

## Distribution, population dynamics and habitat use of the lesser pouched rat, *Beamys hindei*

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The lesser pouched rat, *Beamys hindei* Thomas 1909, is one of Africa's rarest and least known rodents, recorded only from a few localities in Kenya and Tanzania. The results of this study show that *B. hindei* is more widely distributed than previously thought and occurs at high densities in suitable habitat. It breeds throughout the year, but maintains relatively constant population densities as recruitment rates are low. On account of its ability to cache food, it is well adapted to seasonally dry forests where food is in short supply for part of the year. The need for suitable soil in which to construct its burrows and dense vegetation cover may partly account for its patchy distribution. Morphological data collected during this study provide no evidence for separating *B. hindei* from *B. major* and suggest that the differences previously recorded between the two forms may be actually due to clinal variation in size from north to south.

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### Introduction

The lesser pouched rat, *Beamys hindei* (Thomas, 1909), is one of Africa's rarest and least known rodents, recorded only from a few localities in Kenya and Tanzania. Its present conservation status is 'vulnerable' (IUCN, 1990). *Beamys hindei* is currently differentiated

from the closely related *B. major* Dollman 1914 on the basis of hindfoot length (Meester & Setzer, 1971) and foot morphology (Hanney & Morris, 1962) but Ansell & Ansell (1973) suggested a synonymy of the two names. Musser & Carleton (1993) state that *B. hindei* occurs in Kenya and north-east Tanzania, while *B. major* occurs in south Tanzania, Malawi and north-east Zambia. However, they also indicated that a revision of the genus is needed since the specific status of both forms is doubtful.

A number of factors are thought to contribute to the apparent rarity and patchy distribution of *B. hindei*. Hanney & Morris (1962) and Kingdon (1974) emphasize its dependence on surface water, while Kingdon (1974) suggests that it is restricted to sandy soils because of its habit of building deep, complex burrows. *Beamys* are known to feed primarily on seeds and fruits and to inhabit mainly forest and moist woodland (Hanney & Morris, 1962; Kingdon, 1974), but little is known of their behaviour and ecology, and the reasons for their rarity have not been investigated. *Beamys hindei* is closely related to two other cricetid rodents, the giant pouched rat *Cricetomys gambianus* and the pouched mouse *Saccostomus campestris*; all three species possess large cheek pouches, dig burrows and store food (Hanney, 1965; Ewer, 1967; Kingdon, 1974; Ellison, 1993).

In this study we examined, (a) the distribution of *Beamys* on the Tanzanian coast where little survey work had previously been carried out, (b) the morphological differences between animals from northern and southern East Africa, i.e. between *B. hindei* and *B. major*, (c) the factors that influence *Beamys* abundance in Arabuko-Sokoke Forest, Kenya, currently one of the most important known sites for the species, and (d) its population dynamics over a period of one year in Arabuko-Sokoke Forest, with the overall aim of understanding the factors that contribute to the rarity and patchy distribution of these little-known rodents.

## Methods

### *Distribution and morphology*

The distribution of *Beamys hindei* will be discussed using data collected from Arabuko-Sokoke Forest, Kenya, from several localities throughout Tanzania sampled during the Tanzania-Belgium Joint Rodent Research Project (1986–1989), and from several Tanzanian coastal forests as part of a general mammal survey (1989–1993) by volunteers from Frontier Tanzania (Fig. 1, Table I). Animals were collected using combinations of snap and live traps, baited with a mixture of peanut butter and maize scrap, oats or other locally available baits. At each locality, at least 200, but generally more than 600, trapping nights were organized.

The material from southern Tanzania is currently kept at the University of Antwerp (RUCA), Antwerpen, Belgium, the material from the Frontier collections is deposited at the Zoological Department of the University of Dar es Salaam and specimens from Kenya have been deposited at The Natural History Museum, London, UK. For each dead specimen, external measurements were taken of body weight, head-body length and hindfoot length (excluding the toenail). From the material from southern Tanzania, skull measurements were also available, of which occipito-nasal length, upper alveolar row length and upper first molar width are used here. The type specimens of both *Beamys* species (*B. hindei* BMNH 9.6.12.23; *B. major* BMNH 14.10.22.2) and 6 other specimens from the British Museum of Natural History (BMNH 10.9.22.32; BMNH 61.463; BMNH 61.462; BMNH 62.336; BMNH 78.2750; BMNH 61.92) were remeasured. The material was further supplemented with published data on 20 other animals from Malawi (Hanney & Morris, 1962), 14 from northern Tanzania (Hubbard, 1970), 4 from northern Zambia (Ansell & Ansell, 1973) and 1 from southern Tanzania (Christensen, 1987). The published measurements were used for this material, although it was not always clear whether all the measurements had been taken in the same way. Four

