy Rate, expressed as a decimal, multiplied by the Potential Number of Litters that can be produced in one year). Potential Number of Litters for *R. exulans* is obtained by dividing the length of a year (365 days), by the average length of gestation (23 days), which equals 16:
- Crude Incidence of Pregnancy: Per female of greater than nestling age (Crude Pregnancy Rate, multiplied by 16).
- Adjusted Incidence of Pregnancy: Per sexually mature female (Adjusted Pregnancy Rate, multiplied by 16).
- Annual Production: Estimated average number of young produced per parous female each year (Embryo Number, multiplied by Incidence of Pregnancy).
- Crude Annual Production: Per parous female of greater than nestling age (Embryo Number, multiplied by Crude Incidence of Pregnancy).
- Adjusted Annual Production: Per parous adult female (Embryo Number multiplied by Adjusted Incidence of Pregnancy).

rapidly declining to the point of extinction, unless there is a compensating increase in the longevity of adult rats. Rodents generally form the major base of a vertebrate food chain in a natural ecosystem, meaning that they are subject to intense predation by carnivorous mammals, snakes, owls and hawks. In addition, high mortality is caused by diseases (such as plague), parasites, inter-specific and intra-specific competition, adverse climatic conditions and control programs instigated by man. In short, in order for any rodent population to avoid extinction, every 100 individuals in the population must produce more than 100 young to allow for these mortality factors. Any system of computation involving a polyestrous species that is based solely on observation of pregnant females in the field at one point in time continuously will underestimate rates of reproduction.

When examining the reproductive tracts of female rats, new placental scars are readily discernable from old placental scars. Because females with new placental scars recently have given birth to a single litter (generally within a few days to several weeks) and generally still are nursing young, they also should be considered

as reproductive members of the population at time of sampling. In addition, grouping reproductive data into monthly intervals, rather than by weekly intervals, makes dubious post-dating of past litters unnecessary. In the present paper, pregnant females and lactating females with new placental scars are treated together and termed "reproductives" (Table 4).

Reproductive data based on placental scar criteria generally are judged as being unreliable (Davis and Emlen, 1948). Because it is difficult to accurately estimate average litter sizes from old placental scars, which may represent from two to five litters over a relatively long period of time, because little is known of the duration of old placental scars, or of the temporal spacing between the represented litters, and because females with old placental scars may not be reproductive at time of sampling, these individuals were excluded from consideration. One potential source of error when including females with new placental scars in the reproductive sample is that scars may result even though the embryos are resorbed, and thus may not represent actual birth of young. In the present study, it was found that estimated litter sizes based

Table 4. Comparative reproductive data for *Rattus exulans*. Raw data from either authors were modified for direct comparison by analysing them in the same manner as the Boyolali data (see Table 3). Boyolali data are presented both in terms of pregnant and "reproductive" females (either pregnant or evincing new placental scars).

Locality	Source	Males	Females	Comb* Sex Ratio	Embryo* Number	Crude* Preg. Rate	Correct.* Preg. Rate	Crude* Embr. Rate (per 100 fem.)	Crude* Répr. Rate (per 100 rats)	Crude* Inc. Preg. (per par. fem.)	Crude* Ann. Prod. (per par. fem.)
Malaya	Harrison (1951)	182	155	2.17	4.2	23.9	31.1	130.6	60.2	5.0	21.0
Hawaii	Tamarin and Malecha (1972)	43	45	1.96	4.0	20.0	26.0	104.0	53.1	4.2	16.8
Ponape Is.	Jackson (1962)	1092	1114	1.98	2.5	17.7	23.0	57.5	29.0	3.7	9.3
Boyolali	Pregnant Females	557	545	2.02	4.7	26.1	33.9	159.3	78.9	5 †	25.4
Boyolali	"Reproduc- tive" Females	557	545	2.02	4.7	47.7	55.5	260.8	129.1	8.9	41.8

on new placental scars averaged 15.9 per cent greater than those based on live embryo counts. Using data from Tamarin and Melecha (1972) for *R. exulans* in Hawaii, a similar 15.8 per cent difference is found between live embryo counts and estimations from multiparous females (those that have produced more than one litter).

Harrison (1951, 1956) estimated intra-uterine mortality (death of embryos before birth) for *R. exulans* in Malaya at 16 per cent, and Jackson (1962) calculated this parameter as 19 per cent for Polynesian Rats on Ponape Island. Thus, based on differences between live embryo counts and number of new placental scars, an intra-uterine mortality of about 16 per cent is suggested for *R. exulans* in Central Java, and litter sizes estimated from new placental scars were reduced accordingly by this factor prior to analysis.

It is thought by the present authors that exclusion of lactating females with new placental scars from the sample of reproductive members of the population incurs greater error than does their inclusion. Reproduction rates computed from "reproductives" rather than from only pregnant females, agree much more closely with accepted concepts of population dynamics (Table 4). Accordingly, the production of the number of young per 100 individuals in the population in Central Java in 1972-1973 fell below the critical level of 100 only during December and January. Female *R. exulans* in the Boyolali Regency were estimated to produce a maximum of 5.4 (based on pregnant individuals) to 8.9 (based on reproductive individuals) litters per year, meaning an estimated 25.4 to 41.8 young per parous female each year. In the laboratory, females of this species produced from one to thirteen litters (a maximum of about 50 young) annually, averaging 5.2 litters (Egoscue, 1970).

#### Population Dynamics of *Rattus exulans* :

Assuming that the progression of plague during an epizootic is enhanced by temporary linkages between elements of the transmission cycle, then the spread of infection may be directly proportional to the rates of contact between susceptible mammalian hosts and infec-

tious siphonapteran vectors. It would be expected that transmission would be fairly rapid among dense host populations, but would be more gradual and discontinuous among sparse populations. Thus, risk of infection may vary from habitat to habitat, from season to season, or from year to year, due to fluctuations in host densities.

A population is a grouping of individuals of the same species, and the population size of any particular species at a given point in time is the result of three main interacting forces : natality (reproductive potential), mortality (death rate), migrality (mobility). As a consequence of these forces, populations are in a constant state of flux. Even through the overall density may remain relatively stable, new individuals continually enter the population and old individuals perpetually disappear. Thus, new complexes of individuals constantly are being formed and the subsequent rate of population turnover and resultant recruitment of susceptible individuals is of considerable importance in epidemiological studies of rodent-borne zoonoses.

**Population Densities.** — When any area is sampled by trapping, only a certain proportion of the actual population is captured. Calculation of population densities based solely on raw capture data invariably under-estimates the real population, which also includes those individuals that escaped capture. Behavior of individual rodents also is a factor in Sampling (see "Per cent of Individuals Recaptured" in Table 5).

Some individuals in mark-and-release studies may be trapped on several successive nights, whereas other individuals may be captured at the same trapstation after a lapse of three to five months. One of the most fundamental principles underlying reliable estimations of host density is that sampling must be done in a uniform manner. Otherwise comparison of densities between collection sites, seasons, and years is meaningless.

Methods of population estimation used to obtain a more realistic enumeration of the rodents inhabiting the study area are listed below:



Table 5. Capture and recapture success, and known mortality (individuals dead in trap, or killed in processing) of four species of mammals trapped in the Samiran-Jarakan mark-and-release studies in the Boyolali Regency, Central Java, Indonesia (April, 1972-June, 1973).

