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NONFLYING MAMMAL POLLINATION OF SOUTHERN AFRICAN PROTEAS: A NON-COEVOLVED SYSTEM[1]

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ABSTRACT

Traits characterizing those proteas adapted for pollination by nonflying mammals include: bowl-shaped heads bearing fleshy bracts, these borne on short, flexible peduncles, often at or near ground level (geoflorous) and hidden beneath dense overlying foliage (cryptic), and producing copious nectar (ca. 1.8 ml/head, standing crop); individual florets with wiry, yet flexible styles and a nectar-stigma distance of 10 mm; a distinctive yeastlike odor; nocturnal anthesis; sucrose-rich nectar with a high total carbohydrate content (ca. 36%) and a relatively low proportion of amino acids. Evidence of small-mammal visitation to protea flowering heads includes: the presence of pollen on the rostra (carried in a position to effect pollination when foraging for nectar); the transport of fluorescing powders to flowering heads both within and between plants; the accumulation of small-mammal feces in flowering heads, and the destruction of exclosure bags containing nectar-rich heads. The period of greatest small-mammal activity (1800 hr.) coincides with maximum flower opening. T maze experiments showed that small mammals, when given a choice between typically bird-pollinated proteas and those having characteristics of flowers pollinated by nonflying mammals, always foraged on the latter. That small mammals can effect pollination is indicated by their foraging behavior on flowering heads while in captivity, the morphological "fit" between individual florets and the rostra of small mammals, and by selective exclosure experiments that reduced seed set (50% and 95%) when small mammals were excluded and visitation was limited to insects (mostly honey bees). The nectar produced

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by these proteas meets the energy requirements of the small-mammal community for only several days annually, thus coevolution is impossible. Proteas adapted for pollination by nonflying mammals have evolved unilaterally, probably from bird-pollinated prototypes, possibly in response to progressive decrease in population size. Recent discoveries in the Neotropics of flowers with some similar characteristics and also pollinated by nonflying mammals support the existence of a worldwide class of flowers adapted for such pollinators.

The pollination of flowers by nonflying mammals was first mentioned by Kerner (1895, v. 2, p. 230) and was discussed nearly 50 years ago by Porsch (1934, 1935, 1936a, 1936b). The subject was not given further attention, however, until Morcombe (1968) suggested pollinatory relationships between various proteaceous flowers and nonflying mammals in the southwestern Australian flora. Rourke and Wiens (1977) reviewed the problem and noted that various floral features convergent in Australian and South African Proteaceae suggested adaptations for pollination by nonflying mammals. The following year Wiens and Rourke (1978) offered substantive evidence for pollination by nonflying mammals (mostly rodents) in two species of South African proteas. Two previous studies of presumably bat-pollinated African plants, viz., the baobab (Bombacaceae) (Coe & Isaac, 1965) and *Maranthes* (Chrysobalanaceae) (Lack, 1977) demonstrated visitation and nectar feeding by bush babies (*Galago crassicaudatus* Geoffroy) and genets (*Genetta tigrina* Schreber), respectively. Recent interest in the subject has resulted in a number of publications: Sussman and Raven (1978) reviewed the problem and reported pollination by arboreal Madagascan mouselike lemurs; Sleumer (1955) and Carpenter (1978a) reported evidence for the pollination of eastern Australian banksias by sugar gliders (*Petaurus breviceps* Waterhouse) and the indigenous placental bushrat (*Rattus fuscipes* Waterhouse), respectively. Holm (1978) and Ford, Paton, and Forde (1979) commented on the problem and Armstrong (1979) reviewed the subject for Australia generally. Wiens, Renfree, and Wooller (1979) and Hopper (1980) studied the pollination of *Banksia* and other flowers by the southwestern Australian marsupial honey possum (*Tarsipes rostratus* = *T. spenserae* Gray). In the New World, Prance (1980) observed probable pollination by cebus monkeys; and Janson, Terborgh, and Emmons (1981) reported extensive visitation and apparent pollination in Bombacaceae and Combretaceae in the Amazon by monkeys [including the small (100 g) pigmy marmoset], opossums, and procyonids. Lumer (1980) observed pollination of *Blakea* (Melastomataceae) by rodents in Costa Rica, and Steiner (1981) discovered probable pollination by opossums in *Mabea* (Euphorbiaceae) in Panama. The suggestion of rodent pollination in Hawaiian *Freycinetia* (Degener, 1945) is apparently in error (Cox, 1981).

We report the results of three seasons of field studies on several species of southern African species of *Protea* (Proteaceae) with characteristics indicating adaptations for nonflying mammal pollination (hereafter referred to as NMP proteas), as contrasted to proteas with features showing adaptations for bird pollination (BP proteas) (Wiens & Rourke, 1978). Whenever possible the two systems are compared. These observations cover the winter–early spring (August–September) field seasons of 1978–79 and the summer (February) field season of 1980 in the Cape region of South Africa. Wiens and Rourke (1978) established that several murid rodents and a few additional small mammals visited the flowering heads of *Protea amplexicaulis* (Salisb.) R. Br. and *P. humiflora* Andr., as evidenced by the presence of protea pollen loads on the rostra of captured animals. They further demonstrated that the flowers and small mammals possessed the respective structural and behavioral features to effect pollen transfer, and that several rodents foraged readily and non-destructively on the nectar from flowering heads of several proteas while in captivity.

This study has two broad objectives: first, to test further the proposition that these flowers are pollinated by nonflying mammals and to gain a general understanding of how the pollination system functions as an integrated whole; and secondly, to consider why this unusual animal-flower relationship may have evolved. Specific areas of study included: (1) the general nature of the plant association in which NMP proteas occur, (2) the composition and activity patterns of the associated small-mammal community, (3) the temporal patterns of anthesis, nectar secretion, and odor production, (4) nectar volume, total sugar content, carbohydrate and amino acid composition, (5) stylar and general floral struc-

TABLE 1. The number of small mammals examined for pollen loads and the proteas with which they were associated.

Protea	Small Mammal					Study Site
	Acomys subspinosus	*Aethomys namaquensis*	*Elephantulus edwardii*	*Praomys verreauxi*	*Rhabdomys pumilio*	
P. amplexicaulis[c,d]	15	31[a,b]	2	3	16[a]	Jonasplaats, see text
P. cryophila[c]	1[a]	2	5			Sneeubergnek, Cedarberg Mts., E of Citrusdale
P. effusa[c]		1	3	2	4	East bench, Murray Farm, above Gydo Pass N. of Ceres
P. humiflora[c,d]	13[b]	16[a,b]	2[a,b]	3[a]	14[a,b]	Jonasnek
P. recondita[c]		3	3[b]	2	4[b]	Same as *P. effusa*
P. restionifolia		3[a]				Pocskraal, N. shore Stormsvlei reservoir, S. of Worcester
P. scabra		[a]				W. of Villiersdorp
P. sulphurea		2[a,b]			1[b]	W. of Ouberg Pass, NE of Montague

[a] Captive animals of this species foraged on flowering heads of the respective protea in a manner to assure effective pollination.

[b] Animals with numerous protea pollen grains (>100 and often >1,000) in fecal samples taken directly from the colon.

[c] Some heads of these protea species contained fecal pellets.

[d] In addition to the animals listed, single specimens of *Crocidura* sp. and *Graphiuris ocularis* were trapped around *P. amplexicaulis* and one *Dendromus melanotis* and a *Mus minutoides* were captured in *P. humiflora* stands.

ture, (6) genetic compatibility and pollen viability, (7) the energy resources protea nectar provides to the small-mammal community, and (8) the relative importance of insects as pollinators of NMP proteas.

RESEARCH AREAS AND SPECIES STUDIED

The NMP proteas utilized in this research are endemic to the southwestern Cape flora (fynbos) of South Africa. This vegetation is unique, with (1) exceptionally rich species diversity (ca. 8,850 species) and high endemism (73.1%), (2) adaptations for periodic burning, (3) a virtual absence of indigenous trees, (4) a low percentage of annuals, and (5) restriction to the Table Mountain Sandstone, which is highly depauperate nutritionally especially for P and N. Uplift and erosion of this formation have produced a highly dissected landscape comprised of many small mountain ranges with diverse elevations, precipitation, and soils. Predictably, numerous species exist only as small populations and in isolated habitats (Goldblatt, 1978; Taylor, 1978; Kruger, 1979).

Although the vegetation is unique, the animal community is not. The small-mammal community, for example, is composed largely of species with ranges extending far beyond the distribution of the Cape flora. Likewise, the bee fauna is not especially noteworthy (Michener, 1979), although bee-pollinated plants such as legumes constitute an important element of the flora (Goldblatt, 1978).

The NMP protea study sites are indicated in Table 1. BP proteas used for comparative purposes included *P. arborea* Houtt., *P. laurifolia* Thunb. (both from Jonasnek), and *P. repens* (L.) L. (from Jonasplaats, see section on *P. amplexicaulis*). These proteas are illustrated in Rourke (1980).

PROTEA HUMIFLORA AND *P. AMPLEXICAULIS*

Protea humiflora was studied during late winter–early spring (mid-August to mid-September) 1978–79 on Jonaskop, a prominent mountain in the Riviersonderendberge, approximately 50 km south of Worcester and 100 km east of Cape Town. On Jonaskop, *P. humiflora* forms dense stands along a restricted access road to the summit. Two adjacent study sites (A and B), each

TABLE 2. Density, species composition, and composite home range data from live trapping grids in stands of *Protea humiflora* at Jonasnek.

	1978						1979					
	Site A			Site B			Site B			Adjusted Home Range Length (m)		
Species	Number of Ind.	Number/ Hec.	% Comp.	Number of Ind.	Number/ Hec.	% Comp.	Number of Ind.	Number/ Hec.	% Comp.	N	$\bar{X}$	Range
Acomys subspinosus	1	5	2.6	20	95	35.1	7	33	35.0	5	39.3	(35.0–47.5)
Aethomys namaquensis	1	5	2.6	13	62	22.8	12	57	60.0	6	46.2	(27.5–58.0)
Praomys verreauxi	11	52	28.9	4	20	7.0				4	35.4	(27.5–45.5)
Rhabdomys pumilio	25	119	65.8	17	81	29.8	1	5	5.0	17	37.8	(25.0–58.0)
Elephantulus edwardii				3	14	5.3				3	34.6	(27.5–44.2)
Totals	38	181		57	272		20	95				

approximately 2,100 m², were selected along this road at approximately 700 m (hereafter referred to as Jonasnek). During the 1978 field season the species composition, frequency, and cover were determined for the perennial plants on sites A and B. Both sites were divided into 10 m² quadrats, each plant was identified and its position and cover plotted on graph paper and the location of each Sherman trap noted.

Various observations were also made on *P. amplexicaulis* at somewhat higher elevations on Jonaskop (ca. 1,000 m) in an area known locally as Jonasplaats. This locality is relatively flat with many scattered individuals of *P. amplexicaulis* occurring along the east side of the access road (the west side of the road was burned in 1976).

SMALL-MAMMAL TRAPPING SYSTEM

METHODS

At the *P. humiflora* study sites at Jonasnek a square grid of 100 Sherman live traps [45 × 45 m (2,025 m²), approximately 5 m trap distances] was used to establish the species composition, activity, and movement patterns of the small-mammal community. Each trap was fitted with a switch mechanism and wired to a portable Esterline-Angus 20 Channel event recorder that indicated exact capture times and trap positions within the grid. This system facilitated rapid trap checking while minimizing human disturbances to the grid area. Traps were baited with rolled oats and peanut butter and checked at sunrise, sunset, and at variable intervals of 2 to 8 hours over a 24-hour period. Upon initial capture, animals were identified, weighed, sexed, checked for pollen load, marked with numbered ear tags (or toe-clipped), and released at the point of capture. The times and positions of recaptures were merely recorded, but animals were occasionally rechecked for pollen load. Rickart (1981) provides further details. Small mammals associated with the other proteas listed in Table 1 were captured in Sherman live traps (occasionally snap traps) set in irregular transects around, under, or on the branches of flowering proteas.