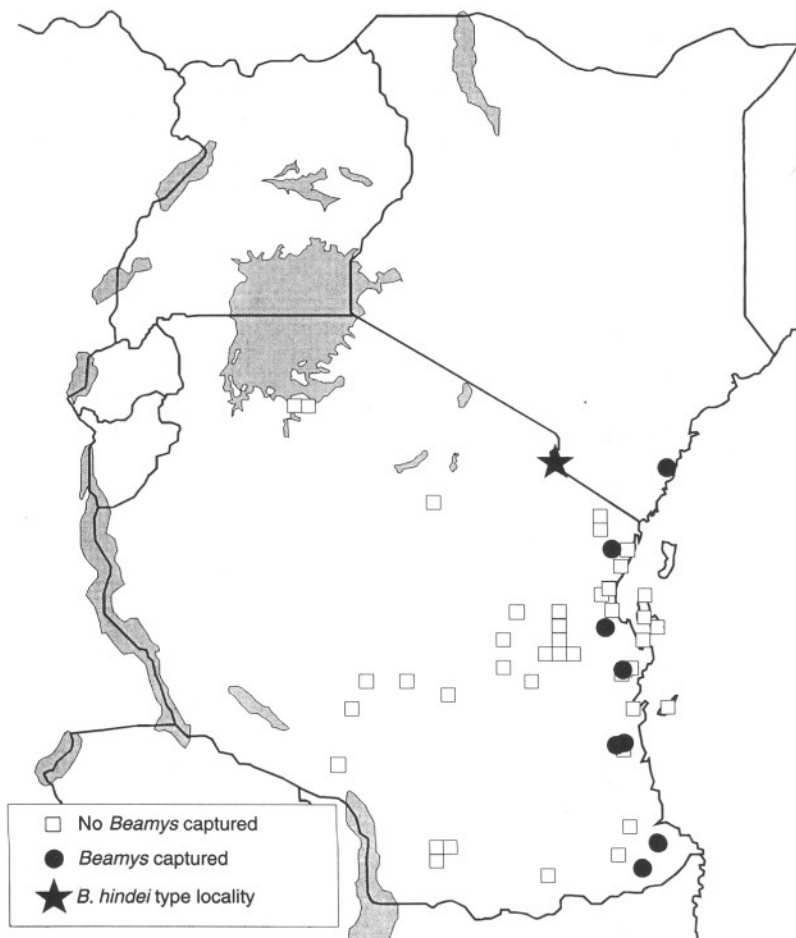


FIG. 1. Map of East Africa showing sites where *Beamys* were and were not recorded during this study.

animals from southern Tanzania were karyotyped from fibroblasts obtained from a peritoneum cell culture.

### Ecology

The ecological study was carried out in Arabuko-Sokoke Forest, 372 km<sup>2</sup> of dry deciduous forest on the Kenya coast. The forest consists of 3 main habitat types: (1) *Brachystegia spiciformis* woodland on loose sandy soils; (2) *Afzelia* forest, on more compact sandy soils and (3) *Cynometra-Brachylaena* woodland, on red *margarini* soils (Kelsey & Langton, 1984). Rainfall in this area usually averages between 600 and 1000 mm per annum and is dominated by a long rainy season in April, May and June (Fig. 2).

To monitor population dynamics, *Beamys* were live-trapped monthly between October 1991 and September 1992 at a study site in the *Afzelia* forest. A preliminary study in this habitat showed that the rats were more likely to be trapped when the moon was new than when it was full (10.1% trap success over 228 trap nights within 3 days of new moon, compared with only 4.4% trap success over 228 trap nights within 3 days of full moon,  $\chi^2 = 5.52$ , *d.f.* = 1,  $P < 0.05$ ), so as far as possible the period of trapping centred

TABLE I

Location and details of coastal trapping sites, for sites where *Beamys* were and were not recorded. The approximate forest area, altitude, number of other small rodent species recorded during the survey (other than *Beamys*), soil type and habitat are described. Non-coastal sites where surveying took place but no *Beamys* were caught are shown in Fig. 1. Data on *Beamys* captures from Kwangumi-Segoma (Usambara mountains) are from Perkin & Watson (1992)