Mammalian Species	No. Ind.	No. Total Capt.	Ind. Known Mort.	Percent Known Mort.	Ist. Capt. Mort.	No. Ind. Recapt.	No. Ind. Releases.	Percent Ind. Recapt.	Average Capt. Per Total Ind.	Average Capt. Per Recapt. Ind.
	<i>Rattus exulans</i>	509	1144	111	21.8	56	271	453	59.8	2.25
<i>Rattus rattus</i>	175	197	22	12.6	21	19	154	12.3	1.13	2.16
<i>Rattus tiomanicus</i>	16	26	3	18.8	2	6	14	42.9	1.63	2.67
<i>Rattus niviventer</i>	10	22	1	10.0	0	5	10	50.0	2.20	3.40
Totals or Averages	710	1389	137	19.3	79	301	631	47.7	1.96	3.26

### Mark-and-Release Studies:

$$\text{Lincoln Index: Density} = \frac{Tn}{t}$$

T = individuals captured and released in the Precensus Period

n = individuals captured in the Census Period

t = mutual individuals captured in both the Precensus and Census Periods.

$$\text{Eberhardt Method: Density} = \frac{(n_1 + 2n_2)(n_1 + n_2)}{2n_2}$$

$n_1$  = individuals captured in the Precensus Period

$n_2$  = individuals captured in the Census Period

**Known Extant Individuals:** the number of individuals known to be alive, based on recaptured in subsequent trapping sessions.

For example, if a rodent is captured in April and August, then it also must have been alive in May, June and July, and therefore is added to the totals for these months, even though it was not captured then.

**Removal Studies:** Because different numbers of trapstations are used in different areas, the raw numbers of captures are not comparable, unless they are divided by the amount of *collection effort* used to obtain these specimens. The resultant estimates are relative and may be expressed as: Number of captures per 100 trapstation-nights; Number of captures per 100 trap-nights.

Field populations of *R. exulans* in the

mark-and-release study area seemed to follow a variable three to five month cycle, with maximum densities occurring in April and May, but with lesser peaks also occurring in August and September, and in December (Fig. VI). Decreasing population levels were encountered in June and July, and in October and November, and intermediate densities were maintained from January through March.

Population trends observed thus far in the second year of study generally follow those witnessed during the first year, except for a dramatic increase in density in July, presumably due to a prolonged wet season.

Variability in population densities was encountered at the other field sites sampled during removal studies (Fig. VII). For example, low densities, similar to those observed in the mark-and-release studies, generally occurred during the dry season; however, with the exception of Plalangan, the August-September peak was lacking. Also, the April-May high densities witnessed in other areas was not evident at Selo. Nonetheless, average trends were as previously described.

**Population turnover.** — In the first year of the mark-and-release studies, 383 *R. exulans* were captured 826 times, the number of captures varying from one to eleven. Each group of individuals first observed in one trapping session were followed through subsequent trapping sessions (Fig. VIII). On the average, 43.0 per cent

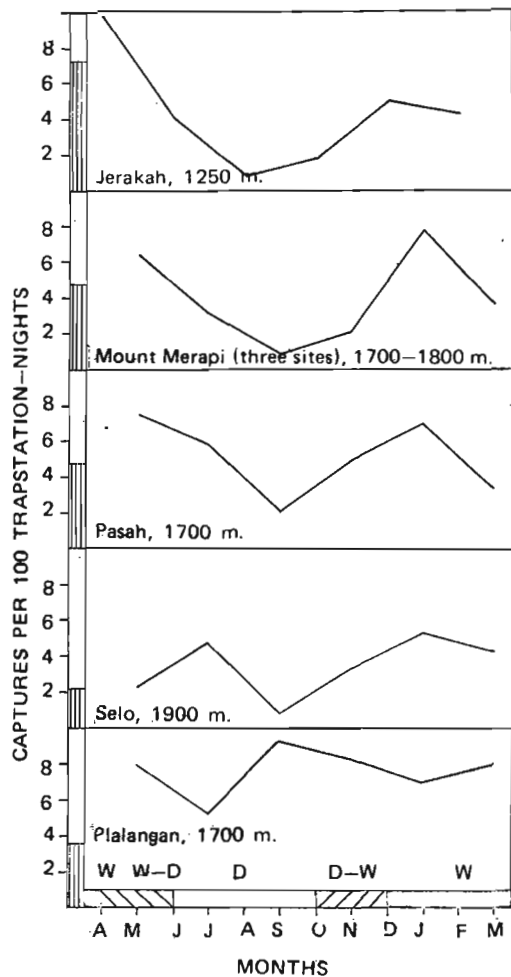


Fig. VII. Comparative capture success for *Rattus exulans* at seven field sites (1972-1973). The lefthand scale indicates the percentage of trapstations in cultivated (vertical lines) and non-cultivated (non-lined) areas.

of the marked individuals that were released (excluding known mortality) remained in the research area for at least one month, 22.9 per cent for at least two months, 13.9 per cent for at least three months, 6.7 per cent for at least four months, 3.5 per cent for at least five months, 2.2 per cent for at least six months, 1.6 per cent for at least seven months, and 0.6 per cent for at least eight months.

Thus, the composite population sampled during any one trapping session includes new individuals, and individuals from each of the previous three to five trapping sessions. Recent trapping (August, 1973) has revealed one individual (captured 16 times) that has remained in the population for twelve months. Harrison (1956) noted that mean survival of marked *R. exulans* in Malaysia was 3.2 months, with maximal observed survival being nine months. The observed low survival rate of *R. exulans* is balanced by a high reproductive potential and obviously is not a disadvantage, as witnessed by the overall abundance of this species and its occurrence in all available habitats.

**Population Gain.** — Unmarked rodents are encountered in every trapping session (Fig. VIII). Capture of new immatures (subadults and juveniles) represent recruitment of presumably susceptible young into the host population, due to reproduction either on the research site, or in adjacent environs. On the other hand, collection of unmarked adults represents either immigration of individuals from nearby areas, or capture of resident individuals that formerly were trapshy.

**Population Loss.** — Approximately 39.4 per cent of the marked and released *R. exulans* were not recaptured, perhaps indicating avoidance of traps after the first capture, or emigration of these individuals from the research area after initial exposure to traps. Examination of recaptured rats indicates that toe amputation and ear puncture of marked individuals have little adverse effect. However, differential mortality between marked and unmarked individuals also may be a factor in increasing the rate of disappearance of rodents from the initial population. The actual rate of death in nature is a parameter that is nearly impossible to measure accurately, and the separate contributions of mortality and emigration to population loss also are rather difficult to evaluate. Accumulated information concerning dispersal and average range of movement will be analysed at a later date and may eventually provide an insight into emigration and immigration rates.

