observed. Occasionally the central core is composed of subunits which also form a tubular structure. Dense core tubuli are linked in regularly spaced arrangements: 12–180 tubules are longitudinally orientated within the threads. In the spermatophore wall the arrangement resembles dense connective tissue of vertebrates.

Clusters of dense core tubuli also occur between developing male germ cells in the testes. Regularly linked tubuli are attached to groups of mature spermatozoa to mould the envelope of the spermatophores in the proximal region of the sperm ducts. Released spermatophores tend to stick firmly to the tube or trunk of the animal even after fixation, dehydration and embedding. This indicates remarkable adhesive properties. When spermatophores are exposed to seawater, the regular arrangement of the dense core tubuli is gradually lost and the spermatophore wall starts to disintegrate[6]. The filament

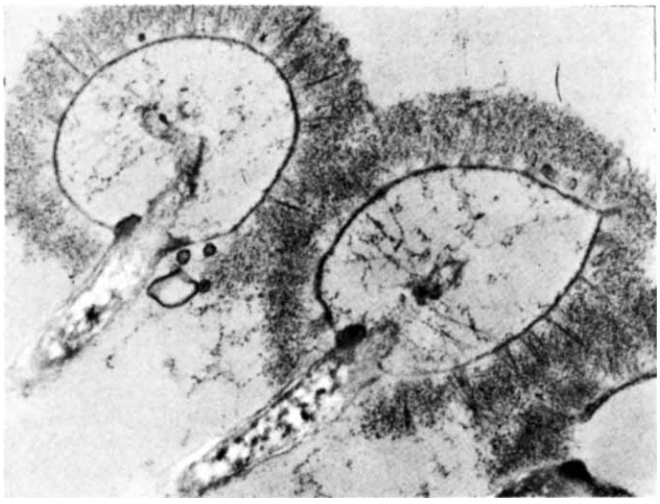

Fig. 3 Two stalked vesicles of the spermatophoral filament. Delicate spines project from the surface into the fibrous cover (×30,500).

uncoils, and at intervals it has areas of radiating stalked vesicles (Fig. 3). Within the sperm ducts these vesicles are smaller, from which I conclude that the filament uncoils through the swelling of the vesicles. They are probably identical with the capitate processes revealed by light microscopy[3,7]. Fibrous, sticky material covers the surface of the vesicles, reinforced by delicate spines (Fig. 3). The dense threads found in the sperm ducts are also released and frequently appear near the spermatophores in sections. Undoubtedly, the stalked vesicles of the filament and the dense threads form an effective adhesive apparatus and flotating device.

My investigation adds further support to the view that the released spermatophores of *Siboglinum* find their way passively without 'some form of copulation' to a receptive female[1,5]. But further observations are required to elucidate the path of the released spermatozoa to the eggs.

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Blood-sucking flies and primate polyspecific associations

PRIMATE polyspecific associations are likely to be an effective means of reducing the number of fly bites individual monkeys receive[1]. The probability of acquiring a vector-borne disease, and the severity of that disease increases with the number of fly bites an animal receives[2–4]. Bait animals placed in groups are known to attract fewer individual mosquitoes per bait individual than are bait animals placed singly[3,5]. Mean group size of the mangabey, *Cercocebus albigena* is about 13 in Kibale Forest, Uganda, and the mean group size of *Colobus badius* and *Cercopithecus ascanius* are 50 and 35 respectively[6]. Associations of groups of these species are likely to reduce significantly the number of dipteran bites individual monkeys receive[1,7]. Other explanations proposed for primate polyspecific associations include increased food location abilities, and increased predator detection and avoidance[8,9]. I report here the correlation of the temporal occurrence of *C. albigena* polyspecific associations with the activity of biting and sucking flies, *C. albigena* feeding and other activities, and the temporal occurrence of attacks by the crowned eagle-hawk (*Stephanoaetus coronatus*) (eagles are the only known predator of these monkeys). The study was carried out in the Kibale Forest, Ngogo Reserve.