Name	Location	Forest area (sq km)	Altitude (m)	No. small rodent spp.	Soil type	Habitat
Sites where <i>Beamys</i> were recorded:						
Arabuko-Sokoke	3°20'S, 39°55'E	372	80	2	Sand	Dry forest
Ruvu South	6°58'S, 38°54'E	98	200-260	1	Sand	Scrub forest
Zaranninge-Kiono	6°10'S, 38°39'E	20	200-300	7	Sand	Dry forest
Kiwengoma	8°22'S, 38°56'E	22	300-750	5	Sand	Riverine forest
Namakutwa	8°19'S, 39°00'E	12	150-380	9	Sandy loams	Groundwater forest
Litipo	10°02'S, 39°29'E	5	150-250	3	Sand	Dry forest
Mnara	10°07'S, 39°24'E		600	4	Sand	Dry woodland
Mnima	10°37'S, 39°13'E		750	6	Sand	Dense fallow, open woodland
Kwangumi-Segoma	4°57'S, 38°42'E	32	200-1000	2	?	Lowland forest
Sites where <i>Beamys</i> were not recorded:						
Gendagenda	5°33'S, 38°38'E	28	100-545	5	Sand	Forest
Tongwe	5°18'S, 38°44'E	3	220-650	1	Sandy clays	Dry riverine forest
Kazimzumbwi	7°00'S, 39°03'E	24	120-280	5	Sandy clays	Forest
Mkwaja	5°52'S, 38°47'E	10	0-100	1	Vertisols	Moist forest
Mchungu	7°44'S, 39°17'E	2	0-15	2	Sandy loams	Forest
Tong'omba	8°25'S, 39°01'E	11	150-540	4	Sandy loams	Forest/woodland
Pangani Falls	5°21'S, 38°40'E	1	20-180	5	Silt loams	Forest
Ruvu North	6°58'S, 39°00'E	31	200-480	3	Sandy loams	Forest/woodland
Vikindu	6°59'S, 39°17'E	10	40-80	0	Coarse sands	Riverine forest
Mkulumuzi Gorge	5°05'S, 39°02'E	4	>50	0	Sandy clays	Forest
Kilulu Hill	4°46'S, 39°07'E	2	100-250	0	Sand	Forest

around the new moon. We captured mice in Sherman live-traps, baited with a peanut butter and oat mixture, using a 100 m × 100 m grid, with a single trap placed at 10 m intervals. Each trapping period lasted 4 nights and traps were checked each morning.

Upon capture, each individual was sexed, weighed and individually marked with a system of earclips. Animals weighing less than 40 g were categorized as juvenile. This weight was chosen because it is the approximate weight that captive animals reach at 1 month of age, when they regularly eat solid food and make excursions out of the nest alone (Egoscue, 1972). An index of population size for each trapping period was calculated using the minimum number of mice known to be alive (Krebs, 1966), while densities were estimated by adding an 11-m band (the radius of the average rat's home range as measured by trapping) to each side of the grid to correct for the edge effect. Home ranges were determined from the minimum convex polygon method using trap positions as locations and only using individuals that were caught at least 10 times during the course of the study. Although using data from only 10 captures may result in underestimation of home-range size, this was unavoidable as few individuals were caught more often than this. The home ranges of 7 individuals (4 males and 3 females) averaged 350 m<sup>2</sup>, with a radius of 11 m.

To examine habitat choice between the 3 main habitat types of Arabuko-Sakoke Forest, 6 trapping sessions were carried out between January and April 1992 at different locations within each habitat. Each trapping session consisted of 33 traps placed along three 100-m grid lines, with 1 trap at 10-m intervals. Grid lines were approximately 100 m apart and trapping continued for 3 nights in each site. An additional 4 trapping sessions were carried out in the *Brachystegia* habitat because some of this habitat is degraded as a result of tree felling, and we were interested in the effects of habitat modification on rat densities. A combination of fire and intensive felling of canopy trees in the degraded *Brachystegia* habitat has reduced levels of shrub cover

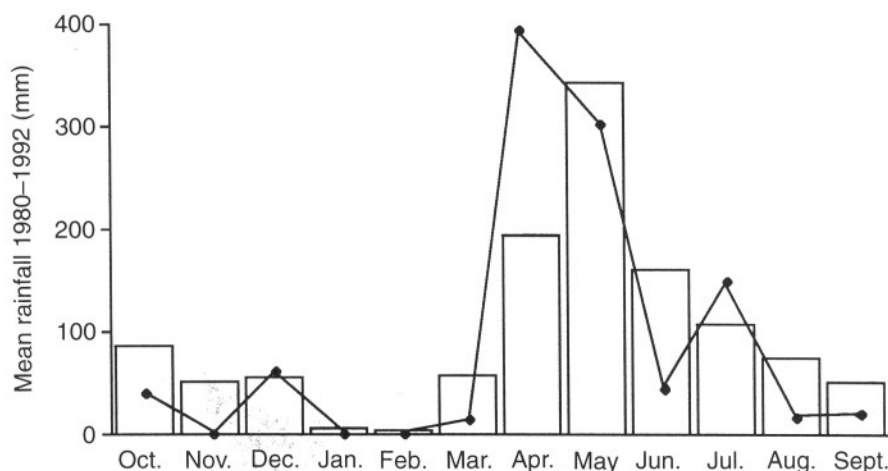


FIG. 2. Mean monthly rainfall at Gede Forest Station, adjacent to the main study site in Arabuko-Sokoke Forest, between 1980 and 1992. The mean monthly rainfall during the study period is also indicated (—◆—).