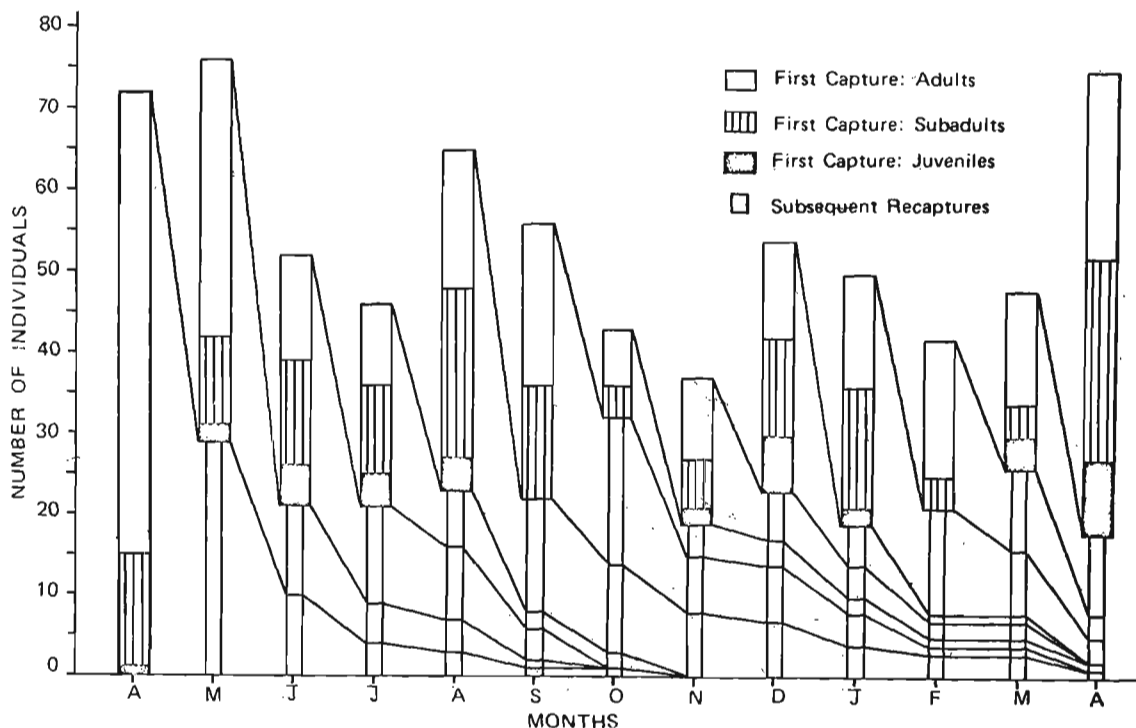


Fig. VIII. Population turnover and longevity of *Rattus exulans* based on recapture data (1972-1973).

#### Host Interaction With The Environment :

The *habitat* is the total sum of physical factors (climate, soils, topography, and so forth) that surrounds a given organism, whereas the *environment* includes both the habitat and the biological factors (competition, parasites, available food, and so forth) that effect the welfare of the individual. The reproductive potential of any rodent species greatly exceeds the capability of the environment to support the resulting numbers of individuals. The interaction of a species with its environment places a limit on the number of individuals that can survive under existing conditions at any given point in time. The forces that limit population size collectively are termed the *Environmental Resistance*, and include such diverse factors as adverse climate, presence of predators, parasites, or diseases, restriction of a valuable food supply, space or harborage, intense inter-specific and intra-specific competition, and control programs instigated by man. The number of individuals that can survive under any particular set of environmental conditions is termed the *Carrying Capacity* for that environment. Understanding of the various forms

of environmental resistance and the concept of carrying capacity is necessary in order to institute efficacious control measures against mammalian components of zoonotic cycles.

As seen in Fig. VI and VII, the carrying capacity of the environment in the plague zone changes seasonally. During the dry easterly monsoon, near arid conditions prevail throughout much of the cropland. In 1972, less than 20 millimeters of rain occurred from mid-July through October, and the vegetative cover dwindled to less than five per cent over much of the cultivated area. In addition, cloud formation in the mountainous zones is nearly nonexistent during the dry season, resulting in high temperatures, low relative humidities and intense solar radiation. Hence, lack of ground cover and harborage, decreased availability of food, and increased climatic stress, all tend to reduce the environmental carrying capacity during the dry season. Conversely, more equitable climatic conditions (at least in cropland) and intense cultivation during the wet westerly monsoon tend to increase the carrying capacity. For example, an

rodents would be concentrated mainly in restricted refugia (densely vegetated bamboo thickets, dykes and terraces, hedgerows, and adjacent

woodland, shrubland and grassland), which presumably serve as centers of dispersal when environmental conditions ameliorate.

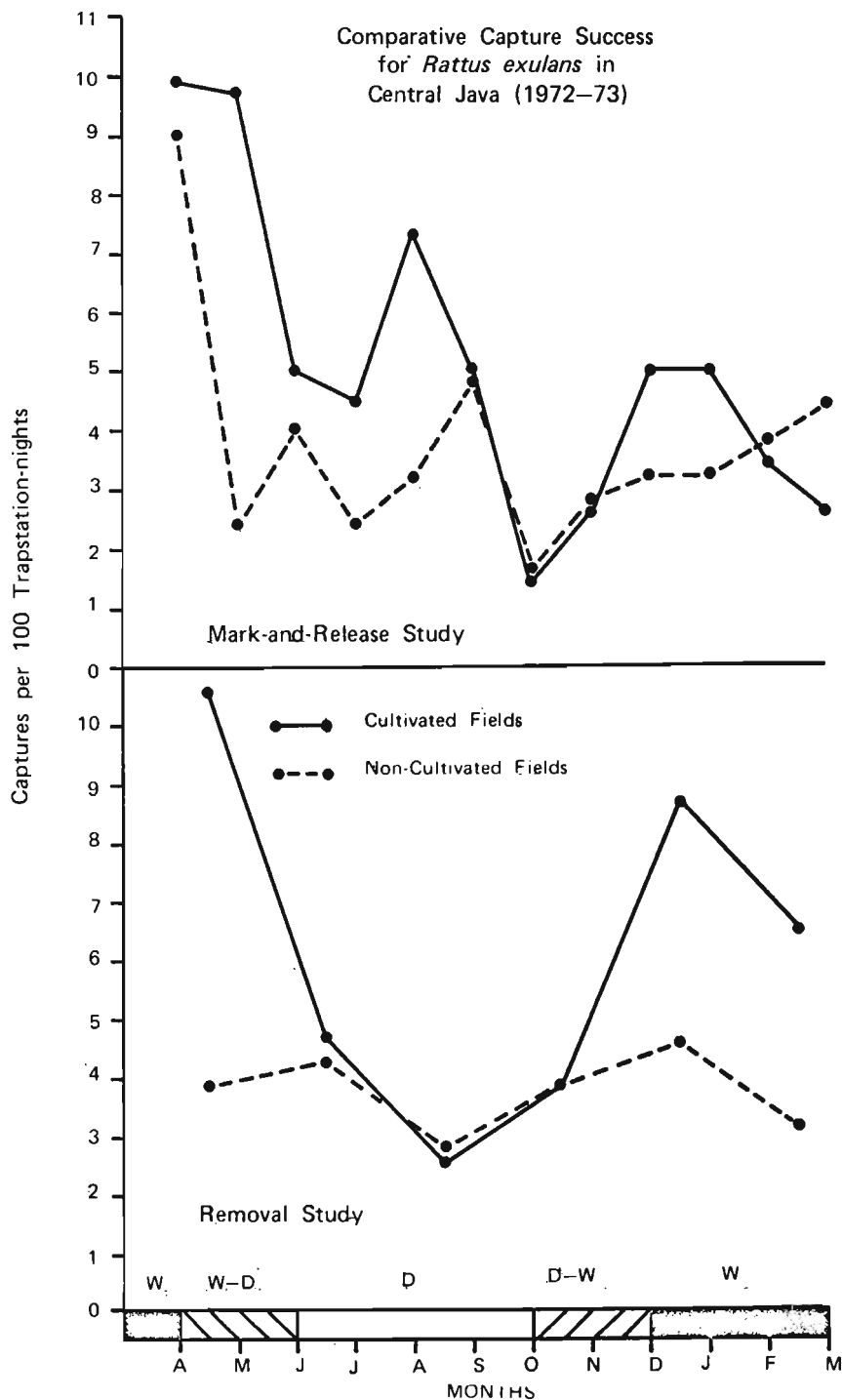


Fig. IX. Comparative capture success for *R. exulans* in Central Java (1972-73).

average of 5.7 *R. exulans* were captured per 100 trapstation-nights from December through May, as compared to 3.7 from June through November.