During the 1978 season, the grid system was operated successively at two sites. The first (Jonasnek A) consisted of a relatively level area and the second (Jonasnek B) was on an adjacent, rocky, north-facing, 25°–30° slope (the warm, dry slope in the southern hemisphere) approximately 100 m from site A. Vegetation was qualitatively similar on both sites, each having the same 34 species dominated by dense stands of *P. humiflora* and scattered individuals of *Leucodendron salignum* R. Br., with generally similar densities of herbaceous ground cover. Soil development was more extensive, however, on site A. The grid was run continuously in 1978 for 121 hours at

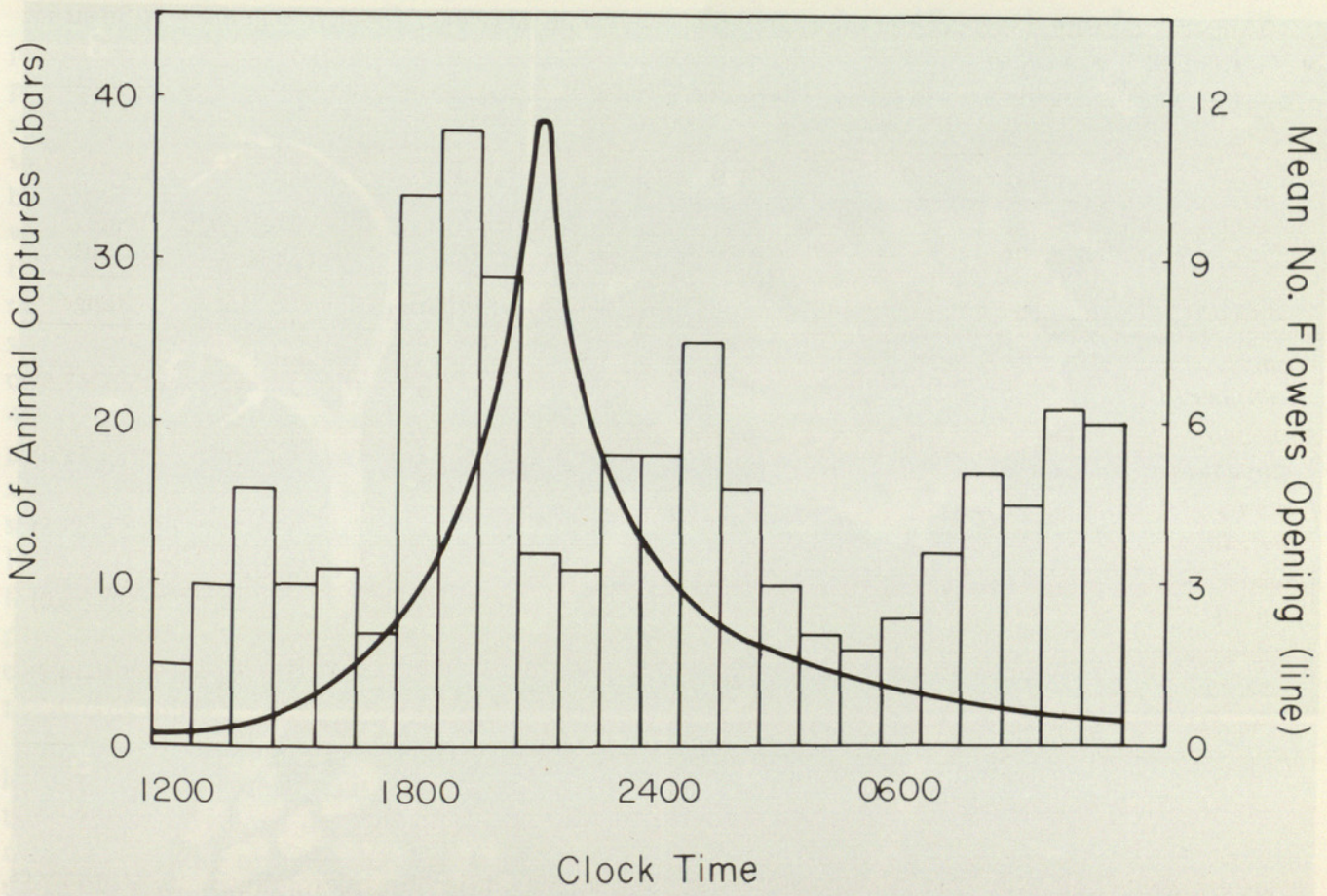


FIGURE 1. Cumulative activity patterns of all five small mammals occurring on the Jonasnek study sites (histograms) and the opening patterns of *P. humiflora* flowers (line).

site A and 193 hours at site B. In 1979 the grid was operated only at site B for a total of 355 hours. By the end of each trapping period, fewer than 5% of the animals captured during a 24-hour period were unmarked.

RESULTS

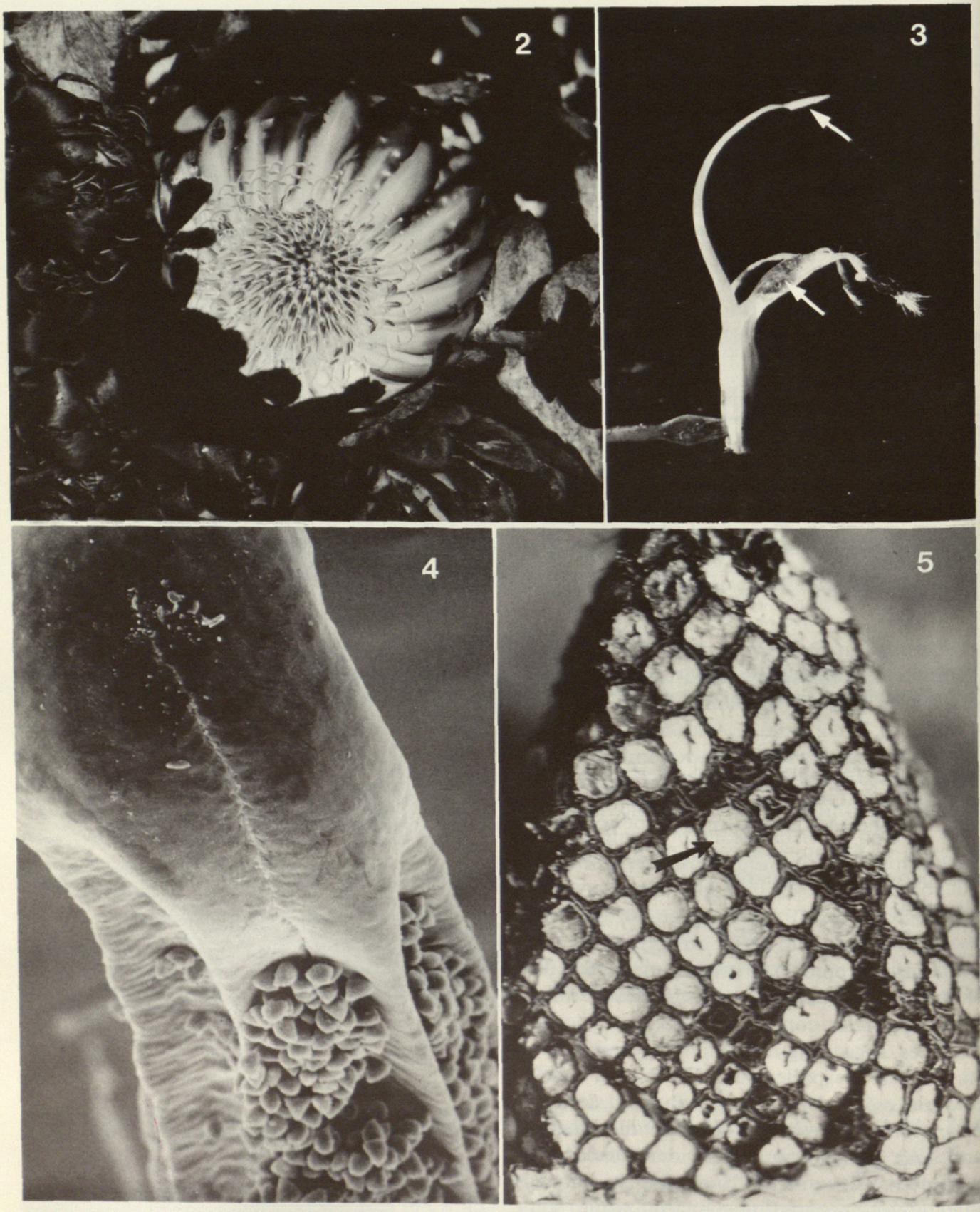
The grid-trapping data are summarized in Table 2. The 1978 data show considerable differences in species composition between the two grid sites, suggesting that microgeographic variation affects the species composition of the small-mammal community within individual stands of *P. humiflora*. The data from 1979 also show a profound reduction in overall densities on site B. Only densities of the Namaqua rock mouse (*Aethomys*) appeared unchanged, while Verreaux's mouse (*Praomys*) and the elephant shrews (*Elephantulus*) were absent. *Praomys* was not recorded anywhere in the study region the second year.

Mean home ranges for the various species were estimated from recapture data by calculating adjusted range length (distance between the farthest two points of capture plus the average inter-trap distance of 5 m) for individuals with five or more captures (Table 2). These values are probably underestimated because they approach the dimensions of the grid, which were relatively small for this purpose, particularly with respect to the Cape striped field mouse (*Rhabdomys*) and *Aethomys*. Figure 1 shows the cumulative activity pattern determined from capture times of individuals of all five species. Because some of the captures were probably artifacts due to the quick retrapping of previously released animals, recaptures that occurred less than one hour after the release were eliminated from the histogram. The diurnal activity shown is almost exclusively due to *Rhabdomys*. The remaining species are predominantly nocturnal. Of the 376 total captures, 232 (61.7%) occurred during the nocturnal-crepuscular period from 1800 to 0700 with highest activity levels occurring just after dusk.

FLORAL MORPHOLOGY OF NMP PROTEAS

PROTEA AMPLEXICAULIS—A TYPICAL NMP PROTEA

The inflorescence is a many-flowered, bowl-shaped head surrounded by dark, fleshy invo-



FIGURES 2–5. Floral and fruiting features of *P. amplexicaulis* and *P. humiflora*.—2. Flowering head (*P. a.*)—3. Individual floret, arrows indicate pollen presenter and nectar reservoir (*P. a.*)—4. SEM photo of style tip showing stigmatic slit and grooves of the pollen presenter region (*P. a.*) (× ca. 200).—5. Fruiting head with pistils cut transversely to expose sterile ovaries and those containing endosperm (arrow) (*P. h.*).

lucral bracts (Fig. 2). The peduncle is stout and short (3–4 mm), yet flexible, the heads appearing sessile along the branches. The heads are often borne near ground level (geoflorous) and are typically deeply hidden beneath dense, overlying foliage (cryptic). The heads are similar to *P. humiflora* in appearance and habit, but are generally more cryptic.

The individual flowers (florets) comprising protea heads are unusual (Fig. 3). The uniovulate pistil is surrounded by four dull-white, nonshowy perianth segments, each bearing a single, sessile anther. The unique feature of the floret, however, is the extremely wiry, yet flexible style, which readily withstands rough treatment. It has the dual function of pollen dispersal and reception. Pollen is deposited prior to anthesis onto a specialized, longitudinally grooved, apical region of the style known as the pollen presenter (Fig. 4). Although pollen covers most of the distal portion of the style, it does not initially reach the stigma itself, this being a highly reduced microscopic groove at the apex of the style (Fig. 4). Physical transfer of pollen is thus necessary even for self-pollination (see section on Genetic Compatibility). Stylar presentation of pollen also occurs in Asteraceae and the Campanulales, but the details differ.

In proteas the base of the style ruptures the lower perianth segments as it grows laterally from the perianth envelope during late bud development. Eventually only the base of the style and the pollen presenter remain enclosed by the perianth segments and the surrounding anthers. The rest of the style forms a bowlike structure outside the perianth just prior to anthesis (Rourke, 1980). Nectar secretion occurs at this time (see section on Nectar Production). Although anthesis, i.e., the emergence of the pollen presenter from the enfolding anthers and perianth segments, is mildly explosive, the pollen, because it is sticky, is not dislodged from the pollen presenter. In *P. amplexicaulis* and other NMP proteas examined, the three united perianth segments form a nectar reservoir about 10 mm below the stigma (Fig. 3). Because the flowers are in close proximity, however, the nectar often pools, particularly around the bracts.

ADAPTATIONS OF PROTEA FLOWERS FOR POLLINATION BY NONFLYING MAMMALS

The basic floral structures of proteas inferring pollination by nonflying mammals were summarized by Wiens and Rourke (1978) and discussed and compared to Australian Proteaceae by Rourke and Wiens (1977). These structures as illustrated for *P. amplexicaulis* include: (1) bowl-shaped heads borne on short (3–4 mm), stout peduncles, often with the outside of the bracts dark-colored, (2) copious, sucrose-rich nectar production with a high (36%) total carbohydrate composition, (3) often inflexed, wiry styles ca. 30–40 mm long, (4) cryptic, geoflorous, axillary positioning of the heads, and (5) a distinctive "yeasty" odor. In contrast, BP proteas produce (1) cylindrical heads with brightly colored bracts, (2) copious, hexose-rich nectar with a low (20–25%) total carbohydrate composition, (3) straight styles ca. 60–90 mm long, (4) conspicuous, brightly colored, terminally borne heads, and (5) no obvious odor.

The following proteas should be added to those previously suggested by Rourke and Wiens (1977) as exhibiting morphologies consistent with nonflying mammal pollination: *P. caespitosa* Andr., *P. convexa* Phill., *P. cryophila* Bolus, *P. denticulata* Rourke, *P. effusa* E. Mey. ex Meisn., *P. pendula* R. Br., *P. piscina* Rourke, *P. pruinosa* Rourke, *P. recondita* Buek ex Meisn., *P. roupelliae* Meisn., *P. tenax* (Salisb.) R. Br. The following species should be deleted: *P. lorea* R. Br., *P. scorzonerifolia* (Salisb. ex Knight) Rourke.