(COVER<4 =  $15.8 \pm 1.2$  and  $24.7 \pm 4.6$  in degraded and intact *Brachystegia*, respectively,  $n = 18, 12$ ,  $t = 3.68$ ,  $P < 0.05$ ) and increased the distance between canopy trees (MTDIS =  $11.8 \pm 1.8$  and  $10.2 \pm 0.8$ , respectively,  $d.f. = 18, 12$ ,  $t = 2.65$ ,  $P < 0.05$ ).

To determine the effects of habitat structure on *Beamys* abundance, we took a number of vegetation measures (Table II) at 20-m intervals along each grid line (6 per grid line) and averaged the results from each grid line. The distance from the trapping line to the nearest known waterhole was also estimated. There are no permanent water sources in the forest but the waterholes provide water for about 10 months of the year.

## Results

### Distribution

*Beamys* were caught at seven sites in Tanzania, and were found to be abundant in Arabuko-

TABLE II  
Description of habitat variables measured

CAN HEIGHT: the maximum height of the canopy in metres.

COVER: the percentage vegetation cover in three height categories (<4 m, 4-8 m, and >8 m).

STEMS: the number of stems within a radius of 4 m in seven size categories (1-5 cm, 6-10 cm, 11-20 cm, 21-30 cm, >30 cm), depending on the diameter at 50 cm above ground level. The number in each size category that had been cut was also noted (diameter estimated from remaining stump).

HS1: shrub density as measured by the mean half-sight distance at 1 m from the ground using a chequered board 50 × 50 cm placed perpendicular to the transect (the distance at which half the board is no longer visible, measured once on each side of the transect).

MIDIS: mean distance to the nearest canopy tree (>8 m height) in each of four quadrats from the centre of the sample size.

% BARE: estimated % of ground area within 4 m with no leaf/plant cover.

% LITTER: estimated % of ground area covered with leaf litter.

TABLE III

Details of specimens collected during this study. The second specimen from Ruvu was found in the stomach of a twig snake *Thelatornis capensis*

Location	Sex	Weight (g)	Head-body length (mm)	Tail length (mm)	Hindfoot length (mm)	Ear length (mm)
Kenya						
Arabuko-Sokoke, Kilifi District	M	46.0	123	123	20.1	19.1
	M	33.0	100	100	19.0	19.0
	?	47.5	131	116	20.0	20.0
	?	40.0	125	120	21.0	20.0
	F	66.0	140	128	23.0	?
	M	56.0	129	128	21.0	?
	M	54.0	112	125	22.0	22.0
	M	59.0	137	126	21.0	21.0
Tanzania						
Namakutwa, Rufiji District	F	46	122.0	103	19.7	18.6
Ruvu South, Kisarawe District	F	82.5	150	107	17.1	19.1
	?		145	95	?	19.0
Mnara, Lindi District	M	77.6	146	126	20.6	19.8
	F	96.2	151	134	20.5	18.1
Mnima, Newala District	M	89.7	153	118	20.3	21.5
	F	94.4	164	128	22.1	21.0
	M	52.0	135	144	21.6	20.2
	F	84.0	156	140	23.5	21.8
	F	47.0	129	130	21.6	20.0
	M	80.0	156	132	20.2	19.5
	F	62.0	139	145	21.2	20.1
	F	51.0	129	119	22.3	19.6
	M	72.0	143	145	22.3	18.7
	F	60.0	118	123	—	—
	F	49.0	115	112	18.2	17.4
	F	55.0	128	129	20.7	19.7
	F	52.0	135	120	21.1	21.0
	M	62.0	141	120	23.5	18.3

Sokoke Forest, Kenya. Most of the sites where *Beamys* were recorded were forests near the coast, while 10 individuals were also caught in fallow land and cassava plantations at Mnima (Fig. 1, Table I). *Beamys* were also regularly trapped during a recent survey of Kwangumi and Segoma Forest Reserves in the Usambara Mountains (Perkin & Watson, 1992). Despite intensive trapping, *Beamys* were not recorded in an additional 13 lowland forest sites within 100 km of the coast and were also absent from other inland and mountain study sites (Fig. 1, Table I). However, we cannot exclude the possibility that *B. hindei* were present at these sites, but not trapped, owing to low densities and relatively few trapping nights.

#### Morphological differences and karyology

On the basis of six body measurements, animals from lower latitudes appear to be larger than those from near the equator but sample sizes did not allow statistical analysis (Table III, Fig. 3a-f). The four karyotypes showed a diploid chromosome number of  $2N = 52$ . This is the first report of the *Beamys* karyotype.