Seasonal fluctuation in carrying capacity may cause differential survival and mortality, corresponding fluctuations in the reproductive rates, or changes in mobility. As mentioned previously, natural mortality is extremely difficult to evaluate. Survivorship based in mark-and-release data also may be biased in that observed increases in the rate of recapture during the dry season probably reflects increased attractiveness of baits during this period of low food availability, rather than increased survival. To the contrary, decreased survival is postulated for this period. The apparent increase in reproduction from September through November (late dry season) may indicate that the two to four month reproductive cycle is superimposed over prevailing environmental conditions. That some reproduction did occur in this period is evidenced by increased captures of immature rats in December and January.

Fig. IX depicts the comparative capture success in cultivated and non-cultivated (woodland, grassland, shrubland, herbalnd, and bamboo thickets) fields throughout the first year of study.

In the mark-and-release studies (original captures only), increased captures in non-cultivated areas coincide with decreased captures in cultivated areas. In the removal studies, relative capture success in non-cultivated areas exceeds those in cultivated areas during much of the dry season. Whether the differences in capture success reflect increased survival in non-cultivated fields during periods of adverse environmental conditions in croplands, or are due to emigration from cropland, or both is problematical.

That prevailing environmental conditions dramatically effect the carrying capacity is illustrated by recent trapping results. The adverse climatic and agricultural conditions, and consequent, decline in population densities for June and July of 1972 already has been mentioned. In contrast, a prolonged wet season is being encountered in 1973, with frequent rains still

occurring in late July. Existing crops in the plague zone were not completely harvested as of 1972, and in fact, new crops were planted. As a result, the population levels of *R. exulans* in July were the highest encountered to date. Thus, favorable climatic and agricultural conditions tend to increase the environmental carrying capacity, thereby increasing the probability of contact between hosts, and making more hosts available to flea vectors. If the plague pathogen is circulating in the area at such time the spread of infection would be greatly enhanced. Hence, either early onset or prolonged duration of the rainy season may have important epidemiological consequences. Comparison of monthly temperature and precipitation records for Central Java (recently provided by the Geophysical and Meteorological Services in Jakarta) with past recorded cases of plague may provide additional insight into this matter.

Bearing in mind that epidemics of human plague are preceded by a complex chain of events in sylvatic and peridomestic environments, the method of breaking this chain should be devised. Control of rodent populations within domestic habitats merely potentiates the spread of infection by creating an abundance of hungry, hostless fleas that will attack man. The upland slopes of Mount Merapi and Mount Merbabu are too vast, and the countless deep ravines dissecting these mountainsides are too inaccessible, to carry out adequate control measures in these sylvatic environments. Thus, the peridomestic habitat remains as the target area in any proposed program of rodent control.

In the event that a systematic effort is initiated to reduce host densities in peridomestic areas, timing of such programs would be of critical importance. During the wet season, rodent population levels are high and the rats are dispersed over the entire cultivated and non-cultivated area. In contrast, during the dry season, host densities are relatively low and the rats are subject to environmental stress, at least in the barren croplands. Control programs instigated during the dry season would not conflict with human agricultural endeavors, but presumably would be more attractive at this time due to the scarcity of natural foods, and

Although most of the recent human cases of plague have occurred during the fourth and first quarters of the year, the epizootics culminating in these epidemics may have been initiated several months before hand. Unfortunately, little is known of the time sequence of such events. Earlier in the present study attempts were made to correlate occurrence of the dry season with the movement of field rodents and fleas into houses. However, as data continue to accumulate, these invasions also appear to be an artifact of field rodent density, with more rats occurring in all habitats (including houses) when population levels are high (compare Fig. VI and XI). Whether these intrusions in fact are due to changes in patterns of movements, density levels, or both, any control efforts made to decrease contact rates between field and domestic elements of the plague infectious cycle should be carried out during the third quarter, prior to the season of maximal incidence of human plague. Control (trapping, poisoning, fumigation, or burrow destruction) applied between July and October, theoretically would further reduce density levels of reservoir species already subject to environmental stress, and by decimating the number of reproductive members, might curtail densities for several subsequent months.

Most control programs are initiated after dramatic increases in local rodent populations already have resulted in extensive destruction of crops, invasion of households, or human epidemics. In areas where infection is endemic and epidemics are a recurring phenomenon, concern for human welfare necessitates a *preventive* approach to control of reservoir species. Application of control measures after high rodent densities already have been attained, and subsequent to extensive epizootics, are both inefficient and ineffective. Control methods applied at such times generally reduce a high population back from the carry capacity into the optimal growth phase once more, thus being of actual benefit to the rats in maintaining a healthy expanding population. Better results would be achieved by applying control during periods of low density, thereby augmenting the existing environmental resistance and limiting population recovery during the potentially dangerous fourth

quarter of the year.

Unfortunately, it must be remembered that, at best, rodent control programs provide only temporary restraint on population densities. Due to the high reproductive potential of these hosts and reservoirs, population recovery can occur quite rapidly, even after maximal control efforts. Thus, some method of vector control might prove to be a more efficient means of interrupting the plague infectious cycle in Central Java.

## DISCUSSION

In an ecological study of plague, it is impossible to assign wholly independent roles in the maintenance and transmission of infection to the flea vectors and mammalian hosts, including man. All phases of rodent and human involvement in the cycle are mediated by the fleas that feed upon these hosts (see the article on Flea Ecology presented in the previous bulletin).

Although many species of mammals may inhabit a given area, not all species are directly involved in the maintenance and propagation of infections. In fact, only one or two species may constitute the principle plague reservoirs in any particular focus (Kalobuhov, 1970). Endemic pathogens may have little adverse effect on their normal hosts, but may persist within the body of these reservoirs as latent infections that are transferred to vectors feeding upon such hosts. In contrast, infection of abnormal hosts (non-reservoirs) may have dire epidemiological consequences by amplifying the spread of the disease.

In a series of systematic experiments, Bahmanyar (1958) inoculated known doses of *Y. pestis* into several species of mammals collected in Central Java. Both *R. r. diardii* (see Table 1) and *R. argentiventer* were found to be highly susceptible to infection and readily succumbed to the pathogen. Even though 72 per cent of the 32 *R. tiomanicus* (listed as *R. r. roquei*) inoculated resisted infection, the species was recorded as being "highly susceptible". Because this interpretation is unclear, the results must be consi-

dered as variable and inconclusive. *R. exulans* was quite easily infected with *Y. pestis* but strongly resisted the disease, and autopsy of surviving individuals several weeks after experimentation yielded evidence of residual plague infection in otherwise apparently healthy rats. Inoculation of *S. murinus* suggested that this insectivore is highly resistant to infection, if not immune. Experiments with *M. musculus* "caught in fields" indicated that it also was surprisingly resistant, especially when considering that the highly susceptible strains of white laboratory mice were originally derived from this species, and that this species generally in non-resistant in other plague focalities throughout the world. Presumably, these specimens actually represent *Mus cervicolor*, which is a common field rodent in several parts of Central Java, whereas *M. musculus* generally is confined to houses in the same areas. Two other species that are quite common in the Boyolali Regency, *R. niviventer* and *C. notatus* were not tested by Bahmanyar.

Examination of Table 6 confirms that *R. r. diardii* and *R. exulans* are involved in the plague infectious cycle in Central Java, in that the pathogen has been isolated directly from their organs. In addition, Dutch workers frequently encountered plague-infected *R. argentiventer* during earlier extensive epizootics in Java. *S. murinus*, *R. tiomanicus* and *R. niviventer* have been indirectly, but not conclusively, implicated by isolates derived from their fleas (Chamsa, 1970). It should be noted that fleas from *R. exulans* also were included in the only plague-positive pool produced by fleas of *R. tiomanicus* and *R. niviventer*, thus confusing possible interpretations.