Many NMP proteas do not have cryptic heads although they are geoflorous, (e.g., *P. cryophila*), while one is cryptic but not geoflorous (*P. recondita*). Some proteas that are neither cryptic nor geoflorous [e.g., *P. nana* (Berg.) Thunb., *P. pityphylla* Phill., *P. pudens* Rourke, *P. witzenbergiana* Phill.] may also be pollinated by nonflying mammals, but verification is needed. Straight, as well as inflexed, styles probably also occur in many presumably NMP proteas; but the relatively short styles (ca. 30–50 mm) that maintain an effective stigma-nectar distance of about 10 mm are probably most important for a functional rostrum-stigma "fit" (Wiens & Rourke, 1978).

Protea cryophila is an impressive exception to the short-style character, yet it appears to prove the rule. Although the styles are ca. 80–90 mm long, the nectar secreted in mature buds is not retained at the point where the style arches out of the perianth tube, as occurs in *P. amplexicaulis* or *P. humiflora*. Instead, the tube is filled with nectar for about 70–80 mm up the tightly stretched perianth tube and approximately 10 mm below the stigma. At this point the tube ends and the perianth flattens out into a strap-shaped structure across which the nectar does not migrate, and where it subsequently forms a nectar droplet. A captive spiny mouse (*Acomys*), when presented with a head of *P. cryophila*, foraged for nectar among mature buds at this level and contacted previously opened stigmas. Thus the critical stigma-nectar distance of ca. 10 mm is maintained.

The structure of the nectar reservoir in *P. am-*

plexicaulis and *P. humiflora* may also be important in pollination. In these species it forms a shallow, "troughlike" structure (Fig. 3), which could facilitate nectar lapping by small mammals. In a BP protea (e.g., *P. repens*) the nectar reservoir, by contrast, resembles a well at the base of the style into which a bird's beak or tongue could be readily inserted and the stigma-nectar distance ratio approximates the length of the entire style (and also the length of the pollinating bird's beak and extensible tongue).

The cryptic positioning of the heads in a number of NMP proteas needs further description. Different strategies are involved: (1) *interior cauliflory*—heads generally borne along older stems densely covered with overlying shoots (*P. amplexicaulis, P. humiflora*); (2) *interior geoflory*—heads borne at or very near ground level and generally covered with overlying shoots, especially in older plants [*P. cordata* Thunb., *P. subulifolia* (Salisb. ex Knight) Rourke]; (3) *interior penduly*—heads borne on pendulous branches generally hidden by overlying shoots, with heads often drooping to near ground level (*P. sulphurea* Phill., *P. witzenbergiana* Phill.); (4) *exterior terminal*—heads enclosed by large surrounding bracts (*P. recondita, P. foliosa* Rourke).

Why crypsis evolved is unclear; but a possible explanation is the reduction of occasional nectar robbing by flower birds that presumably cue visually. Dr. E. Granger (pers. comm.), however, suggests that crypsis might reduce predation on small-mammal pollinators by nocturnal raptors (owls), of which there are a dozen species in southern Africa (Oatley, 1971). Small mammals foraging on exposed flower heads should be more vulnerable to aerial predation than animals foraging inside a foliage cover. These four forms of crypsis also occur in the proteaceous genera *Banksia* and *Dryandra* of Australia (George, 1981), which also has a large owl fauna (Morcombe, 1974).

STIGMA MORPHOLOGY

METHODS

Because of its reduced nature, the stigma morphology of the NMP proteas *P. humiflora* and *P. amplexicaulis* and the BP proteas *P. cynaroides* (L.) L. and *P. repens* was studied with a Hitachi 450 scanning electron microscope to determine whether its structure might provide evidence relating to more efficient pollination by particular animals. Proteaceae are generally protandrous and we suspected there might be differing periods of slit opening or receptivity. Seven specimens were collected every 3 hours for a period of 24 hours. Both individual flowers and entire flowering heads were collected at each sampling, and special care was taken not to disturb the flowers prior to fixation.

Styles were fixed for 24 hours in one of the following: (1) liquid nigrogen (N_2), (2) supercooled 95% ETOH, (3) a mixture of 50% formalin and 95% ETOH, or (4) a solution of magnesium phosphate ($MgPO_4$). Styles of individual flowers were prepared by one of the following methods: air dried directly after removal from the fixative, washed in 95% ETOH prior to drying, or processed with a critical point drier. These different methods of fixation and drying produced no detectable changes in stylar structure. Stigmatic morphology was compared among flowers (1) fixed at different times of the day, (2) occurring at varying positions on the flowering head, and (3) representing different age classes.

RESULTS

Observation of approximately 300 stigmas of *P. humiflora* and 200 stigmas from the other species (see above), plus *P. minor* (Phill.) Compton, produced little or no evidence that the stigmatic slit ever opened to any appreciable degree (Fig. 4). Neither did we observe structural changes suggesting differing cycles of receptivity, nor evidence indicating differential pollination success by a certain group of pollinators. Nonetheless, further studies of this subject might prove interesting.

TEMPORAL PATTERNS OF ANTHESIS AND NECTAR PRODUCTION

METHODS

To learn whether anthesis and nectar production are correlated with the activity patterns of small mammals, we determined the time of flower opening for *P. humiflora* under field conditions by counting and marking the number of newly opened flowers at the Jonasnek site A. Flowers on six heads were counted at three-hour intervals over a period of nine days. The erect styles that identify open flowers were marked with red fingernail polish at each time check. Field observations to determine time of flower opening were also made for *P. amplexicaulis* at Jonasplaats and for *P. cryophila* at the Sneeuberg site, but at different time intervals.

TABLE 3. $\bar{X}$ No. flowers opening/head between prescribed time intervals for nonflying mammal and bird pollinated proteas.

Species	Pollination System	0800–0900	1700–1800	2100–2200
P. amplexicaulis	NMP	5.4 (N = 24)	2.6 (N = 24)	9.5 (N = 24)
P. cryophila	NMP	47.4 (N = 50)	4.9 (N = 40)	—
P. effusa	NMP	9.5 (N = 31)	4.0 (N = 34)	—
P. recondita	NMP	8.0 (N = 4)	3.5 (N = 4)	—
P. sulphurea	NMP	22.6 (N = 46)	6.2 (N = 48)	—
P. arborea	BP	19.3 (N = 26)	5.2 (N = 48)	15.7 (N = 26)
P. laurifolia	BP	9.7 (N = 28)	8.0 (N = 33)	3.7 (N = 27)
P. repens	BP	0.36 (N = 22)	12.8 (N = 23)	1.1 (N = 22)

Additional observations on *P. effusa, P. recondita,* and *P. sulphurea,* were made under laboratory conditions, at room temperature, and without special lighting regimes. Flowering heads, which recover easily from wilting and maintain flowering function for a number of days following removal from the plant, were stored in closed plastic bags for 24–48 hours, after which we placed the peduncles in water and cut away the erect styles of open flowers with scissors. Observations were made at 12-hour intervals and the styles of newly opened flowers cut away after each observation. In addition to NMP proteas, three BP proteas (*P. arborea, P. laurifolia, P. repens*) at the Jonasnek and Jonasplaats sites were studied for comparative purposes.

We measured nectar under a dissecting microscope from freshly picked flowering heads using a 15 μl capillary tube. Magnification was necessary to ensure that the nectar droplets from the tightly grouped florets had not pooled.

RESULTS

Time of Anthesis

Protea humiflora clearly shows a maximum rate of flower opening between 1800 and 2100, which is also the period of maximum small-mammal activity (Fig. 1). Other species of NMP proteas also exhibit a primarily nocturnal anthesis, but the periods cannot be bracketed as precisely because the observations were not regularly made at short intervals as in *P. humiflora* (Table 3). *Protea amplexicaulis,* however, would appear to have a pattern of anthesis similar to *P. humiflora,* and judging by casual observations of NMP proteas made during the evening hours, it seems likely this is a general pattern.

Among BP proteas (Table 3), *P. repens* has a midday flower-opening pattern, whereas in *P. laurifolia* Thunb. more florets open in the early morning (0930) and also between 1800 and 2100. The actual time at which anthesis occurred in the newly opened flowers observed at 0930 is unknown because data are lacking for the critical periods (Table 3).

Protea arborea appears to have a largely nocturnal anthesis, for which we have no apparent explanation. Presumably the species is pollinated by the Cape sugar bird, as are the other two BP species. No sugar birds were ever observed on *P. arborea* in the study areas, however, they were common in nearby (ca. 1 km) stands of *P. laurifolia.*

Nectar Production

No nectar production could be detected in the heads of *P. humiflora* utilized for determining periods of anthesis. Nor were there consistent patterns of nectar production noted in any of the heads on the study areas. A few scattered observations, however, provide some information. Freshly secreted nectar was observed in *P. humiflora* flowers on three separate days (Aug. 16, 26, 30) between 1630 and 1800 hours. These days were relatively cold, windy, and generally stormy, but were without rain during the previous 12 hours. These preliminary observations suggest that nectar secretion is initiated in *P. humiflora* in late afternoon or early evening during periods of relatively low daily temperature and just prior to the period of greatest small-mammal activity.

What appeared to be freshly secreted nectar was also observed in *P. cryophila* at 2030 hours on Feb. 13, but secretion was confined to relatively few flowers on a single head among the 10 under observation. In this instance, however, the

TABLE 4. Total sugar content of nectar (g solute/100 g solution) from nonflying mammal and bird pollinated proteas.

Species	Pollination System	$\bar{X}$ Total Sugar Content	N	S.D.	Range
P. amplexicaulis	NMP	37.2	42	6.3	27.9–47.9
P. cryophila	NMP	33.3	13	7.2	25.2–49.4
P. humiflora	NMP	37.8	59	6.9	28.2–65.4
P. arborea	BP	18.8	5	—	16.8–20.4
P. laurifolia	BP	24.4	20	1.0	20.3–26.6
P. magnifica	BP	20.6	16	2.9	16.2–24.8
P. repens	BP	18.8	45	1.8	14.6–23.6

day was sunny and warm as is common during midsummer.

In *P. angustata* R. Br., *P. cryophila,* and *P. humiflora* nectar was first secreted from mature buds, i.e., while the pollen presenter was still enclosed by the perianth segments, although the style had generally already arched laterally away from the perianth over most of its length. This should not impede pollination, however, because the incurved styles of open flowers easily contact the rostra of small mammals foraging for nectar among the outer few whorls of mature buds. Following warm days, however, the nectar reservoirs of some previously opened flowers in *P. amplexicaulis, P. cryophila,* and *P. humiflora* appeared to develop a moist film by 2000 hours, but no obvious nectar build-up was observed. Laboratory studies such as those by Cowling (1978) may be necessary to obtain an adequate understanding of temporal patterns of nectar secretion.

NECTAR COMPOSITION

METHODS

The nectar of NMP and BP proteas was analyzed for (1) total sugar content (g solute/100 g solution), (2) percentage of different sugars comprising the carbohydrate fraction, and (3) amino acid content. The nectar was extracted from the heads with a capillary tube and the total sugar content was measured with an AO Goldberg refractometer (Model 10923) corrected for temperature. Because of the high total sugar content of NMP protea nectar, it was often diluted with appropriate parts of distilled water in order to retain the value on the refractometer scale. The values were then corrected by the appropriate dilution factor. Only apparently freshly secreted nectar was used for identifying the major components of the carbohydrate fraction and the amino acid content. Nectar for these analyses was immediately spotted on Whatman #1 filter paper, quickly dried, and later chromatographed by I. and H. G. Baker following methods they previously described (Baker, Opler & Baker 1978; Baker & Baker, 1979). Considerable care was taken to reduce the possibility of pollen contamination in the samples used for determining amino acid content. Because freshly secreted nectar was rarely available for analysis of total sugar content, nectar that had accumulated in older heads was utilized. Since nectar remaining in older flowers is more variable than that freshly secreted, the sample size was increased.

RESULTS

Total sugar content of nectar. The three NMP proteas analyzed all have nectar with total sugar content in the mid-thirties ($\bar{X} = 36.1\%$) (Table 4). The four BP proteas have nectar with total sugar content ranging from the high teens to mid-twenties ($\bar{X} = 20.7\%$), which is typical for most bird-pollinated flowers. There is virtually no overlap in the values between the two BP proteas and the NMP proteas and the differences are statistically highly significant ($P \ll .01$). The difference in total sugar content of the nectar in the two groups should be an important distinguishing feature between BP and NMP proteas.