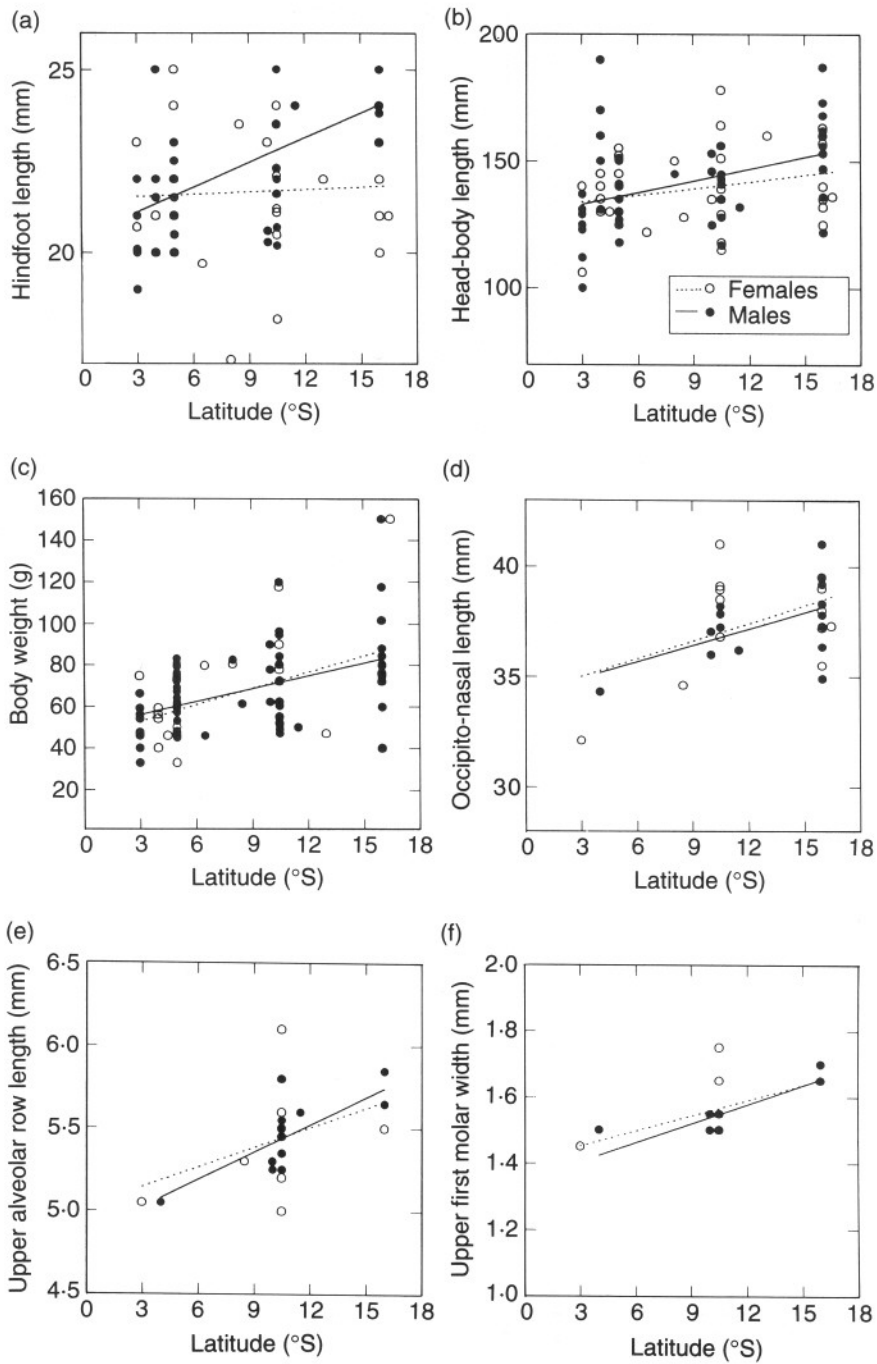
FIG. 3. (a-f) Variation in morphological measurements of *Beamys* with latitude.

TABLE IV

Number of lesser pouched rats (*Beamys hindei*), spiny mice (*Acomys wilsoni*) and soft-furred rats (*Praomys sp.*) caught in four different habitats within Arabuko-Sokoke Forest

	Number of trap nights	<i>Beamys</i>		<i>Acomys</i>		<i>Praomys</i>	
		No. caught	% capture success	No. caught	% capture success	No. caught	% capture success
<i>Afelia</i>	594	68	11.4	2	0.3	2	0.3
<i>Brachystegia</i> —intact	396	15	3.8	0	0.0	1	0.3
<i>Brachystegia</i> —degraded	594	7	1.2	6	1.0	1	0.3
<i>Cynometra</i>	594	0	0.0	0	0.0	0	0.0