Based on ecological distribution, patterns of movement, and known resistance to the plague pathogen, it is readily apparent that *R. exulans* functions as the primary maintaining plague reservoir in the Boyolali Regency, a postulate championed by Bahmanyar (1958). It is possible that the less common, but ecologically similar *R. tiomanicus* serves as a secondary reservoir, however the potential role of the common but ecologically restricted *R. niviventer* remains unknown. *M. cervicolor* and *S. murinus*, due to their strong resistance to infection and

rarity in the normal Boyolali plague zone (95 per cent of 112 human cases of plague in 1968 and 1970 occurred in areas above 1000 meters, see Fig. II), are thought to play no important part in the natural infectious cycle.

Low resistance of both *R. r. diardii* and *R. argentiventer* to initial infections, and nearly complete susceptibility of infected rats to the pathogen, most certainly exclude these species from any possible role in the conservation of plague in Central Java during inter-epidemic periods. Local populations of these rodents may be almost entirely decimated during an epizootic, with only a few resistant individuals surviving (Pollitzer, 1954). Transmission of plague requires the co-existence of both resistant and susceptible individuals, each making different contributions to the continuance of an epizootic. Both species have high reproductive capacities (breed at an early age, and have large frequent litters of young), and during periods of increased population turnover induced by epizootics, rapid recruitment of young susceptible individuals is crucial to propagation of the infection. Thus, *R. r. diardii* and *R. argentiventer* probably function as amplifying hosts for the pathogen (in the sense of Mull, 1970) and serve as liaisons between field fleas, wild reservoir, and man — *R. r. diardii*, once the infection reaches the villages, and *R. argentiventer*, once the epizootic progresses downslope to ricefields.

Baltazard and Bahmanyar (1960) produced an excellent epidemiological map depicting plague events in the Surakarta Residency (including the Boyolali Regency) from 1952 to 1957. Based on the distribution of human cases, they described for types of zones in relation to plague infection :

- Zone 1. Pure ricefields, distant from mountainous areas, that are inhabited almost exclusively by *R. argentiventer* : no plague encountered.
- Zone 2. Pure ricefields, near mountainous areas, that are inhabited almost exclusively by *R. argentiventer*: frequent incursions of plague, but a few cases, limited in territory, and of extremely brief duration.

Zone 3. Ricefields bordering dry croplands on mountain slopes (Wonogiri focus on Mount Lawu) that are inhabited by *R. argentiventer*, *R. exulans* and other field rodents' remarkable "persistence" (more correctly, the recurrence of human cases) of plague infection over several years, large number of cases, progression in "slow waves" through numerous villages.

Zone 4. Pure dry croplands (including Boyolali focus on the Mount Merapi-Merbabu complex) that are inhabited mainly by *R. exulans* and other field rodents, excluding *R. argentiventer*: regular occurrence of plague, fewer human cases, sporadic progression, cases often separated in distance and time.

It should be noted that an epidemiological map does not describe the "persistence" of infection, but rather the a posteriori distribution and recurrence of human cases subsequent to the

spread of infection from sylvatic centers of maintenance. Actual persistence of the infection can be studied only during inter-epidemic periods, and not in times of general epizootics.

The differing epidemiological patterns described for Zones 3 and 4 may be based on the different population densities of the liaison rodents involved in the propagation of infection. During the first year of investigation, an average of less than one *R. r. diardii* per house was found throughout much of the plague zone; these findings agree with those of Baltazard and Bahmanyar (1960). Although some houses yield up to ten *R. r. diardii*, from 30 to 40 per cent of the houses sampled yielded none, hence, progression of the infection is sporadic and saltatorial. On the other hand, tremendous populations of *R. argentiventer* are encountered in ricefields, with several thousand individuals inhabiting a relatively small area; hence the infection spreads in "waves" over a large expanse encompassing many villages. Human populations

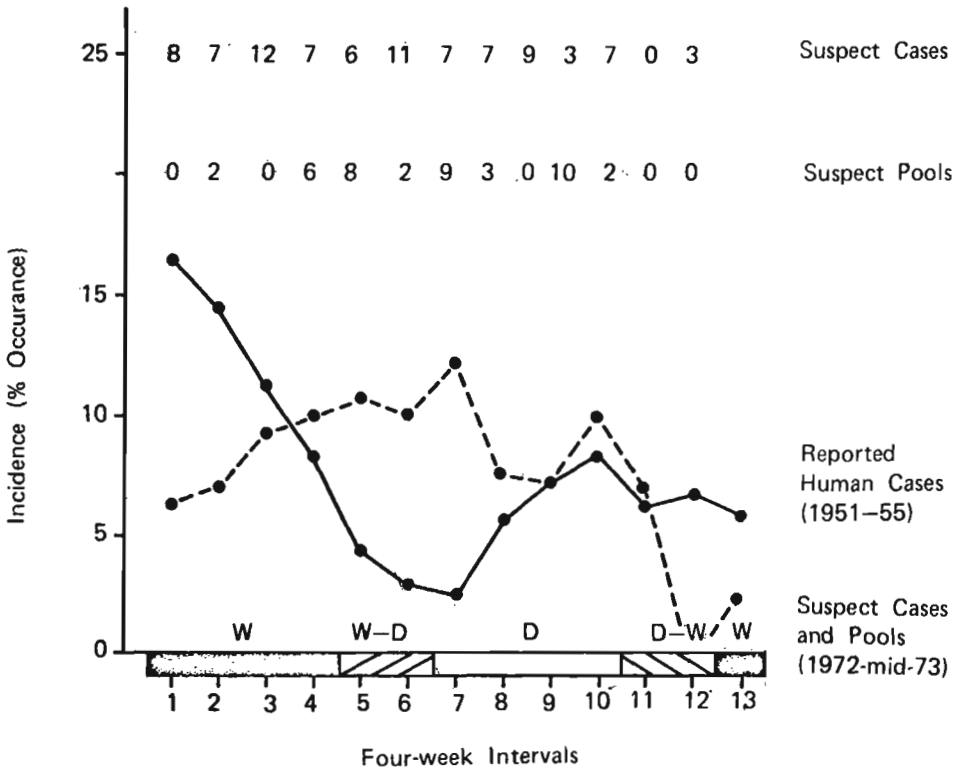


Fig. X. Potential seasonal distribution of plague in Central Java.



also are much more dense at these lower elevations, increasing the probability of spread of the disease.

In mid-May 1972, plague was isolated from eleven field fleas (*Stivalius cognatus*) removed from five *R. exulans* captured in open acacia woodlands on the upper flanks of Mount Merapi (at approximately 1800 meters), about two kilometers from the nearest village. Upon bacteriological confirmation of these suspect materials in early June, all villages in the area were sampled and five additional positive isolations were achieved from *S. cognatus* and domestic fleas (*Xenopsylla cheopis*) infesting *R. exulans* and *R. r. diardii*, and from the organs of *R. exulans*, in houses of the subvillages of Bulurejo and Kenteng (1500 and 1250 meters, respectively).

Although 87 persons (Fig. X) with fevers and painfully swollen lymph glands have been encountered in the plague zone during the first year, all recovered from clinical symptoms after three-day treatment with antibiotics and no human plague cases actually were confirmed.