On 5 d each month from January to September 1975, I followed a group of *C. albigena* from dawn to dark. Data on mangabey activity and polyspecific associations were recorded during four 5-min periods each hour (0–5, 15–20, 30–35 and 45–50 min). During each 5-min period as many individual *C. albigena* as possible were located, and the predominant activity of each during a 10-s interval was recorded. 'Moving', 'sitting', and 'feeding' are the activity categories used here. The location of each *C. albigena* observed was plotted on a map (4 cm = 100 m) of the study area. To record daily and hourly movements, net group displacements were measured from one 5-min period to the next. The actual distance measured was from the central focus of individuals in one 5-min period, to the central focus of the next. A polyspecific association was defined as the presence of more than one individual of another species within 20 m of the nearest mangabey. Times of eagle attack were recorded as they occurred. Attacks took the form of an eagle flying fast and low through the tree tops and branches, usually through the midst of the mangabey group. Activity of biting and sucking flies was determined using myself as bait. On 4 d I placed myself (naked arms and legs) on a platform 20 m above the forest floor, and remained there from dawn to dark. All flies (mosquitoes and others) biting me were recorded each hour, and when possible I killed all flies actually biting. Data from all days have been aggregated.

The *C. albigena* group took part in polyspecific associations on 43 of the 45 d of observation. Of a total 513 associations, 90.8% involved *C. ascanius*, 22.01% *C. badius*, 5.07% *Colobus guereza*, 1.75% *Papio anubis* and 0.59% *Cercopithecus Thoesti*. There was little interaction between species during the associations. On two occasions juvenile *C. albigena* attempted to join play groups of the other species. Other interactions were confined to adult *C. albigena*, displacing or occasionally chasing *C. ascanius*.

The occurrence of *C. albigena* in polyspecific associations was not equally distributed throughout the day ($\chi^2 = 19.71$, d.f = 9, $P < 0.05$) (Table 1). There was a significant correlation between the hourly occurrence of polyspecific associations and the hourly activity of biting flies ($r_s = 0.63$, $N = 10$, $P < 0.05$) (Table 1). Because the data on Kibale fly activity are sparse, I also compared the temporal pattern of associations with the timing of mosquito activity in rainforest in Bwamba County, Uganda[10]. The correlation is significant ($r_s = 0.66$, $N = 10$, $P < 0.05$) (Fig. 1).

There were no significant correlations between the hourly occurrence of primate polyspecific associations and eagle attacks ($r_s = 0.119$, $N = 10$, $P > 0.05$), mangabey feeding activity ($r_s = 0.08$, $N = 10$, $P > 0.05$), sitting activity ($r_s = -0.08$, $N = 10$, $P > 0.05$), movement activity ($r_s = 0.42$, $N = 10$, $P > 0.05$), and the hourly distance travelled ($r_s = -0.05$, $N = 10$, $P > 0.05$) (Table 1).

Table 1 Polyspecific associations, feeding moving and sitting activities, hourly distances travelled, eagle attacks and the number of biting flies of a group of mangabeys

Time	Total associations	Feeding observations	Sitting observations	Moving observations	Mean distance travelled (m)	Eagle attacks	Biting flies
0800–0900	57	308	170	200	107	3	12
0900–1000	41	367	123	209	133	1	5
1000–1100	42	410	145	187	100	4	5
1100–1200	35	400	157	196	118	4	1
1200–1300	24	298	178	241	141	1	9
1300–1400	54	364	167	168	95	2	11
1400–1500	36	321	158	218	164	2	11
1500–1600	42	408	105	225	121	0	8
1600–1700	46	452	108	198	147	1	31
1700–1800	49	338	126	211	118	0	61
r_s		0.08	−0.08	0.42	−0.50	0.119	0.63
P		NS	NS	NS	NS	NS	<0.05

The diurnal periodicity found in the occurrence of primate polyspecific associations is in agreement with studies on other African primates[11], and previous work on Kibale primates[8]. During the early mornings I noted that several species had frequently slept adjacent to one another. The dawn and dusk peaks in polyspecific associations probably represent the iniation and termination of night-long associations. As the *C. albigena* group slept in 45 different places on 45 different nights, there does not seem to be any shortage of sleeping sites.