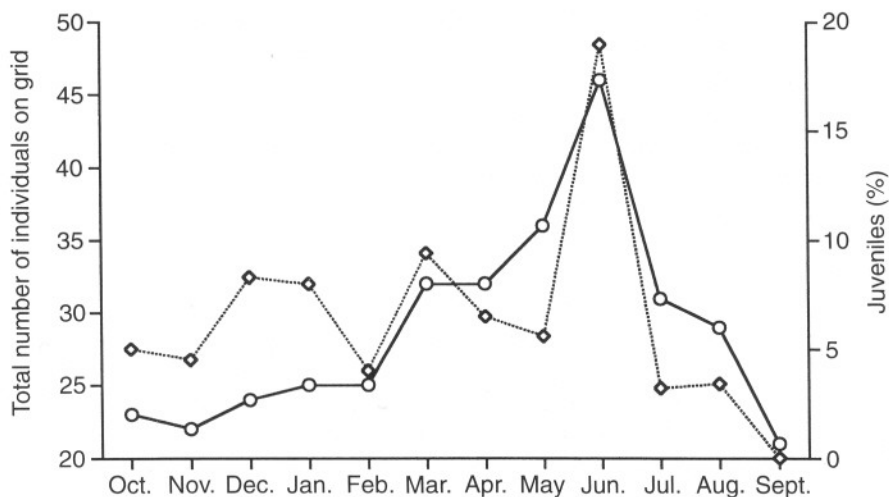


FIG. 4. Total number of animals captured on the grid (—○—) and the percentage of juveniles (---◇---) in each month of the study.

#### Habitat use

Sites where *Beamys* were recorded during this study were all evergreen or slightly deciduous forests, on sandy soils and less than 400 m in altitude. Since only Litipo contained a permanent river, a continuous supply of water is clearly not a requirement. There were no obvious differences in the habitat or altitude at the sites where *B. hindei* were and were not trapped (Table I). Forests containing *Beamys* were no larger and did not support a less diverse rodent community than those where *Beamys* were not recorded (comparing forest area,  $t = 1.74$ ,

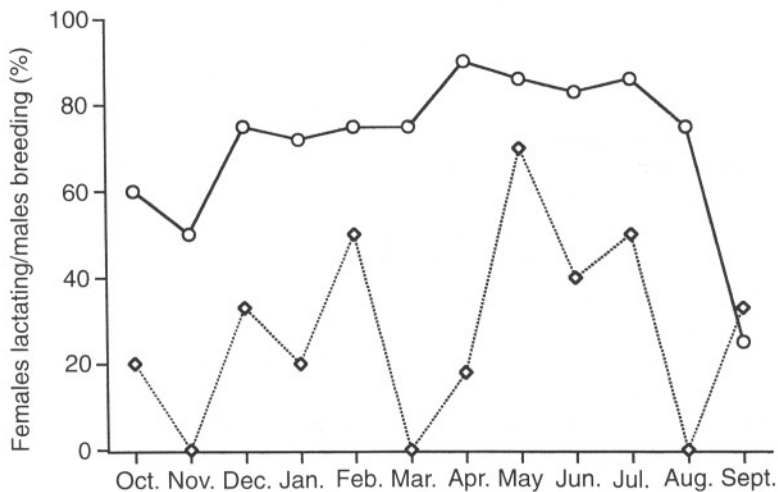


FIG. 5. The percentage of females lactating (---◇---) and males in breeding condition (with scrotal testes —○—) in each month of the study.

$n = 7, 11$ , NS; comparing number of small rodent species recorded during surveys other than *Beamys*,  $t = 1.85$ ,  $n = 9, 11$ , NS; Table I).

Within Arabuko-Sokoke Forest, the *Afzelia* habitat supported the highest densities of *B. hindei*, while the *Brachystegia* habitat supported relatively low densities (Table IV,  $\chi^2 = 119.1$ ,  $d.f. = 3$ ,  $P = 0.0001$ ). No small rodents of any sort were captured in the *Cynometra* habitat. Trapping success was significantly lower in the degraded *Brachystegia* than in undisturbed *Brachystegia* ( $\chi^2 = 7.52$ ,  $d.f. = 1$ ,  $P < 0.01$ , Table IV). The small rodent community was dominated by *B. hindei* in both the *Afzelia* and the *Brachystegia* forest, comprising 88% of captures (Table IV).

Using stepwise regression techniques to examine the relationship between habitat variables and the abundance of *B. hindei* in the *Brachystegia* and *Afzelia* habitats (data from the *Cynometra* habitat were not included since no *B. hindei* were trapped there) showed that they were more abundant where the density of understorey cover below 4m was higher (COVER<4) and the mean distance to canopy trees (MTDIS) lower. Using the total number of *B. hindei* trapped over three nights along each grid line as the dependent variable Y, the predictive equation was:

$$Y = 1.785 - 0.187 \text{ MTDIS} + 0.077 \text{ COVER} < 4, F = 37.9, P < 0.05$$

On the basis of vegetation structure, there appeared to be no reason why *B. hindei* should not occur in the *Cynometra* habitat, as the *Cynometra* forest actually had more cover in the <4m band, and canopy trees were closer together than in either the *Brachystegia* or *Afzelia* habitats (mean cover <4m in *Cynometra*, *Afzelia* and *Brachystegia* habitats = 51.8%, 39.0% and 24.7%, respectively, ANOVA,  $d.f. = 2, 62$ ,  $F = 24.9$ ,  $P < 0.01$ ; mean distance to nearest canopy tree in the three habitats = 5.9m, 7.6m, and 11.2m, respectively, ANOVA,  $d.f. = 2, 62$ ,  $F = 18.6$ ,  $P < 0.05$ ). There was no effect of distance to nearest surface water on *Beamys* abundance in either the *Brachystegia* or *Afzelia* habitats.