The last reported instances of human plague in the Boyolali Regency were in April 1970, from the subvillage of Jeruk, five kilometers to the north on the slopes of Mount Merbabu, at 1300 meters. Although the areas from which the 1972 plague-positive isolates originated were sampled an additional six times at bimonthly intervals, no further infection was found there. However, an additional 36 suspect pools (*i.e.* caused death of inoculated experimental animals through three or more subpasses, and bipolar-staining coccobacillary forms often discernible in tissues of symptomatic experimental animals) of fleas and host-organs were encountered elsewhere in the plague zone. Unfortunately, heavy contamination prevented definitive bacteriological culturing of these suspect materials and the actual presence absence of *Y. pestis* could not be confirmed. Nonetheless, it is highly probably that the plague pathogen still is circulating among rodents and their fleas in the Boyolali plague focus and continues to pose a threat to human welfare in the area.

Presumably, the infection is maintained in sylvatic mountainous areas of the Boyolali Regency where optimal combinations of field vectors and reservoirs favor persistence of ever-shifting enzootic-epizootic infections. During intensive epizootics, the disease may progress downslope through peridomestic cropland, eventually reaching villages and, if the spread of infection is extensive enough, may reach rice-fields that border dry croplands. The factors that cause shifts from *sylvatic-enzootics*, to *sylvatic-epizootics*, to *peridomestic-epizootics*, to *domestic-epizootics*, and finally to *epidemics* in human populations are poorly understood. It is difficult to imagine that these events can occur without some prior changes in the relationships between individual vector and reservoir species, in man's relationship to these species, or in some other environmental parameter(s).

One potential factor in enzootic-epizootic shifts may be seasonal peaks in the emergence of presumably susceptible nestling *R. exulans* into the field reservoir population. The increased proportion of immatures captured in June, July and August, and in December and January (Fig. VI) are roughly correlated with periods of increased prevalence of plague in the human population (Fig. X). Note that the time scales are slightly different in Fig. XI and Fig. X.

From the data presented in this bulletin and in the article on flea ecology presented in the previous bulletin, it is evident that domestic species of rodents (*R. r. diardii*) and fleas (*X. cheopis*) rarely venture into peridomestic and sylvatic environs in the Boyolali plague zone, or at least fail to become firmly established in these habitats. On the other hand, peridomestic and sylvatic species of rodents (*R. exulans*, *R. tiomanicus*, and *R. niviventer*) and their fleas (*S. cognatus* and *Neopsylla sondaica*) often enter human domiciles for varying periods of time. The frequency of visits of field rodents to houses seems to increase in direct proportion to population densities of these hosts (with spill over from the fields into the houses) and during times of prolonged environmental stress (movement from barren croplands into houses during the dry season). That the frequency of potentially

infective field fleas (*S. cognatus* and *N. sondaica*) in houses is well correlated with the visits of

field rodents to domestic habitats is shown in Fig. XI.

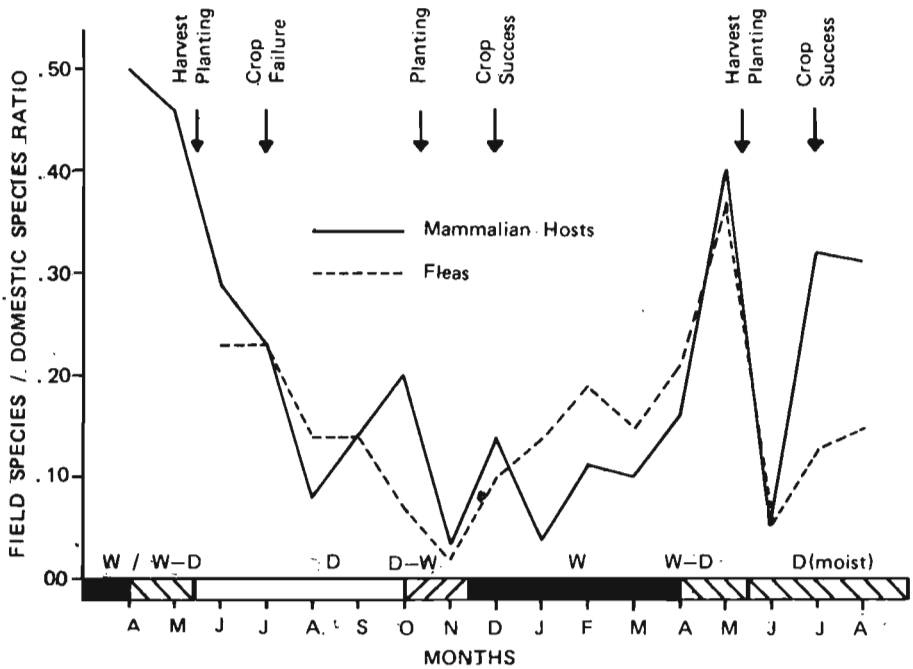


Fig. XI. Prevalence of field rodents (*R. exulans*, *R. tiomanicus* and *R. niviventer*) and field fleas (*S. cognatus* and *N. sondaica*) in houses in the Boyolali plague focus (1972–1973). Note that the dry season of 1973 remained moist.

Table 6. Components of the plague transmission cycle in Central Java, as revealed by plague-positive isolations from pools of fleas and organs of mammalian hosts. Data are from the present study (Underlined) and from Baltazard and Bahmanyar (1960, U.S. Public Health Service (1968) and Chamca (1970).

Mammalian Host	General Habitat	<i>Xenopsylla cheopis</i>	<i>Stivalius cognatus</i>	<i>Neopsylla sondaica</i>	Host Organs
<i>Suncus murinus</i>	House	Positive	Negative	Negative	Negative
<i>Rattus rattus diardii</i>	House	<u>Positive</u>	Negative	Negative	Positive
	Field	Negative	Negative	Negative	Negative
<i>Rattus exulans</i>	House	<u>Positive</u>	<u>Positive</u>	** Questionable	<u>Positive</u>
	Field	<u>Positive</u>	<u>Positive</u>	** Questionable	<u>Negative</u>
<i>Rattus tiomanicus</i>	House	Negative	Negative	Negative	Negative
	Field	* Questionable	Negative	Negative	Negative
<i>Rattus niviventer</i>	House	Negative	Negative	Negative	Negative
	Field	* Questionable	Negative	Negative	Negative

\* Fleas from *R. exulans*, *R. tiomanicus* and *R. niviventer* were included in the same pool (Chamsa 1970), so that the actual source of infection remains unknown.

\*\* *N. sondaica* previously has been confused with *S. cognatus*, and both flea species may have been included in the same pool inadvertently.

Finally, in considering the prevalence of plague in mountainous areas, the altitudinal distribution of the rodent and flea species involved in the transmission cycle is of critical importance. As noted in Fig. IV, both the known primary mammalian reservoir (*R. exulans*) and potential secondary reservoir (*R. tiomanicus*) are much more abundant at higher elevations in the Boyolali Regency than in the lowlands. In addition, the suspected primary maintaining

vector (*S. cognatus*) and potential secondary maintaining vector (*N. sondaica*) are absent or rare below 1000 meters in elevation. The domestic flea (*X. cheopis*) is the predominant flea in both houses and fields below 1000 meters, but is fairly well confined to houses above 1000 meters.

A schematic representation of the potential elements of the plague transmission cycle in the Boyolali focus is given in Fig. XII-A, B, and C.