Carbohydrate composition. The nectar of NMP proteas are generally "sucrose-rich," i.e., the ratio of sucrose to glucose-fructose is >0.5 (Baker & Baker, 1979) (Table 5). Thus all the NMP proteas analyzed for carbohydrate composition may be characterized as sucrose-rich, with the exception of *P. angustata* (0.326) which

TABLE 5. Carbohydrate composition (mean proportions) in nonflying mammal and bird pollinated protea nectar.[a]

Species and Pollination Type	Melezitose	Maltose	Sucrose	Glucose	Fructose	Ratio (Sucrose/ Glu + Fru)
P. amplexicaulis (NMP)	.036	.029	.345	.330	.260	.593
P. humiflora (NMP)	.019	.021	.394	.364	.203	.728
P. cryophila (NMP)	.0335	.015	.276	.343	.333	.410
P. repens (BP)	.017	.042	.123	.531	.286	.152
P. angustata (NMP?)	.049	.275	.2215	.419	.283	.326

[a] Analyses kindly provided by Prof. H. G. and I. Baker from samples supplied by the authors.

is marginal in this respect. *Protea repens,* a BP protea, has a sucrose-poor nectar ("hexose-rich") (0.152), which is confirmed by other studies (Mostert et al., 1980; Cowling, 1978). Cowling (1978), however, reported that some presumably BP proteas (*P. longifolia* Andr.) also have high sucrose concentrations. The importance of the differences in the small amounts of melzitose and maltose present in the samples is difficult to assess, although *P. angustata* has considerably higher values than the other species.

Amino acid composition. The significance of the amino acid composition of the nectar is difficult to evaluate (Table 6), but the relatively small quantitites present suggest they have no important nutritional value for small mammals. This should be expected in non-coevolved systems, where the nectar is apparently not an essential component of a pollinator's diet (see section on Reward). The amino acids may, however, impart taste to the nectar (Baker et al., 1978).

Nectar odor. The heads of all NMP proteas emit a "yeasty" or fermented odor, as previously mentioned, but two variations are apparent. *Protea amplexicaulis, P. cryophila, P. humiflora, P. recondita,* and *P. sulphurea* superimpose a sweetish scent to the basic yeasty theme, whereas *P. angustata, P. restionifolia* (Salisb. ex Knight) Rycroft, and *P. scabriuscula* Phill. produce a pungent odor reminiscent of rancid butter. Nectar freshly extracted from the heads of *P. amplexicaulis* and *P. humiflora* retains the odor, indicating that the volatile fraction occurs in the nectar itself.

The heads of *P. effusa, P. recondita,* and *P. sulphurea* maintained in water under laboratory conditions emitted perceptively stronger odors at night. A similar situation appeared to exist in both *P. amplexicaulis* and *P. humiflora* under field conditions. Although these observations are subjective, they complement the data on both flower opening and nectar secretion.

That the odor of *P. amplexicaulis* and *P. humiflora* attracts small mammals first became apparent when flowering heads were placed in the cages of captive animals while they were in their sleeping tube. Although the flowering heads were not visible from the tubes, the animals usually emerged within a few minutes, sniffed the air with upraised snouts, and then proceeded directly to the heads and began to forage.

FLORAL AND NECTAR PREDATION

The loss of reproductive potential in protea through predation was not a major consideration in this study, but several observations warrant mention. The fleshy bracts and styles of flowering heads in the species studied occasionally showed clear evidence of being chewed by small mammals, but in *P. amplexicaulis* this occurred on only about 1–2% of the heads. Thus predation by chewing is probably of little importance, especially since fertilized ovules might develop even if the styles were subsequently destroyed. Cowling (1978) presented evidence that the bracts might act as a carbohydrate sink, thus providing a possible reason for thier occasional exploitation by small mammals.

A more unusual and significant form of predation in proteas is the removal of entire flowering heads. The extent of such predation is indicated by the number of heads removed from *P. humiflora* on study stie B in 1978. Quadrat seven (10 m^2) had 307 flowering heads removed from the 45 individual plants occurring on the quadrat; quadrat ten (10 m^2) had 164 heads removed from 13 *P. humiflora* plants. Since *P. humiflora* averages 17.3 seeds per head (Table 9), about 8,148 potential seeds were lost. The num-

TABLE 6. Amino acid composition of nonflying mammal and bird pollinated protea nectar, graded on a scale of increasing concentration from 1–6.[a]

Amino Acid	*P. amplexicaulis*[b] (NMP)	*P. cryophila*[b] (NMP)	*P. angustata*[c] (NMP?)	*P. humiflora*[c] (NMP)	*P. repens*[b] (BP)
Alanine	1	2	1	1	1
Arginine	—	tr[d]	?	—	—
Asparagine	2	1	1–2	1	—
Aspartic	—	1	—	—	—
Cysteine, etc.	tr	tr	2	1	—
Glutamic	1	2	—	4	1
Glutamine	2	2	1–2	1	2
Glycine	1	3	1	2	2
Histidine	—	—	—	—	—
Isoleucine	1	1	—	2	1
Leucine	—	1	1	1(?)	—
Lysine	—	1	—	—	1
Methionine	1	2	—	2	1
Phenylalanine	—	2	1	1	—
Proline	2	1–2	2	1	2–3
Serine	1	2–3	1	1	2
Threonine	—	—	—	—	—
Tryptophan	1	2	—	—	—
Tyrosine	2	1	—	—	2
Valine	1	1	2	—	1

[a] Analyses kindly provided by Prof. H. G. and I. Baker from samples obtained by the authors.
[b] 5 = .1212 μg/μl.
[c] 6 = .2424 μg/μl.
[d] tr = trace.

ber of heads removed by predators in these quadrats was not obviously different than the number removed from others in the immediate study area, although the overall predation of entire heads was patchy.

The peduncles of heads removed through this form of predation were not obviously chewed, as might be expected from rodent activity, instead the heads appeared torn from the plants. Furthermore, the heads were often concentrated in discrete piles of up to 15, and many showed evidence of severe disturbance and damage. These observations suggested removal by an organism capable of pulling the heads from the plants. The chacma baboon (*Papio ursinus* Kerr), which occurs in the study area (pers. obs.), is the most likely predator because it forages in this manner (Roberts, 1951). Similar predation was also observed on a BP protea, *P. repens*. Since the heads are either severely disturbed or torn apart (but not eaten) it appears most likely that the predators are seeking either the sweet, copious nectar and/or the large scarab beetles (*Anisonyx ursus* F.) that occasionally occur in the heads in large numbers. Floral predation by primates is known in the Neotropics (Mori et al., 1978; Janson et al., 1981).

Nectar and pollen robbing may be a form of serious predation in both NMP and BP proteas. When the standing crop of nectar averages several milliliters, it offers an unusually rich energy resource and is heavily exploited by numerous insects. Mostert et al. (1980) found a total of 2,215 insects in 20 heads of *P. repens*. The largest percentages consisted of ants (19%), beetles (67%), and flies (12%). Whether these insects, which also occur in the NMP *P. amplexicaulis* and *P. humiflora*, contribute significantly to pollination is unknown. Bees also extract considerable nectar and pollen from the heads (Table 15), but whether this should be considered predation is difficult to assess because they probably also contribute to pollination (see sections on Nectar Consumption by Bees and Selective Exclosure Experiments).

Predation by ants should be expected in such a rich nectar source, but few ants were noticed around flowering heads of most proteas observed in this study. In *P. cryophila*, however, the heads were often heavily infested, especially at night.

Mostert et al. (1980), however, reported that nearly 20% of the insects on flowering heads of *P. repens* were ants.

Small Mammal and Abiotic Dispersal of Protea Pollen

METHODS

Many of the small mammals captured in flowering stands of NMP proteas were tested for the presence of pollen on their rostra, and in some instances the feces were also examined for pollen.

The presence of pollen on the rostrum was tested by rubbing the area with gelatin blocks (several mm^2) containing basic fuchsin stain (Beattie, 1971), but neither the sampling procedure nor the size of the gelatin blocks was standardized. The gelatin block was then melted on a microscope slide and spread under a cover glass. Pollen is readily captured and stained by this method and the slides are essentially permanent. Fecal pellets were also analyzed for pollen using the same general technique. To avoid possible contamination, however, fecal samples were removed directly from the colon of sacrificed animals and partially dissolved in water to soften and spread the fecal material on the gelatin blocks.

To eliminate the remote possibility that these pollen loads originated by the chance accumulation of abiotically dispersed pollen, the following materials in dense stands of the NMP protea, *P. humiflora* (Jonasnek—site A), and a BP protea, *P. laurifolia* (below Jonasplaats), were analyzed for the presence of (presumably) wind-dispersed protea pollen: (1) rocks and leaf litter between protea plants, (2) living leaves not closer than ca. 20 cm from flowering heads, and (3) the bracts of flowering heads.

RESULTS

Some protea pollen was found on the rostrum of all animals examined, but the amount varied widely, from only a few scattered grains to many thousands (Table 7). Of the 151 animals examined for protea pollen, only 15 samples contained less than 100 grains of protea pollen and only 9 had less than 50. The samples typically also contained a few non-protea pollen grains, but they averaged only 3.1 per sample; the highest number was 44. No average for the number of protea pollen grains was obtained because thousands of grains were present on many of the slides. The number of pollen grains on the rostrum is a function of how recently the animal foraged in relation to the number of groomings and wet-preenings. Snap-trapped animals often carried higher pollen loads than live-trapped animals; presumably the latter groom and preen while in the traps. During wet-preening, pollen should be ingested and feces did contain protea pollen, often in large numbers.

Table 7. $\bar{X}$ No. pollen grains in samples (N = 2) collected from various objects in a stand of flowering *P. humiflora*.

	Protea Pollen	Non-protea Pollen
Non-protea exposed leaf litter	6	56
Exposed rocks	2	11
P. humiflora bush[a]	33	82
P. humiflora heads[b]	492	75

[a] Samples collected from leaves <2 dm from flowering heads.

[b] Samples taken from bracts of flowering heads; pollen occurred primarily in dense clusters on the trichomes of the bracts.

Even in dense stands of protea, non-protea pollen usually predominated on the various objects examined, except on the bracts of flowering protea heads (Table 7). If protea pollen accumulated on the rostra of small mammals by chance, then the concentration should be proportional to that of non-protea background pollen which is not the case. Only visitation to flowering heads of protea can adequately explain both the size and composition of the small-mammal pollen loads.

Small mammals may also visit the flowering heads of BP proteas, e.g., *P. laurifolia*. In this species evidence of light chewing is occasionally evident on the bracts of the heads, but no indication of intensive rodent activity was observed on any BP protea. We sampled pollen on the rostra of five gerbils (*Tatera afra* Gray) and a single *Rhabdomys* trapped in a stand of *P. laurifolia* with no NMP proteas within at least 500 m. These animals all possessed low counts of protea and non-protea pollen on their rostra. Three of the animals sampled showed approximately equal numbers of protea and non-protea pollen grains, but had only a low total pollen count (<15 grains/sample). Two of the gerbils, however, showed approximately three to four

times more protea than non-protea pollen grains and also relatively larger pollen loads, although these were still small in absolute terms (13:55, 18:68). It is unlikely that the protea pollen in these two samples could have originated from sources other than direct visitation to the heads, since the stickiness of BP protea pollen is similar to that of the NMP proteas. The entire pattern of small-mammal visitation to various flowers needs further study and can be initially approached by simply measuring pollen loads.

TABLE 8. Energetic relationships between *P. humiflora* and small mammals (Jonasnek sites).

$\bar{X}$ Nectar/ Fl. (μl) (N = 20)	$\bar{X}$ Standing Crop Nectar/Head (ml) (N = 11)	Nectar Cal/g	$\bar{X}$ No. Fls./Head (N = 12)	$\bar{X}$ No. Heads/ Plant (N = 19) Sites A & B	No. Protea Plants Sites A & B	$\bar{X}$ No. Heads/ Quad. Site B	No. Animals Sites A & B	$\bar{X}$ Cal/g/hr for *Aethomys* (Active & Grooming) (N = 4)
8.8	1.8	3,693	303	1977, A = 56.6 1979, B = 5.2	A = 221 B = 603	1979 = 58	1978, A = 38 B = 57 1979, B = 20	11.83

POLLINATION ENERGETICS: *P. HUMIFLORA* AND *AETHOMYS*

METHODS

One object of the study was to determine the potential contribution of NMP protea nectar to the energy regime of the associated small-mammal community. The nectar production of *P. humiflora,* Jonasnek site B (for which the small-mammal composition and density are known), was analyzed in terms of the following parameters: (1) the potential volume and caloric content of *P. humiflora* nectar, (2) the metabolic rate of *Aethomys* as a representative small mammal, (3) the maximum amount of nectar that *Aethomys* will consume during a given period when maintained on a strict nectar diet, and (4) the density of the small-mammal community.

The caloric content of *P. humiflora* nectar was measured using an IKO Adiabatic Bomb Calorimeter. The basal metabolism of *Aethomys* was obtained by measuring O_2 consumption in a closed manometric system, corrected for temperature and atmospheric pressure. The accumulated standing crop of nectar per head (not freshly secreted nectar) was determined by shaking the droplets from the head and measuring the accumulated nectar. This procedure obviously leaves considerable nectar on the head and is thus highly conservative. Individual flowers with apparently freshly secreted nectar were utilized to determine nectar volume per flower.