#### Population dynamics

We caught and trapped 101 different *B. hindei* over 12 months on the one ha grid in the *Afzelia* habitat, with an average trapping success of 6.7%. The total number of animals on the grid ranged from 21 to 46, reaching a peak in June (Fig. 4), and densities ranged from 14.0/ha to 30.7/ha. The overall sex ratio of the population using individuals weighing over 40g was 1.3:1 (males:females). Breeding appeared to continue throughout the year, with lactating females being caught in all months except November, March and August (Fig. 5). The percentage of females lactating was not significantly correlated with monthly rainfall ( $r = 0.405$ ,  $n = 12$ ,  $P > 0.05$ ), although the highest percentage was recorded in May, at the peak of the rainy season. Females bred at least once per year. The percentage of juveniles in the population showed no obvious seasonal changes, except for a peak in June (Fig. 4, correlation between % of immatures and monthly rainfall = 0.093,  $n = 12$ , NS).

The percentage of males found with descended testes was fairly constant between December and August, only dropping in the middle of the dry season between September and November (Fig. 5). There was no significant correlation between the percentage of males in breeding condition, and monthly rainfall ( $r = 0.505$ ,  $n = 12$ , NS). However, retraps of known individuals showed that this was not due to individual males remaining in breeding condition throughout the year, but because different individuals came into breeding condition at different times of the year.

The range in weights of breeding adults was considerable, for males from 50 to 97g, and for

females from 45 to 72 g. Males were on average heavier than females (mean  $\pm$  S.E. for males = 61.0 g  $\pm$  1.6,  $n = 121$ , and for females = 52.0 g  $\pm$  1.1,  $n = 66$ ;  $t = 3.89$ ,  $P < 0.001$ ). Using only the data from individuals in breeding condition (scrotal testes/parous females), neither males nor females showed any significant weight change between the dry and wet season (two-way ANOVA: effect of sex,  $F_{1,99} = 66.4$ ,  $P = 0.0001$ ; effect of season,  $F_{1,99} = 2.33$ , NS).

## Discussion

### *Distribution and taxonomy*

Although *B. hindei* is considered to be rare (Kingdon, 1974), the new records from this study suggest that it is more widely distributed than previously thought and is abundant in suitable habitats. It has now been recorded from several forest sites on the Tanzanian and Kenyan coast where surveys have been carried out. Inland, *Beamys* seems to be rare, although the type specimen of *B. hindei* was trapped near Taveta and the genus has also been reported from Kilimanjaro (Kingdon, 1974). In Malawi, *Beamys* occurs in the broad-leaved forests on the highlands between approximately 700 and 2000 m (Hanney & Morris, 1962). Although *B. hindei* can no longer be considered as particularly rare, the coastal forest which provides its main habitat is becoming increasingly threatened (Burgess *et al.*, 1992; Burgess, FitzGibbon & Clarke, 1994) and the large number of localities where *B. hindei* were not trapped still suggests a patchy distribution.

*Beamys major* Dollman 1914 was originally described as being much larger than the type species *B. hindei*, although Dollman must have known that the *B. hindei* type was a very young female (Hubbard, 1970). Hanney & Morris (1962) discussed the number of foot pads and the presence or absence of a hallux as a possible discriminatory character, but Meester & Setzer (1971) again separated *B. hindei* and *B. major* on the basis of hindfoot length only; approximately 25 mm in *B. major* and only 20 mm in *B. hindei*. Although our data were too incomplete for a statistical description of sexes, age groups and localities, we could show geographical differences. The overlap in hindfoot length (and other external measurements) of individuals from different sites is so large that any discrimination based on this character is impossible. Nevertheless, there seems to be a tendency for animals to be larger further south (Fig. 3).

Thus, our data do not provide any evidence for the existence of two distinct species. Instead, the results suggest that there is a clinal variation in size of *Beamys* from north to south, and there is probably just one single species, as already suggested earlier by Ansell & Ansell (1973) and accepted by Corbet & Hill (1991). Our data certainly confirm the earlier call for a serious revision of the genus (Musser & Carleton, 1993), including karyological, biochemical and molecular data.