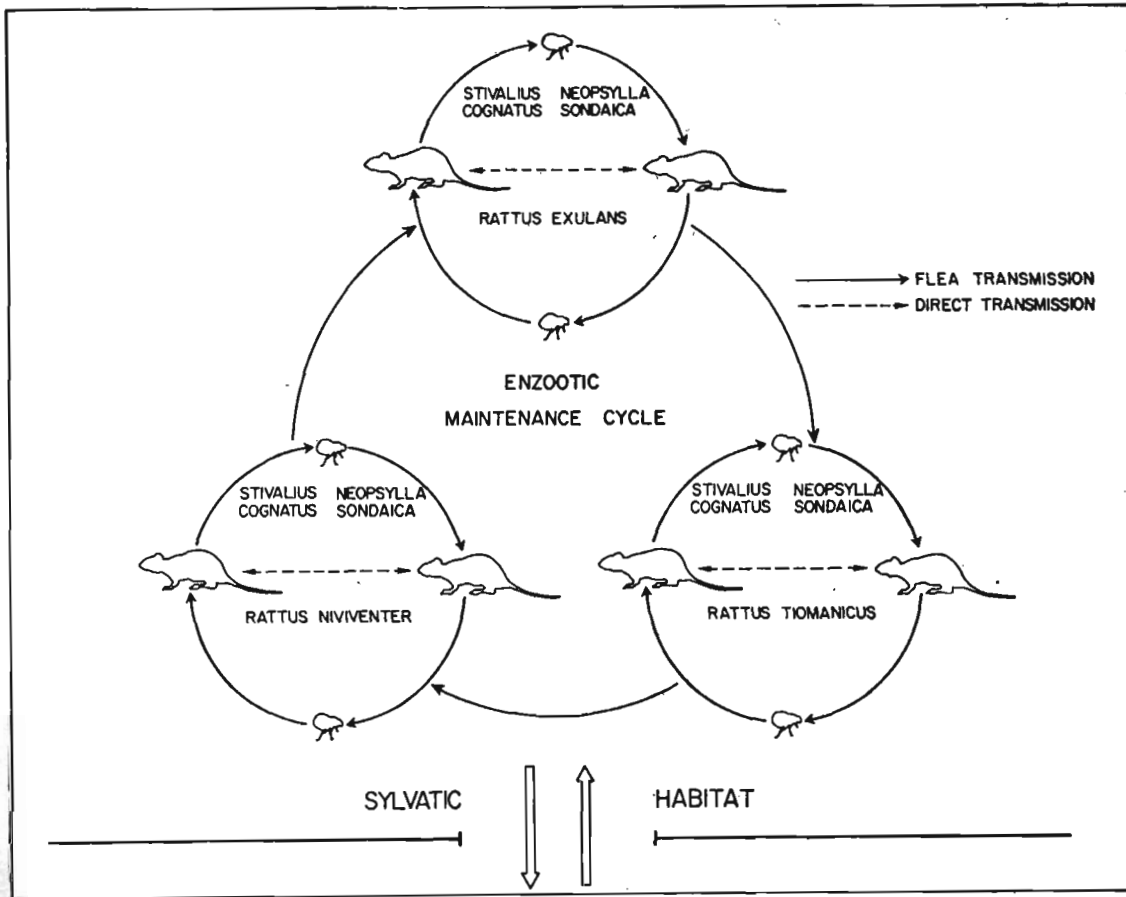


Fig. XIIA. Potential components of the plague transmission cycle in sylvatic habitats.

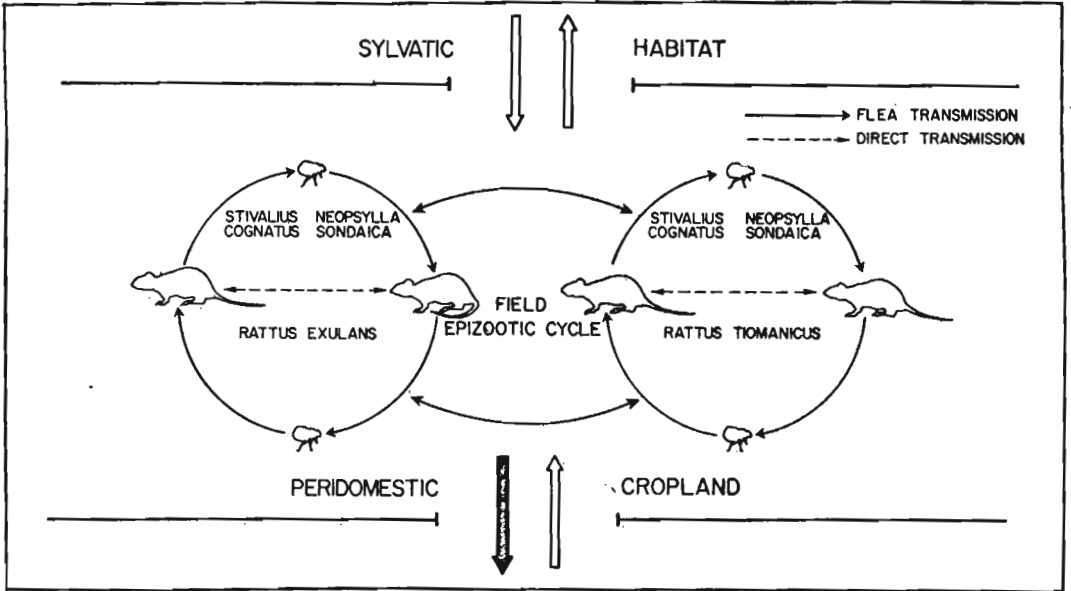


Fig. XIIB. Potential components of the plague transmission cycle in peridomestic habitats.

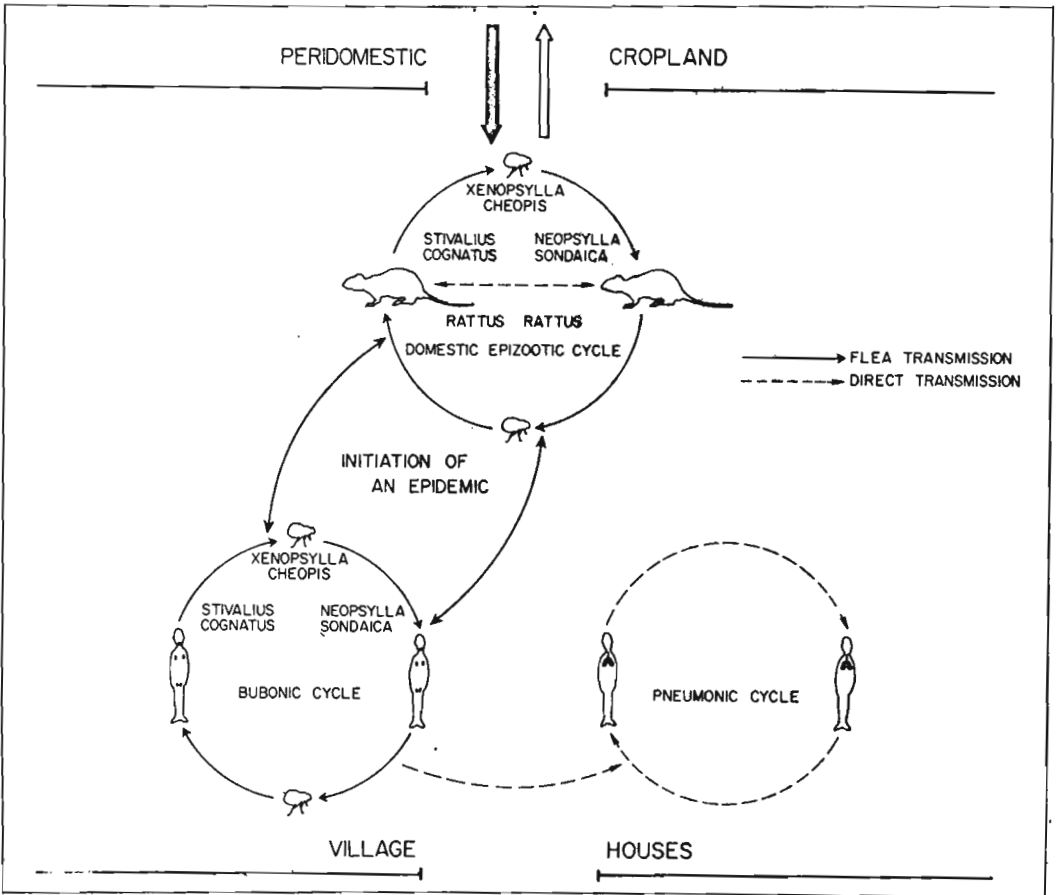


Fig. XIIC. Potential components of the plague transmission cycle in domestic habitats.