The annual amount of protea nectar on the study site was calculated by determining the mean number of flowers per head, and the number of heads occurring in several randomly determined quadrats on grid B as a representative distribution for the entire grid (Table 8).

To approximate the amount of nectar *Aethomys* might ingest, a single animal was fed a strict diet of *P. humiflora* nectar (44% sucrose equivalents) from a graduated pipette and the con-

sumption recorded at 12-hour intervals (the quantities of nectar required for the experiment precluded a larger sample of animals).

RESULTS

The amount of energy in the annual nectar crop of *P. humiflora* can be roughly approximated from the data in Table 8. Multiply the amount of nectar produced per flower (8.8 μl) by the average number of flowers per head (303). Multiply this result (2.7 ml) by the number of heads per 10 m^2 quadrat (58) and multiply that sum (156.6 ml) by 25 (the total number of quadrats). Thus, roughly 3,915 ml of nectar can be expected from the *P. humiflora* plants on site B. One milliliter of nectar yields 0.31 g of solids, and one gram of solids produces 3.7 Calories. Thus the 3,915 ml of nectar on the study site yields 4,490 C. *Aethomys* requires approximately 14.1 C. per 24 hours. The 20 animals occurring on grid B in 1979 would require 282 C. per day to satisfy their basic energy requirements. If 50% of the nectar is lost to predation, sufficient nectar would remain to supply the energy requirements of the small-mammal community for 8.0 days from an approximately 45 day flowering period. Because of the many variables involved, however, this calculation provides only a crude estimate of the actual energy relationships. It does, however, indicate that only a small fraction of the annual energy needs of the small-mammal community can be met by protea nectar.

The single *Aethomys* maintained on *P. humiflora* nectar consumed an average of 6.55 ml/day, which was approximately equal to the amount of nectar taken during the first feeding bout of about 10 minutes at the initiation of the experiment (6.4 ml). Predictably, a strict diet of *P. humiflora* nectar results in progressive weight reduction (16.1% of body wt.) and death (in five days).

Seed Set in Protea

METHODS

Seed set was determined by cutting transversely through the fruiting heads at mid-ovary level with a sharp, thin blade. This is possible because the fruits (achenes) are tightly packed and remain firmly attached to the receptacle of the head for several years. Interestingly, the individual fruits remain attached to the head during this period whether or not they develop into viable seed. Furthermore, viable and sterile achenes do not obviously differ morphologically. When the heads are cut transversely at mid-ovary level, however, viable, endosperm-containing seeds are readily identifiable by their soft, milky-white texture; whereas seeds interpreted as sterile have a dull-white, dry, fibrous content (Fig. 5). Seed set in this study is thus defined as the number of achenes per head containing endosperm expressed as a percentage of the total number of flowers.

RESULTS

Seed set is generally low in both BP and NMP proteas, and in Proteaceae in general. Excluding species with small sample sizes (<10), average seed set ranges between 6 and 15%, with the exception of *P. recondita,* which developed 18 and 29% seed set from two populations (Table 9). Although the sample sizes are not large for most of the species (ca. N = 10), we found no significant variation in the 1978 seed crop for *P. humiflora* when more than 10 heads were sampled. While the annual seed set in *P. humiflora* differed significantly between 1977 and 1979 (P = .01) and between 1978 and 1979 (P = .01), the absolute change itself was not great. No significant difference was observed between seed set in 1977 and that in 1978 (P = .18), but the annual rainfall differed greatly. Although the percentage of seed set may not vary greatly from year to year, the number of heads per plant may well differ appreciably, but few data are available on this point (Table 8).

Little evidence of insect predation was noted in fruiting heads. Larval insects were infrequently observed, and were only occasionally abundant in a particular head. Such predation seems unlikely to affect the statistical data significantly.

Finally, what factors produce the typically low seed set (1–30%) in these and other proteas (Table 9)? Lack of pollination and resource availability are commonly accepted explanations for low seed set, but Casper and Wiens (1981) demonstrated that in *Cryptantha* (Boraginaceae) a significantly greater number of embryos are initiated than develop into seeds. More recent studies of *Cryptantha* (Casper, 1982) showed that embryo reduction cannot be attributed to inadequate pollination nor to resource availability, thus suggesting genetic control.

The consistently low seed set in both BP and NMP proteas, and the apparent occurrence of similarly low seed set in Australian proteaceous

TABLE 9. Seed set in nonflying mammal and bird pollinated proteas.

Species	$\bar{X}$ No. Flowers/Head	Range	$\bar{X}$ No. Seeds/ Head[a]	Range	% Seed Set	Pollination Type	Study Site
P. amplexicaulis	157 (N = 15)	136–176	11.5	0–42	7.3	NMP	Jonasplaats
P. arborea	244 (N = 2)	221–267	9.5	6–13	3.9	BP	Jonasnek
P. cryophila	1,024 (N = 12)	749–1,217	154	90–227	15.0	NMP	Sneeubergnek
P. effusa	157 (N = 10)	136–178	17.4	2–30	10.8	NMP	Murray Farm
P. humiflora	303 (N = 12)	248–373	17.3	0–95	6.0	NMP	Jonasnek
P. laurifolia	283 (N = 10)	230–346	19.4	0–55	7.0	BP	Murray Farm
P. magnifica	374 (N = 2)	349–398	5	4–6	1.3	BP	Jonasplaats
P. pendula	157 (N = 10)	136–178	17.4	2–30	11.1	NMP(?)	Murray Farm
P. punctata	138 (N = 11)	112–155	12.3	2–32	9.0	BP	Sneeubergnek
P. recondita (1)	258 (N = 10)	118–379	75.9	23–149	29.3	NMP	Sneeubergnek
P. recondita (2)	393 (N = 11)	338–436	69.6	18–148	18.1	NMP	Murray Farm
P. scolependrifolia	194 (N = 13)	160–260	16.9	0–51	9.0	NMP	Jonasplaats
P. subulifolia	105 (N = 21)	88–128	15.5	0–51	14.3	NMP	Jonasplaats
P. sulphurea	500 (N = 8)	416–588	15.3	0–53	3.0	NMP	Ouberg Pass

[a] N same as column 1 unless otherwise indicated.

genera (Rourke & Wiens, 1977; Carpenter & Recher, 1978b) also suggest that genetic factors may play a role in controlling seed set in Proteaceae, but experimental verification is needed.

GENETIC COMPATIBILITY

METHODS

Protea humiflora was tested for genetic compatibility by enclosing individual flower heads in bags of lightweight, small-mesh nylon with a basal drawstring designed to exclude potential pollinators. Exposure to wind and rain sometimes matted the nylon exclosure bag against the wiry styles, which may have exposed the stigmas to cross-pollination. In 1978 a large percentage of exclosure bags had holes chewed in them or were partially pulled from the heads (presumably by mice attempting to gain access to the highly nectarous heads). Crossing experiments with these species are difficult to implement under field conditions.

Pollen must be physically moved to the stigma to effect pollination (Fig. 4). In 1978 we attempted to cross-pollinate flowers by reciprocally exchanging pollen-laden exclosure bags between heads of different plants. Immediately after transfer the bags were manipulated to distribute pollen over the stigmas. The remaining nylon exclosures were undisturbed throughout the flowering season. In 1979, however, some heads were manipulated inside the pollen-laden exclosure bags daily for four days in an attempt to spread pollen over the stigmatic slits of newly opened flowers. The remaining heads were not manipulated. The results were analyzed statistically with the Mann-Whitney U test and χ^2.

RESULTS

In 1978 no statistical differences were observed in seed set between selfed and crossed plants ($P = .19$), but the sample size was small ($N = 6$) (Table 10). Furthermore, in 1978 both the selfed group and the outcrossed group produced significantly fewer seeds than the control group ($P \ll .01$).

In 1979 the difference in seed set between the enclosed heads which were manipulated, and

TABLE 10. Seed sets of enclosed heads of *P. humiflora* tested for genetic incompatibility.

Year	Unmanipulated Heads $\bar{X}$	Unmanipulated Heads % Control	Manipulated Heads $\bar{X}$	Manipulated Heads % Control	Artificially Outcrossed Heads	$\bar{X}$ Control
1978	4.2 (N = 6)	.23			1.2	18 (N = 103)
1979	3.4 (N = 12)	.16	2.7 (N = 9)	.13		21 (N = 35)

those which were not, was difficult to evaluate. In the non-manipulated group (N = 12) only two heads produced seed, one with 42 seeds and the other with six. In the manipulated group (N = 9), however, six heads produced seed, but none more than 10. The single head with 42 seeds in the non-manipulated group affects the statistics when using the Mann-Whitney U test. Perhaps cross-pollinating insects or some other perturbation produced this exceptionally high seed set. To avoid this problem, we compared the percentages of heads that produced any seed in the manipulated group (60%) and in the non-manipulated group (14.3%) by the McNemar variation of χ^2. This shows that the percentages are significantly different ($P \ll .01$), and suggests that self-pollination (but not necessarily autogamy) is successful to a limited extent in *P. humiflora.*

The data are difficult to evaluate because all heads placed under nylon enclosures (including those artificially crossed in 1978) typically produced significantly fewer seeds than did the control group in 1978 and 1979 ($P \ll .01$ in all cases). Thus either the enclosure treatment itself may retard seed set, or manipulation by hand does not effectively transfer pollen to the minute stigmatic slit in *P. humiflora.*

Many Proteaceae are protandrous, but this should not have affected the results since in 1979 manipulations were carried out for four days. In any case, many more of the 300 stigmas in a head should have been receptive than produced seed. Moreover, the pollen remains viable for several days (Table 11), so this should likewise not have been a problem.

To determine the breeding system in these proteas, plants should be grown under greenhouse conditions. Furthermore, a better understanding is needed as to how, when, and in what amounts pollen must be deposited on the minute stigmatic slit to effect pollination.

Pollen Viability

METHODS

To determine whether residual pollen (i.e., pollen retained on the rostrum following grooming) was functional, we tested *P. amplexicaulis* and *P. humiflora* pollen for length of viability. Pollen was tested for percent germination on a boron-enriched sucrose agar medium similar to that used by Taylor (1972), except that the sucrose concentration was lowered by 75%. All the pollen utilized in this study was collected from flowers that opened between 1800 and 2130 on the day the tests were initiated. A single flower of each species was removed from the original group of experimental heads and the pollen plated on agar every 12 to 24 hours for four days, and at 2130 on the sixth day following anthesis. At least two replicates were plated from each flower. Plates were maintained at ambient temperature and humidity. The percentage of pollen germinated was determined at least 16 hours after plating by counting the number of germinated and ungerminated grains visible in a single microscope field (×160) in each replicate.

RESULTS

A substantial proportion of pollen retained the ability to germinate on agar for two full days following anthesis in *P. amplexicaulis* and at least three days in *P. humiflora* (Table 11). Thus residual pollen should be capable of fertilization during this period. Some inconsistency both between replicates and for different times of plating is apparent in our results. The extremely low germination of *P. amplexicaulis* pollen on the morning of the second day, for example, is difficult to explain. Perhaps the viability of pollen from this single flower was anomalously low. Pollen plated in the evening showed a tendency to yield a higher percentage of germination than that plated in the morning, particularly in *P. humiflora.* Perhaps pollen is physiologically adapted for maximum germination under conditions to be expected at the time dispersal normally occurs.

Selective Exclosure Experiments

METHODS

To determine the effects of excluding small-mammal visitation on seed set in *P. amplexicaulis* (Jonasplaats) and *P. humiflora* (Jonasnek), flowering heads were enclosed in a cage of hardware cloth (mesh size 13 mm), the base of which was fitted with a nylon skirt that was tightened around the peduncle by a drawstring. The cage was supported over the inflorescence by wiring it securely to adjoining branches, thus preventing movement of the cage and possible damage to the flowers or peduncle. This cage effectively excluded all known mammals in the area (including *Mus minutoides* A. Smith, the smallest known

TABLE 11. Pollen longevity in *Protea amplexicaulis* and *P. humiflora*.

	Day No. and Observation Time						
	1		2		3		
P. amplexicaulis	0930	2130	0930	2130	0930	2130	0930
	–	(N = 3)	(N = 2)	(N = 3)		(N = 2)	(N = 2)
$\bar{X}$ % germination/fl.	–	.66	.01	.60	.49	.36	–
P. humiflora	0930	2130	0930	2130	0930	2130	0930
	–	(N = 4)	(N = 4)	(N = 4)		N = 4	N = 4
$\bar{X}$ % germination/fl.	–	.68	.41	.74	.45	.57	–

TABLE 12. Seed set in protea heads caged to preclude small mammal foraging, but open for visitation

	1978						
	Control		Mammal Excluded			Control	
	$\bar{X}$	Range	$\bar{X}$	Range	Significance	$\bar{X}$	R
P. amplexicaulis						24.04 (N = 27)	
P. humiflora	18.43 (N = 51)	0–95	8.73 (N = 11)	0–19	P = .06	21.23 (N = 35)	(

TABLE 13. Interplant distribution of fluorescing powder by (presumably) small mammals.