### *Habitat use*

Density estimates from the *Afzelia* habitat in Arabuko-Sokoke Forest show that *B. hindei* can reach high densities comparable with those recorded for other small forest rodents (Delany, 1986), when conditions are favourable. Densities were, however, far lower in the two other main habitat types, *Brachystegia* and *Cynometra*, while *B. hindei* were completely absent from many of the coastal forests surveyed in Tanzania. A number of factors have been predicted to influence the distribution of *B. hindei*, in particular the availability of water, competitive exclusion, the

structure of the vegetation, the suitability of the soil for burrow construction, and the availability of suitable food plants.

Although the availability of surface water was thought to be a major factor influencing the distribution of *B. hindei*, this study provided no support for this hypothesis. In addition, the available data do not provide support for competitive exclusion—forests where *B. hindei* occurred supported as many species as forests where they were not reported. The coastal forests are particularly depauperate, but the fact that *B. hindei* have not been recorded in the species-rich forests of inland East Africa is probably due more to the patterns of colonization (Rodgers, Owen & Homewood, 1982) than to competitive exclusion.

Although *Beamys* have now been recorded in a wide range of forest types, as well as open woodland and cassava plantations, in Arabuko-Sokoke Forest *B. hindei* were more common in areas with a dense shrub layer and where canopy trees were closely spaced. A combination of fire and intensive felling of canopy trees in the degraded *Brachystegia* habitat has reduced the amount of cover and resulted in less favourable habitat for *B. hindei*. Although modified forest habitats are often reported to support a more diverse rodent community, this is often at the expense of forest-adapted species (Jeffrey, 1977; Delany, 1986).

The fact that *B. hindei* tend to be restricted to coastal forests suggests that soil type may be influential in determining the distribution of this species, in particular that they may prefer areas with sandy soils that facilitate burrow construction. These burrows may provide protection from predators, reduce daily and seasonal variation in ambient temperatures, and provide a store for cached food (Ellison, 1993). In Arabuko-Sokoke Forest, *B. hindei* were recorded in the two sandy soil habitats but absent from the *Cynometra* habitat on hard *margarini* soils, despite apparently suitable dense vegetation. However, because no information is available on the diet of *B. hindei*, we are unable to rule out the possibility that a lack of suitable food plants may explain the absence of *B. hindei* from this particular habitat.

#### Population dynamics

Although *Beamys* from Malawi were reported to be seasonally polyoestrus during the wet and early dry season (Hanney & Morris, 1962), reproduction in the Arabuko-Sokoke population and in captivity is not limited to a particular time of year (this study and Egoscue, 1972, respectively). The ability of *B. hindei* to use stored food supplies (Hanney & Morris, 1962) may facilitate breeding when food is not plentiful (Vander Wall, 1990) and this is supported by the finding that body weight did not vary significantly with season (as also reported in a closely related species, the pouched mouse, *Saccostomus campestris*, Ellison, Bronner & Taylor, 1993). Since the main food source of *B. hindei* is fruits and seeds (Hanney & Morris, 1962), the peak in proportion of females lactating in the middle of the rainy season would be adaptive, with young being produced in the late wet season and early dry season, as fruits and seeds became abundant.

Compared to African savanna habitats, forests—both deciduous and evergreen—are relatively stable environments and, as a result, forest-adapted species usually show different reproductive parameters to species that are widely distributed and inhabit both savanna and forest (Wirminghaus & Perrin, 1993). In captivity, female *B. hindei* did not usually start to breed until they were at least five months of age, average litter size was 2.8 (range 1–5 young), the period of sucking was relatively long (5–6 weeks), the minimum interbirth interval was 62 days, and individuals lived to three to four years of age (Egoscue, 1972). Compared with rodents inhabiting less stable environments, these parameters are indicative of a forest-adapted species.

In addition, *B. hindei* in Arabuko-Sokoke Forest maintained a relatively stable population density and a low but almost continuous level of juvenile recruitment throughout the year. In contrast, densities of savanna species such as *Mastomys* often increase by 5–7 times and sometimes over 20 times during the year, particularly when they occur in agricultural or fallow land (Leirs, Verhagen & Verheyen, 1993).

In conclusion, the results of this study suggest that *B. hindei* is more widely distributed than previously thought, although the large number of sites where they were not trapped still suggests a patchy distribution and the reasons for this remain unclear. *Beamys*' preference for dense understorey vegetation and soft sandy soil in which to construct its burrows may be contributory factors, while its ability to cache food make it particularly well adapted to seasonally dry forests where food is in short supply for part of the year. In addition, Rodgers *et al.* (1982) noted that the coastal mammal fauna is, in general, characterized by low species diversity and a low similarity index between forests, and suggested that this was due to the small size of the forests and their low habitat diversity, which increased the probability of chance extinctions during the unstable history of fluctuating sea and ground levels and water and river regimes.

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