These data do not support the possible existence of increased predator surveillance, increased food detection abilities or chance as causal to primate polyspecific associations. Predator detection may well be improved during the associations, but it does not explain the temporal patterns. Feeding by two or more species in the same tree or in the same area was common, and one species may well use another as an aid in food location. But again, *C. albigena* feeding activities bore no significant relation to the temporal pattern of association. Predation, food and chance seem to do little more than add noise to a pattern that is probably due to another factor.

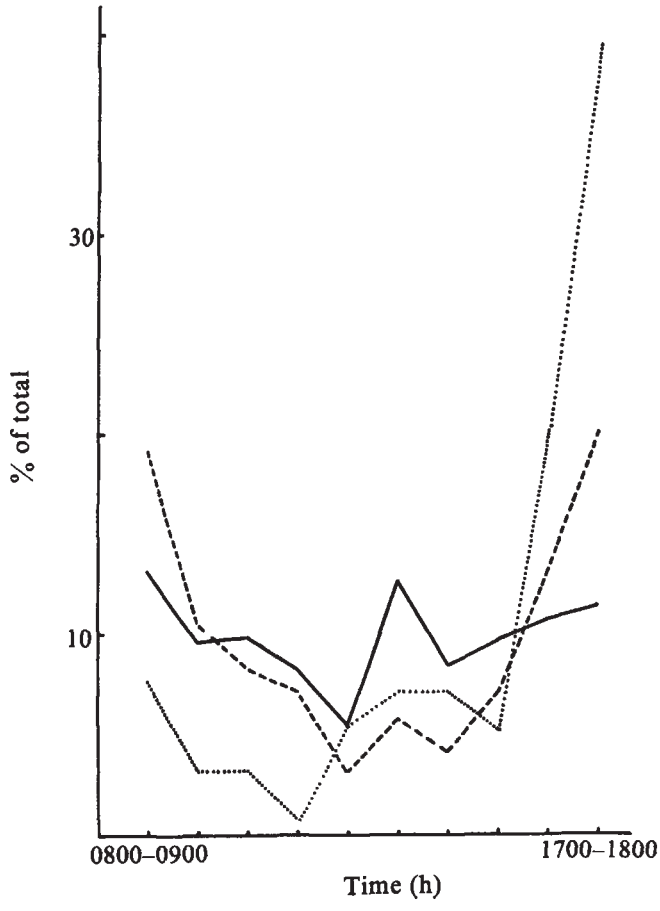

Fig. 1 *Cercocebus albigena* polyspecific associations and the activity of Kibale biting flies and Bwamba mosquitoes. — · — · —, polyspecific associations: — — — Bwamba mosquitoes; · · · · Kibale biting flies.

The importance of the significant correlation between polyspecific associations and biting fly activity is dependent on the importance of dipteran-borne disease to monkeys, and on the probability of polyspecific associations lowering the number of fly bites individuals receive. The size of the primate groups involved, and the published data on effects of number of bait animals suggest that polyspecific associations could easily reduce the number of bites received by individual monkeys. *C. albigena*, *C. ascanius*, and *P. anubis* all suffer from *Hepatocystis kochi* ('monkey malaria') which is present in Kibale[12]. *C. albigena*, and *P. anubis* suffer from *Dirofilaria sp.* and *C. ascanius* have been found with microfilaria[12]. All Kibale monkeys suffer from yellow fever, and other arboviruses are probably present[12]. Experimental infection of three *C. ascanius* with yellow fever resulted in fevers for 1–3 d, and the death of one due to an 'intercurrent infection'[12]. Such effects are likely to have considerable impact on free-living monkeys. A mechanism exists for reducing the number of fly bites received per individual monkey. The temporal pattern of this mechanism correlates with the times of day when it could function to reduce the number of fly bites per individual monkey. Disease organisms using flies as vectors are prevalent among the Kibale monkeys, and seem capable of being a strong selective factor acting to promote primate polyspecific associations.

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