Protea Species	Approximate Distance from Source (m)	Points of Deposition
P. amplexicaulis[a]	1.0	Fl. head of another *P. a.*
	0.1	Runways to (but not on) fl. heads of another *P. a.*
	7.0	Runways to (but not on) another *P. a.*
	4.0	Runways to (but not on) another *P. a.*
P. humiflora[b]	3.5	Fl. head of another *P. h.*
	8.0	Runways to and on fl. head of another *P. h.*
	0.5	2 fl. heads of another *P. h.*
	2.5	2 fl. heads of another *P. h.*
P. subulifolia[a]	2.0	Runways to (but not on) another *P. s.*
	0.5	Fl. head of another *P. s.*
	1.5	Shoots (but not fl. heads) of another *P. s.*
	7.0	Runway and shoots (but not fl. head) of another *P. s.*
	0.5	Shoots and fl. heads of another *P. s.*
	0.5	Runways and shoots (but not fl. heads) of another *P. s.*
	15	Runways and fl. heads of another *P. s.*

[a] Jonasplaats study area.
[b] Jonasnek study area (site B).

rodent to occur in the study area), but allowed easy access to insects, especially honey bees. Seed set in the caged heads was compared with that of control heads, i.e., heads on the same or adjoining branches left open to natural pollination. The data were analyzed for significance utilizing the Mann-Whitney U test.

RESULTS

Excluding small mammals from the heads of NMP proteas reduces seed set by approximately 50% in *P. humiflora* (Table 12). In 1978 the differences in *P. humiflora* between the controls and the rodent-excluded heads approached significance ($P = .06$), but in 1979 the differences are considered significant ($P = .01$). We have no obvious explanation for the variable results obtained from the experimental groups between 1978 and 1979, except for the reduced sample size in 1978 ($N = 11$) and general improvement in the technique for placing exclosures over the heads in 1979.

Experiments on *P. amplexicaulis* were conducted only during 1979, and seed set in caged heads was reduced more than 95% in comparison to controls ($P \ll .01$). The sample size, however, was small ($N = 9$) and the experiments were undertaken comparatively late in the flowering season.

FLUORESCING EXPERIMENTS

METHODS

To determine the extent of intra- and interplant movement of pollen and small mammals, the flowering heads of three species of protea (*P. amplexicaulis, P. humiflora, P. subulifolia*) were dusted with fluorescing powders (Hercules Radiant Pigment Type R 103 G) of various colors. Approximately a half teaspoon of powder (or paste produced by adding 50% ETOH) was applied over unopened florets at the center of a flowering head, avoiding the more peripheral open (and presumably nectar-containing) flowers. The heads of each plant were treated with a single color of fluorescing powder. Captive *Aethomys* foraged as readily on powdered heads as on non-powdered heads. By using the paste, which left a delicate, easily broken crust, we avoided possible contamination of adjoining plants by wind-blown powder.

Heads were normally treated at dusk to avoid possible distribution of the powder by diurnal insects. Observations of other flowering heads, or animals trapped in the area, for traces of fluorescing powder were made with a long-wave UV lamp late the same night or early the following morning before the initiation of insect movement. Observations on mice, however, were con-

TABLE 14. Small mammals captured carrying fluorescing powders applied to *P. humiflora* flowering heads (Jonasnek, site B).[a]

Animal	Approximate Distance from Source to Capture Point (m)	Portions of Animal Carrying Fluorescent Powder
Acomys	5	Hind feet, tail
Acomys	12	Rostrum, rear feet
Aethomys	9	Rostrum, front feet
Rhabdomys	3	Rostrum, chest, front feet
Rhabdomys	13	Rostrum, front feet
Rhabdomys	20	Rostrum, front feet

[a] A single *Aethomys* was captured at the *P. restionifolia* study site (Pocskraal) that bore two colors of fluorescing powders on the rostrum and front feet indicating visits to both heads approximately 15 m apart.

tinued on *P. humiflora* for three days. After the first night, only animals bearing large concentrations were recorded because many of the traps became lightly contaminated from recaptured animals carrying fluorescing powder. The high concentrations of fluorescing powder seen on some mice, however, could only have originated directly from the powdered heads.

RESULTS

Small mammals visit not only different flowering heads on the same plant, but also the heads of other protea plants for distances up to 15 m (Tables 13, 14). The large proportion of trapped animals carrying fluorescing powder on their rostra (5 or 6) provides further evidence that the small mammals foraged on these heads. In many instances the general movement patterns of the small mammals were clearly evident from the scattered fluorescing particles around the dusted heads and along the rodent runways that often interconnect NMP protea bushes.

SMALL-MAMMAL FECES IN PROTEA FLOWERING HEADS

METHODS

If small mammals regularly frequent the flowering heads of proteas, it was reasoned that they might leave behind artifacts as evidence of such visitations. The taking of nectar is difficult to detect, and the removal of pollen from newly opened flowers could occur by agents other than small mammals.

TABLE 15. Number of heads containing any fecal pellets in *P. recondita* as a function of age.[a]

Age of Heads	Fecal Pellets Present	Fecal Pellets Absent
Flowering heads fully open	6	0
Flowering heads ca. ½ open	2	4
Flowering heads <½ open	0	6

[a] While the data are highly suggestive, the sample sizes are too small to permit a χ^2 analysis for significance.

RESULTS

Small-mammal feces in the flowering heads of *P. amplexicaulis, P. cryophila, P. humiflora, P. effusa* and *P. recondita* were the only obvious artifacts discovered. Feces accumulation was found to be age dependent, the older heads containing significantly more fecal pellets than younger ones (Table 15). The presence of feces in the heads demands the presence of animals on (or above) the head at the time of defecation, and fecal accumulation within the heads indicates frequent and/or relatively long visits. In *P. recondita,* however, defecation from above is virtually impossible because this protea produces a terminal (but cryptic) head (Rourke & Wiens, 1977).

Moreover, protea pollen was present within the fecal pellets indicating that the animals made at least two visits to a flowering head: the first when the pollen that later occurred in the feces was obtained, and the second at the time of defecation.

NECTAR CONSUMPTION BY BEES

METHODS

A set of experiments was designed to determine the extent of nectar consumption in *P. humiflora* by the African honey bee (*Apis mellifera adansoni* Latreille). Two experiments compared weight losses between experimental heads (accessible to bees) versus control (inaccessible) heads. Both experiments were conducted on warm, clear, sunny days with the temperature at or above 25°C when bee activity was relatively high. Only flowering heads with at least one row of open, undisturbed flowers and observable nec-

tar were used. Heads were weighed at the beginning and end of the experiments.

In the first experiment, 20 heads were collected the afternoon of the day before the experiment and kept overnight with their peduncles in water. The next morning all heads were weighed and individually placed in a small can of water with the peduncles submerged. Ten of the containers with their single heads were placed on the ground near a flowering plant of *P. humiflora* and left uncovered (experimental group). The other ten were similarly positioned but were covered with plastic window screen (control group) to prevent insect visitation. The experiment was initiated at 1345 and terminated at 1700. Although the actual number of bee visitations to the experimental heads was not recorded, bees only rarely visited the experimental heads clustered in cans. To correct this problem the second experiment was initiated.

This experiment was similar to the first except that all heads were collected the morning of the experiment and the experimental heads (after weighing) were wired directly onto two *P. humiflora* bushes to simulate their natural distribution on the plant. Since the experimental heads could not be kept in water, the control heads were simply placed in trays under plastic screens near the bushes with the attached experimental heads. Bees appeared to visit these experimental heads just as readily as the naturally occurring heads. This experiment was initiated at 1030 and terminated at 1700. Both experiments were analyzed by the Mann-Whitney U test.

RESULTS

The difference in weight loss between the two groups in the first experiment was not significant statistically, whereas it was significant in the second experiment ($P < .01$). The average weight loss for both experimental and control heads was predictably greater in the second experiment than in the first, since heads in neither the experimental nor the control groups were kept in water (Table 16). Decrease in mean weight in the experimental group is assumed to be the result of nectar loss due to the foraging activities of bees.

Interpretation of the second experiment is complicated because the window screen covering the control group possibly reduced evaporative loss. There was little wind on the day of the experiment, however, and the experimental population was also mostly shaded by the foliage and relatively close to the ground. Thus in the second experiment we interpret possible reduction in evaporative loss produced by covering the control group with window screen as inconsequential, and assume that the differences in weight loss resulted primarily from the removal of nectar by foraging bees.

TABLE 16. Bee nectar consumption in *P. humiflora*.

Experiment	$\bar{X}$ Nectar Loss/Head (g) Resulting from Bee Foraging	S.D.	Control (g)	S.D.	Significance
1	2.04	0.63	1.75	0.86	n.s.
2	3.54	0.36	2.42	0.51	$P < 0.01$

FLOWER PREFERENCE EXPERIMENTS

METHODS

Choice tests using a T maze were conducted to determine if mice are preferentially attracted to, or preferentially forage from *P. humiflora* heads (an NMP species) rather than those of *P. repens* or *P. laurifolia* (BP species). Several species of rodents from two populations were tested: (1) individuals from the *P. humiflora* study area (*Acomys, Aethomys, Dendromus, Elephantulus*) and (2) individuals from an area at least several km away from any known NMP proteas (*Aethomys, Rhabdomys, Tatera*). The first group represented animals that were live-trapped in *P. humiflora* stands and were presumably familiar with the *P. humiflora* nectar resource ("experienced" animals), while the second group represented animals that were unlikely to have encountered *P. humiflora* or similar flowers ("naive" animals). Animals were maintained in wire cages with cardboard "sleeping tubes" prior to the experiment.

The sides and bottom of the T maze were constructed of masonite and covered above with screen mesh to permit observation. The base and arms were 38 cm long and the individual runways 10 cm wide and 15 cm high. Each end of the maze could be opened to facilitate positioning of test animals and flowering heads. Tests were conducted between approximately 2000 and 2400 hours to coincide generally with the animals' normal activity periods (Fig. 1).

TABLE 17. Flower preference of small mammals in T maze experiments.

Experimental Group	Bird Adapted Flowering Head	Nonflying Mammal Adapted Flowering Head	Significance
I. "Experienced"[a]			
Initial arm choice	17	17	n.s.
Foraging[b] choice	1	26	$P \ll .01$
II. "Naive"[c]			
Initial arm choice	17	17	n.s.
Foraging choice	0	21	$P \ll .01$

[a] Five *Aethomys* were utilized in the 34 trials.

[b] Trials resulting in no foraging were generally attributable to specific animals.

[c] Naive animals utilized in the 34 trials included: five *Tatera* (21 trials), two *Aethomys* (11), two *Rhabdomys* (2).

The experimental procedure consisted of placing a freshly picked head of *P. humiflora* in one arm of the maze and a head of either *P. repens* or *P. laurifolia* in the other arm. The position of the heads in the maze arms was determined by a coin toss. A test animal enclosed in its sleeping tube was then transferred into the base of the maze. Initial response time (time before emergence from the tube) and subsequent behavior was monitored for up to five minutes. If animals did not emerge within two minutes, the tube was tapped several times. The first direction of movement in the arms was recorded as "initial choice" (+ if toward *P. humiflora* and − if toward the alternative). The first head on which the animals foraged for ≥15 seconds was recorded as "foraging choice." If animals did not enter the maze arms, or did not forage, their responses were recorded as 0 for either initial and/or foraging choice. In both groups, initial and feeding choices were analyzed utilizing the binomial test, with H_0 that responses are random and thus should be distributed evenly between the two arms of the maze. Analysis of the experienced group excludes the single individuals of *Acomys*, *Elephantulus*, and *Dendromus* tested. Analysis of the naive group is broken into *Tatera* and all others.

RESULTS

Initial choice of maze ends was evenly distributed in both the experienced and naive animals (Table 17). In the experienced group, 17 of the 34 animals initially moved toward *P. humiflora* and the remaining 17 toward the alternative ($P = .13$, n.s.). In the naive group, initial choices were also split evenly, 17 to *P. humiflora* and 17 to the alternative ($P = .13$, n.s.).

Foraging choice, however, was not random (Table 17). Of 27 foraging responses in the experienced group, 26 were on *P. humiflora* ($P \ll .01$). Of 21 foraging responses in the naive group, all were on *P. humiflora* ($P \ll .01$). These results clearly indicate that the heads of *P. humiflora* are the preferred of the two rewards offered for both groups of animals.

The role of experience in feeding-responses was evaluated by basing expected χ^2 values on the assumption that *all* animals should forage and no animals should fail to forage. Of the 36 trials in which experienced animals initially responded, 25 foraged and 11 did not ($\chi^2 = 3.36$, n.s.), and during 38 such trials in the naive group, 21 animals foraged ($\chi^2 = 7.61$, n.s.).