## SUMMARY AND CONCLUSIONS

The present interepidemic study of the ecology of the plague transmission cycle in Central Java was designed to elucidate the temporal and spatial relationships that may exist between the various components of the infectious cycle, and in attempt to identify important environmental parameters that may affect these interrelations. The project is co-sponsored by the Indonesian Ministry of Health and the Southeast Asia Regional Office of the World Health Organization. Intensive field work commenced in April 1972, and will continue until December 1974. Preliminary data from the first year of research are presented herein.

Mammalian hosts were live-trapped : at monthly intervals on a one kilometer mark-and-release grid; at bimonthly intervals at 20 permanent research sites; and at semi-annual intervals in 60 villages in and near the Boyolali plague zone. Approximately 87,350 trapnights were accumulated during the first year of investigation. Specimens of mammals thus obtained were: examined for ectoparasites; bled for antibody-antigen serological tests; measured and weighed; sexes and aged; dissected for internal reproductive data; and autopsed. Homogenates of fleas, or of spleens from the hosts, were inoculated into experimental animals which were observed for morbidity and mortality. Tissues of symptomatic experimental animals were examined bacteriologically for the presence of the plague pathogen. Approximately 2500 pooling-tests were performed during the first year of study.

Based on human case distribution in the 1968 and 1970 epidemics, a zone of infection was apparent in the Mount Merapi—Mount Merbabu volcanic complex, above 1000 meters in elevation. Successful isolation of *Y. pestis* from rodents and their fleas, both in field environs and in villages houses, substantiates the continued circulation of the plague pathogen among host and vector populations in the Boyolali plague focus and indicates that this disease still poses a threat to human welfare in the area.

Based on the known resistance to the plague pathogen, *Rattus exulans* is the probable

primary mammalian reservoir in Central Java. This species ranges throughout all available habitats in the area. Approximately 22 per cent of the *R. exulans* captured were from houses and it accounted for 8.4 per cent of all mammals trapped in human domiciles. This rodent breeds throughout the year, with peaks in reproduction occurring from February through March, and September through November. Preliminary data indicate that from 5.4 to 8.9 litters are produced each year, averaging an annual production of 25.4 to 41.8 young per reproducing female. Population densities of *R. exulans* in the Boyolali plague zone seem to exhibit a variable three to five month cycle, with peak densities in April and May, in August and September, and in December. Population levels varied from research site to research site, but generally tended to follow the same annual pattern. Longevity and population turnover of reservoir species are of great epidemiological importance. Based on recapture data from the mark-and-release study, an average of 43.0 per cent of the marked *R. exulans* remained in the research area for at least one month, 22.1 per cent for two months, 13.9 per cent for three months, 6.7 per cent for four months, 3.5 per cent for five months, 2.2 per cent for six months, 1.6 per cent for seven months, and 0.1 per cent for at least eight months.

Little is known concerning the plague resistance-susceptibility of *Rattus tiomanicus*; however, it has an ecological distribution that is quite similar to that of *R. exulans* and possibly could function as a secondary mammalian reservoir in the Boyolali focus. Approximately 43.0 per cent of the *R. tiomanicus* captured were from houses, and it accounted for 1.2 per cent of all mammals trapped in human domiciles. Reproductive and population parameters for *R. tiomanicus* have not been analysed as yet.

The plague resistance-susceptibility status of *Rattus niviventer* never has been investigated. Because the ecological distribution of this rodent is restricted mainly to deep semi-wooded ravines and other sylvatic habitats, it has little contact with man and probably plays little if any role in the plague transmission cycle in Central Java.

Only 4.9 per cent of the *R. niviventer* captured were from houses, and it accounted for only 0.2 per cent of all mammals captured in human domiciles. Reproductive and population parameters for *R. niviventer* have not been analysed as yet.

Because *Rattus rattus diardii* is highly susceptible to infection by the plague bacillus and readily succumbs to the pathogen, it most certainly can play no role in the maintenance of infection in Central Java during interepidemic periods. However, *R. r. diardii* does function as a liaison rodent between wild reservoirs, infective fleas and man, once the infection spreads to the villages from sylvatic and peridomestic habitats. Thus, *R. r. diardii* probably serves as an amplifying agent for the pathogen. Approximately 99.2 per cent of the *R. r. diardii* captured were from houses, and it accounted for 89.4 per cent of all mammals captured in human domiciles. Thus, this species seems to be fairly well restricted to houses in the Boyolali plague zone, accounting for only 2.0 per cent of all mammals trapped in field environs. On the average, less than one *R. r. diardii* per house was found throughout villages in the Boyolali Regency. Although some houses yielded up to ten *R. r. diardii*, from 30 to 40 per cent of the houses sampled yielded none. It should be noted however that these results are based on trapping data, and *R. r. diardii* seems to exhibit a definite trapshy behavior. For example, only 12.3 per cent of the marked-and-released *R. r. diardii* have been recaptured, as compared to 59.8 per cent for *R. exulans*. Also, individuals often are recaptured in the same house five to six months after release, even though the house was trapped repeatedly during the intervening period. *R. r. diardii* appears to produce young throughout the year, but reproductive data have not been thoroughly analysed as yet.

*Suncus murinus*, *Bandicota indica* and *mus cervicolor* are thought to be strongly resistant to plague infection in Central Java, and are rarely encountered in the Boyolali plague zone (above 1000 meters). *Callosciurus notatus* and its fleas have not yet been implicated in the normal plague cycle. Like *R. r. diardii*, *Rattus argen-*

*tiventer* is quite susceptible to the plague pathogen, but in does not occur in the Boyolali plague zone. This species evidently functions as liaison rodent in the spread of infection, and thereby serves as an amplifying agent for the pathogen, once epizootics have spread downslope and into ricefields that border mountainous areas in Central Java.

Seasonal variation in climatic conditions, through the direct effect on the annual crop-cycle, seems to be the most important environmental factor regulating reproduction and population levels of field rodents in the plague zone. Adverse climatic and agricultural conditions during the dry easterly monsoon drastically reduce the carrying capacity of the cropland. Near-arid conditions prevail and vegetation cover dwindles to less than five per cent over much of the cultivated area. There is an apparent increase in the frequency of field rodents (and their fleas) in houses at such times. Amelioration of climatic conditions during the wet westerly monsoon allows intense cultivation once more. With the resultant increase in cover and food supply, field rodent population reach maximum densities in the rainy season. As an artifact of these high population levels, rodents are abundant in all habitats and there is a spill-over of field rodents (and their fleas) into village houses. Thus, environmental conditions at certain times in both the dry season and the wet season favor increased visits of potentially infective field rodents and fleas to human habitations.

Considering the prevalence of plague in mountainous zones in Central Java, the ecological distributions of the various components of the transmission cycle are of critical importance.

Population levels of the primary mammalian reservoir (*R. exulans*) and possible secondary reservoir *R. tiomanicus* are much greater on the middle and upper slopes of Mount Merapi and Mount Merbabu than in the surrounding lowlands. Also, the suspected primary maintaining vector (*Neopsylla sondaica*) are absent or rare below 1000 meters in elevation.

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