DISCUSSION

SMALL MAMMAL VISITATION TO PROTEA FLOWERING HEADS

Rourke and Wiens (1977) and Wiens and Rourke (1978) presented preliminary evidence that small mammals regularly visited and pollinated the flowers of various South African proteas with which they were associated. That small mammals actually visit the flowering heads of particular proteas is supported by the following new information: (1) the presence of pollen on the rostra and in the gut of small mammals, (2) the nocturnal interfloral and interplant transfer of fluorescing powder and its occurrence on captured small mammals, and, (3) the accumulation of rodent feces in the flowering heads of various proteas.

Pollen loads. Protea pollen was found on the rostra and in the feces of all small mammals captured in association with flowering species of NMP proteas, although the amounts were highly variable (Table 1). Because protea pollen is rather sticky, it is not subject to widespread wind dispersal as demonstrated by its infrequent occurrence in background samples collected away from the flowering heads (Table 7). Table 7 also gives an approximation of the density of background pollen in the environment. The small percentage of non-protea pollen in the pollen loads carried by animals tested demonstrates that

background pollen does not accumulate in dense concentrations on the rostrum. The non-protea pollen could also originate from animals foraging on these non-protea flowers, but the low concentration argues against this, or at least suggests a considerable time lapse. If the occurrence of protea pollen on the animals were the result of chance accumulation from background pollen, then the ratios of non-protea and protea pollen on the rostrum should be approximately equal to the background samples. In fact, the ratios differ radically. Protea pollen is present in the samples taken from small mammals in concentrations averaging at least 100 grains, whereas non-protea pollen averages three grains per sample. This result is greatly underestimated for proteas because no more than 500 grains were ever counted per slide, although some slides obviously contained many thousands of protea pollen grains. The pollen in feces is almost exclusively that of protea, and is probably ingested during grooming (little pollen is apt to be ingested during nectar lapping). The data are most consistent with the explanation that the pollen on small mammals originated from frequenting the heads of flowering proteas.

Fluorescent powder experiments. The results of placing fluorescent powder on the flowering heads of several ground-flowering proteas demonstrates that interplant and interhead nocturnal distribution of fluorescing powder occurs up to 15 m from the source (Tables 13, 14). Numerous particles of fluorescing powder were repeatedly found scattered along rodent runways, strongly suggesting transport by small mammals. Nocturnal terrestrial insects would be unlikely to travel equivalent distances in the available time, nor would they be likely to follow rodent runways. Furthermore, the capture of a number of animals with relatively large amounts of fluorescing powder on their bodies, especially on the rostrum, supports their role as vectors of most of the fluorescing powder transported nocturnally.

Small-mammal feces in protea flowers. The accumulation of small-mammal feces in protea heads strongly supports the hypothesis that they regularly and frequently visit the flowering heads of NMP proteas. The presence of protea pollen in the feces provides further evidence of multiple visitation.

Exclosure experiments. Experiments designed to test for genetic compatibility inadvertently provided additional information relating to rodent visitation of *P. humiflora* heads. Twenty-four fine-mesh nylon exclosure bags were placed over heads with mature buds, but within six days 14 of the bags (58%) had holes chewed through them or were pulled partially away from the heads, or both. Placing the heads under exclosures appeared to increase the amount of nectar in the heads, thus (presumably) making them more desirable nectar sources. The only other animals in the area capable of such behavior might be chacma baboons, but this seems improbable since they were never observed near the study areas.

Although captive animals regularly foraged on NMP protea heads, no wild animals were ever observed visiting the heads. Such observations are technically difficult because the species we studied most extensively (*P. amplexicaulis, P. humiflora*) have both geoflorous and cryptic heads, and the small mammals, except *Rhabdomys,* are nocturnal. A single *Aethomys* was seen in a bush of *P. amplexicaulis* at approximately 2230 hours, but it did not visit a flowering head during the several minutes of observation. Two rodents, (*Aethomys* and *Rhabdomys*) were caught in snap traps high in the branches of *P. humiflora* near flowering heads, and many animals were captured beneath protea bushes.

DOES SMALL MAMMAL VISITATION EFFECT POLLINATION?

Several lines of evidence support the contention that small mammals visit the flowering heads of proteas. But what information indicates that these visits also result in pollination? The best evidence originates from observations of: (1) the foraging activities of captive small mammals on the flowering heads of various proteas, (2) floral morphology, and (3) selective exclosure experiments.

Nectar foraging and putative pollination by small mammals. Some individuals of each species listed in Table 1 (plus *Dendromus*) foraged on the heads of NMP proteas when in captivity. The responses of the various species and individuals, however, were not consistent. For example, *Aethomys* generally foraged readily, whereas *Rhabdomys* rarely foraged and its activities were sometimes destructive. *Elephantulus* occasionally licked the surface of the heads without actually lapping nectar from the nectar reservoirs. Nonetheless, every species in Table 1, at some time, foraged on the heads of NMP pro-

teas in a manner that should have effected pollination (the process is convincingly recorded cinematographically on 16 mm film).

One aspect of rodent visitation to flowering heads mentioned by Rourke and Wiens (1977) needs correction. They speculated that rodent visitation was largely destructive. This is clearly not the case. Except for pollen loss, there is little evidence of rodent visitation following nectar-foraging. The occasional chewing of florets and bracts that prompted the suggestion occurred on only about two percent of the heads in *P. amplexicaulis* and is unlikely to have effected pollination.

The orientation of the styles and nectar reservoirs restricts effective foraging only from the center of the head outward along the radii and ensures contact with the stigmatic surface (Figs. 3, 4). The critical stigma-nectar distance of ca. 10 mm makes inevitable the deposition of pollen in the region of the stigmatic slit during nectar lapping and guarantees the maintenance of pollen loads.

Selective exclusion experiments. When small mammals were excluded from flowering heads, seed set was reduced approximately 50% in *P. humiflora* and 95% in *P. amplexicaulis*. Thus it might be argued that insects and mammals are equally important in the pollination of *P. humiflora*. This conclusion would be premature, however, in the absence of data from the reciprocal experiment involving the exclusion of insects while permitting mammal visitation. Unfortunately, experiments along these lines were technically unsuccessful. On the bases of floral morphology, physiology, and animal foraging behavior, small mammals should be more efficient than insects in pollinating *P. amplexicaulis* and *P. humiflora*. More information is needed, however, to establish the relative pollination efficiency of insects and small mammals in this system.

The floral features characterizing NMP proteas presumably evolved in response to visitation by a variety of small mammals. However, some of these features (e.g., easily accessible, highly concentrated nectar and exposed pollen) also promote visitation by numerous insects, especially honey bees, that doubtless effect occasional pollination. Based on floral morphology, however, pollination by insects can occur only haphazardly when they forage for pollen or otherwise land on the stigma. While foraging for nectar (which they normally do), insects do not contact the stigma and pollination is impossible. Bees are possibly the most likely of insects to accomplish cross-pollination since they visit many plants, but scarab beetles might also function in this capacity (Rourke, 1972). Honey bees appeared to collect pollen from all species flowering during the period in which these studies were conducted (late winter–early spring). As Faegri and van der Pijl (1979) pointed out, "social bees . . . will visit any blossom that yields sufficient nectar." Bees and beetles may, however, regularly pollinate other proteas not closely related to the species in question, e.g., *P. odorata* Thunb. and *P. laetans* L. E. Davidson, respectively. Insects probably add to pollination success in some NMP proteas. Traits enhancing their visitation should therefore be selected for, or at least maintained at equilibrium, so long as those characteristics do not retard visitation by small mammals, which are presumably the more efficient pollinators.

Birds are rare and inconsequential visitors to the NMP proteas we studied. During a period of four years, involving over 2,000 hours of observation, one malachite sunbird was seen taking nectar from the rim of a flowering head of *P. humiflora,* but the styles were not contacted. Two Cape buntings (granivores) were captured in Sherman live traps arround *P. humiflora.* Although they carried protea pollen on their foreheads, we did not observe them on the inflorescences. On one occasion an automated camera photographed an orange-breasted sunbird at the flowering head of *P. cryophila.* This is in sharp contrast to the visitation pattern in Australia where flower birds as well as nonflying mammals are common visitors to proteas and other plants (Hopper, 1980, 1982; Turner, pers. comm.). The often cryptic flowering habits of many NMP proteas, the absence of visual cues associated with typical BP proteas, and the high sugar content of the NMP protea nectar, do not suggest that NMP protea flowers are important sources of nectar for flower birds (Pyke & Waser, 1981).

THE ATTRACTING SYSTEM

The most obvious attraction is odor, since the flowers of many NMP proteas are cryptic and pollination by small mammals is largely nocturnal. As previously mentioned, the yeastlike odor with its various modifications attracted captive animals.

The T maze experiments tested critically both olfactory response to protea heads and the ulti-

mate foraging choice. Because the proffered heads could not be seen by the captive animals, olfaction is the only stimulus to which they could have responded. The experiment, however, did not test whether the animals were initially responding to the heads of the BP protea (*P. repens* or *P. laurifolia*) or the NMP protea (*P. humiflora*). The results (Table 16) show that initial choice of maze arm was random, i.e., the experimental animals did not initially discriminate between the arm holding the NMP protea and that holding the BP protea, but did so only after receiving additional cues. Since the heads were randomly switched between the two maze arms, the runways may have become saturated with the scents of both heads, thus initially precluding selective odor cues. The heads of BP proteas have little scent discernable to humans and have no yeasty odor. While the initial response to the heads was olfactory, the ultimate foraging choice (virtually always the NMP protea) could also have involved visual cues.

The styles and inner surface of the bracts of *P. amplexicaulis, P. humiflora* and some other NMP proteas are whitish, whereas the outer surface of the bracts is often dark brown or purplish. The contrast produces a "target effect" by emphasizing the white center of the head in poor light. This is apparent to the human eye, but we have no experimental evidence regarding its apparency to animals, although differences in shades are presumably evident to most mammals. Hawkmoth-pollinated plants are typically white; even generally dark bat flowers often display some white which might act as a nectar guide. Different NMP proteas utilize different strategies to produce the effect and the subject deserves further study.

THE REWARD

Small mammals visit proteas to obtain nectar (as do myriads of insects and possibly also baboons). As indicated previously, the amount of nectar available to the small mammals is difficult to evaluate, although we estimated it would supply their energy needs for approximately eight days of their annual requirement.

The flowering period of *P. humiflora* lasts perhaps six weeks, and it is reasonable to assume that the small-mammal energy budget would be supplemented during this period by protea nectar. The NMP proteas, however, occur over only an infinitesimally small portion of the overall geographical distributions of the small mammals in question. In areas no more than several hundred meters from stands of *P. humiflora*, the small-mammal community is totally without this resource and is presumably not adversely affected.

The nectar resource from NMP proteas could, however, be more important to the total energy budget than the previous comments indicate. Some local immigration from adjoining areas could increase the density of the small-mammal population on the study areas. That this happens, is suggested by the apparently high density of small mammals on grid B (58 in 1978, 20 in 1979). While we have no comparable population density data for areas without NMP proteas, the small-mammal populations on our study sites appear generally high.

We consider the nectar resource of NMP proteas as primarily a supplement to the basic small-mammal diet (a sweet treat or junk-food trip?) rather than an important component of their annual energy budget. Such a "dessert" hypothesis is in clear contrast to coevolved systems, where nectar (and sometimes also pollen) forms the primary or exclusive component of the energy budget.

Furthermore, the flowering of most NMP proteas correlates with the reproductive period of the small mammals and the extra energy resource could be important to females during gestation and lactation, and also in juvenile survival. Blooming at this time should certainly enhance the possibility of flower visitation by small mammals, and selection could have shifted flowering by the NMP proteas into this period. Most BP proteas have peak flowering periods at other times. In unilaterally evolved flowers (see following section), the flowering periods appear to coincide with environmental factors that should maximize visitation. For example, pseudocopulatory orchids flower before the female wasps appear; and Janson et al. (1981) indicated that Neotropical Bombacaceae and Combretaceae pollinated by nonflying mammals flower during the dry season when fruits or other flowers are at seasonal lows. The nectar in this latter case could also be an important source of water for these relatively large pollinators. As Porsch (1934) pointed out, water is not always so readily available in the tropics as is generally assumed. Morcombe (1968) made the same argument for southwestern Australia. He commented that the majority of banksias flower during the height of the dry season, although George (1981) indi-

cated flowering in *Banksia* may not correspond so closely with the dry season as Morcombe suggested. If water is an important resource provided by nectar, this should be reflected in a low sugar concentration. In this connection, Schemske (1980) reported that *Combretum farinosa* Kunth (= *C. fruticosum*?), which flowers during the pronounced dry season in Guanacaste, Costa Rica, produces copious nectar and has among the lowest nectar-sugar concentrations (7.1%) of which we are aware. The water-resource argument needs further analysis as an explanation for dilute nectar concentration in unilaterally evolved plants occurring in at least seasonally arid regions (Watt et al., 1974; Pyke & Waser, 1981).

THE EVOLUTION OF NMP PROTEAS

COEVOLUTION, CO-OCCURRENCE, OR UNILATERAL EVOLUTION?

The South African NMP proteas are not coevolved (Rourke & Wiens, 1977; Wiens & Rourke, 1978). This statement often elicits questions from ecologists and evolutionary biologists, suggesting that coevolution is perhaps too deeply established as *the* raison d'être for the evolution of pollination or dispersal systems as Janzen (1980) has already suggested. Coevolution (Ehrlich & Raven, 1964) has provided a central paradigm for the study of plant-animal interactions and is an immensely useful concept. Pollination systems, however, are also commonly "unilaterally" evolved, i.e., plants that have profoundly altered floral function to attract a pollinator that itself has not become specialized to the flower. In other words, the system does not elicit "reciprocal selective responses" typical of coevolved systems, but rather "unilateral selective responses" on the part of the plant. A number of biologists have suggested that plants make initial evolutionary adjustments to animals, e.g., Grant and Grant (1965), Baker and Hurd (1968), Baker (1973) and Feinsinger (pers. comm.). Clearly, many generalist animals take nectar (or fruit) during times of seasonal abundance (Snow & Snow, 1971; Heithaus et al., 1974; Carpenter, 1978b). The concept of unilateral evolution is not meant to replace coevolution, but to complement it in the sense that it represents one end of a spectrum of biological interactions and coevolution another. Transitional situations will occur, but this is hardly uncommon in evolutionary classifications. Pollination systems involving single, coevolved pollinators are rare (e.g., *Ficus* and *Yucca*). Typically, guilds of pollinators act upon a series of sequentially flowering, coevolved plant species. The same principles that apply to nectar-foraging animals also apply to fruit- or seed-eating animals. Howe (1980) strongly questioned whether coevolution is always involved in interactions between the plant and the animals that disperse its seeds, preferring to consider the situation an example of "co-occurrence." Howe does not discuss whether the fruits he studied presumably evolved to entice various animals to eat them, or were at least preadapted to the extent that the animals readily foraged on them.

The NMP proteas are clear examples of unilateral evolution, since virtually all the basic features of the flowers appear adapted for the attraction and reward of nonflying mammals that presumably effect pollination while foraging for nectar. NMP proteas co-occur with honey bees, which also take nectar and pollen from the flowers and may occasionally effect pollination. The highly concentrated nectar, however, is the only trait held in common with bee-pollinated flowers. Conversely, good evidence exists that other proteas, e.g., *P. repens,* have coevolved with the Cape sugar bird (*Promerops cafer* L.). The latter commonly takes nectar (and insects) from the flowering heads and its breeding season is synchronized with the peak flowering activity of this protea. Even the young are partially fed on its nectar (Broekhuysen, 1959; Winterbottom, 1962; Mostert et al., 1980). In our view, all three of these mutualistic situations, i.e., coevolution, unilateral evolution, and co-occurrence describe common interactions between plant and animal species; the recognition of the latter two categories, each of which must involve tens of thousands of plant species, is overdue. While coevolution is a general concept, it was never intended by its formulators to be as all-inclusive as the current literature suggests (Raven, pers. comm.).

Of the pollination systems described by Faegri and van der Pijl (1979), wind, water, ant, and at least elements of bee, (social groups), bird, [various passerine groups, cf. Stiles (1981)], most flies, perhaps beetle systems, and all pollination involving mimicry (Wiens, 1978) are probably unilaterally evolved. Many of the plants known or thought to be pollinated by nonflying mammals are apparently unilaterally evolved (see Introduction). Coevolved guild systems probably occur in southwestern Australia, however, where some Proteaceae may be regularly pollinated by

the marsupial honey possum, *Tarsipes* (possibly also the southwestern pygmy possum, *Cercartetus concinnus* Gould), which shows clear adaptations for nectar and pollen feeding (Wiens et al., 1979; Hopper, 1980). The floral spectrum on which *Tarsipes* feeds and the degree to which it shares floral resources with birds is currently under study (Hopper, pers. comm.; Turner, pers. comm.).

The Origin of Nonflying-Mammal Pollination Systems

Rourke and Wiens (1977) suggested that at least some of the NMP proteas evolved from bird-pollinated prototypes in both Africa and Australia, as evidenced by branching patterns of the inflorescences. Many of the NMP proteas have an axillary inflorescence apparently derived by reduction from the large terminal inflorescences of the BP proteas. Fire was also a possible stimulus in the evolution of NMP proteas through the development of rhizomaty which may have promoted geoflory.

Another hypothesis for the origin of NMP proteas is suggested by this study. Virtually all NMP proteas are characterized by small, highly localized populations often associated with specific soil types. These species are typically low shrubs largely restricted to relatively high elevations in the outlying Cape mountain systems bordering the arid Karoo (Rourke, 1980). As previously stated, the Cape flora occupies an elevated and greatly dissected landscape closely associated with the Table Mountain Sandstone. Consequently, many species in this rich flora occur only as small populations in scattered, isolated habitats, as do the NMP proteas. In contrast, many of the BP proteas are large shrubs or small trees often occurring in dense populations covering many hectares. Flowering stands of these proteas apparently attract large numbers of locally migrating flower birds with which they are commonly associated.

We propose that differences in population structure may be the single most important factor regulating the evolution of pollination by nonflying mammals in *Protea*. The continuing dissection of the Table Mountain Sandstone and the progressive restriction of species having highly specialized ecological requirements (especially for soil types), may have provided nonflying mammals with several advantages over birds as pollinators. The small mammals involved are ubiquitous, non-hibernating, and non-migratory residents, and generalist feeders (Roberts, 1951). Such pollinators permit temporal partitioning of flowering times among sympatric NMP proteas, and may be more readily attracted to an ephemeral and highly restricted resource than more specialized feeders. They may also provide more reliable pollination service than insects (e.g., bees and beetles) whose activities are often restricted by the long periods of low temperatures characteristic of late winter and early spring when most NMP proteas flower. The occasional fluctuations in population size of small mammals, however, might be a disadvantage. No other flowers are known to be visited by nonflying mammals in these communities, and sympatric NMP proteas flower sequentially, thus presumably no competition exists for mammal pollinators among NMP species.

If the system were, indeed, derived from bird-pollinated species, the prototypes were presumably pre-adapted for nonflying-mammal pollinators in having (1) large heads with copious nectar secretion, and (2) an inflorescence with mechanically strengthened tissues (particularly those of the style), which could accommodate a relatively large animal without undue destruction of floral parts. Physiological and structural modifications involved in the change to the present NMP type include: (1) the shift to nocturnal anthesis and (presumably) nectar production, (2) the production of nectar with high concentrations of sucrose and other sugars, (3) reduction of the stigma-nectar distance to about 10 mm, and (4) the production of a volatile, olfactory attractant.

The hypothesis explains why pollination by nonflying mammals probably had multiple origins, since species with cryptic, terminal heads (*P. recondita*); rhizomatous stems (*P. angustata*); cryptic, geoflorous heads (*P. amplexicaulis*); and aerial, pendulous heads (*P. sulphurea*) all represent different lines of evolution in which nonflying-mammal pollination presumably evolved independently. The common denominator among these species is their occurrence in relatively small, isolated populations. The shift to the NMP type in protea shows every evidence of being a strategy superimposed on many different life forms, each of which responded in differing ways depending on the phyletic constraints within the system.

Whether the "restricted population hypothesis" is also applicable to other examples of pollination by nonflying mammals remains to be

determined. Certainly many of the cryptic and/or geoflorous species of *Dryandra* and *Banksia* in Australia occur in small, isolated populations. In Southwestern Australia, *Tarsipes* (perhaps *Cercartetus*) is highly adapted for a diet of nectar and pollen and represents a distinct line within its family. This suggests an older and long-established, flower-animal interrelationship in Australia, as Sussman and Raven (1978) and Ford et al. (1979) suggested, even though many of the cryptic, geoflorous banksias and dryandras are probably specialized within their genera.

Sussman and Raven (1978) proposed that nonflying-mammal pollination is an old phenomenon, possibly originating in the tropics. They postulated a grand scale competitive exclusion of nonflying mammals as pollinators by flower-feeding bats, which are presently unknown in the Cape region of southern Africa or in southern Australia. Less distinctive climatic gradients, however, probably existed in the early Tertiary (Sussman & Raven, 1978). Because of the low frequency of individuals of a species in tropical forests, the "restricted population hypothesis" might not be expected to apply unless (1) plants are self-compatible [an uncommon condition according to Bawa and Opler (1975] and produce sufficient flowers to induce regular visitation by nonflying mammals, or (2) the particular plant species do not occur as highly scattered individuals in tropical forests. Bats and birds solve the problem of scattered distributions by possessing flight and trap-lining capablilities, which should make them much more competitive in tropical forests than nonflying mammals.

Since the publication of Sussman and Raven's paper, three examples of pollination by nonflying mammals have been discovered in the New World tropics. Lumer (1980) reported that rodents (*Oryzomys devius* Bangs and *Peromyscus mexicanus* Saussure) pollinate *Blakea* (Melastomataceae) in a Costa Rican cloudforest. Lumer (pers. comm.) indicates that this *Blakea* often occurs as clusters of several individuals. But *Blakea* also grows in a windy, cold environment along the continental divide. Baker (pers. comm.) suggests that the harsh, windy environment may preclude effective bat visitation to such flowers. Little is known about the occurrence of flower-feeding bats in this area, but even if flower-visiting bats were present, they might well avoid the environment where these plants occur, thus providing support for Sussman and Raven's argument. *Blakea* appears to offer some evidence for both the competitive exclusion and restricted population hypotheses.

Two additional discoveries of nonflying mammal pollination are reported for the New World lowland tropical forests. Janson et al. (1981) indicated that in the Peruvian Amazon 13 species of nonflying mammals (monkeys, marsupials, procyonids) take nectar and presumably pollinate species of *Combretum* (Combretaceae), *Quararibea,* and *Ceiba* (Bombacaceae). Steiner (1981) reported that the red woolly opossum (*Caluromys derbianus* Waterhouse) visits and presumably pollinates *Mabea* (Euphorbiaceae). This opossum also visits the typically bat-pollinated flowers of *Ochroma* (Bombacaceae) and *Trichanthera* (Acanthaceae). Steiner also suggested that the common opossum (*Didelphis virginiana* Kerr) may likewise be involved in pollination.

Janson et al. (1981) observed that species of *Combretum, Quararibea,* and *Ceiba* are unilaterally adapted for pollination by various nonflying mammals, as is *Blakea* (Lumer, 1980) and probably also *Mabea* (Steiner, 1981). Whether other tropical flowers subject to nectar foraging by nonflying mammals are adapted for pollination by these animals or by bats is uncertain. Mori, Prance, and Bolten (1978) indicated that opossums, cebus, and squirrel monkeys observed on *Lecythis* flowers are feeding opportunistically, as are (presumably) marsupials on the typically bat-pollinated flowers of *Ochroma* and *Trichanthera* (Steiner, 1981). Janson et al. (1981) stated that some primate visitation is clearly opportunistic and destructive.

With respect to population structure, Steiner (1981) reported that *Mabea* may also have a clumped distribution, and suggested that such distributions may be more common in the tropics than was previously thought likely (Hubbell, 1979). Janson et al. (1981) mentioned that *Combretum* and *Quararibea* are not uncommon in the study area, but that *Ceiba* has a widely scattered distribution.

The reports of pollination of the baobab by the bush baby (Coe & Isaac, 1965) and of genets taking nectar from the flowers of *Maranthes* (Chrysobalanaceae) (Lack, 1977) in tropical Africa need further study to determine the basic pollinator adaptations of the flowers, although Lack indicated that *Maranthes* is primarily bat-pollinated. Baobabs are bat-pollinated in west Africa (Baker, 1961 and pers. comm.; Jaeger, 1954—cited by Faegri & van der Pijl, 1979).

A number of low or prostrate proteas occur in tropical Africa, e.g., *P. enervis* Wild, *P. heckmanniana* Engl., *P. paludosa* Welw., *P. secundifolia* Hauman (Beard, 1963), but the pollinators are unknown. A study of these species may well provide additional information on Sussman and Raven's competitive exclusion hypothesis as applied in the Old World tropics. Data currently emerging from the Neotropics indicate that nonflying mammals are not necessarily out-competed by bats.

Is There a Class of Flowers Adapted for Pollination by Nonflying Mammals?

The existence of a class of flowers adapted for pollination by nonflying mammals was suggested by Rourke and Wiens (1977). Their argument was based primarily on the parallel floral evolution between South African species of *Protea* and a number of Australian proteaceous, and possibly some myrtaceous genera. The problem was discussed by Sussman and Raven (1978) and by Armstrong (1979). The discovery of additional instances of nonflying-mammal pollination in the Neotropics by Lumer (1980), Janson et al. (1981), and Steiner (1981), and in Australia (Hopper, 1980, 1982; Turner, in prep.) provide additional information on the subject.

Janson et al. (1981) in their extensive studies of Amazonian nonflying-mammal pollinators provided the most important new data. They generally supported the concept of a class of flowers adapted for pollination by nonflying mammals, but stressed that sufficient attention has not been given to the possible role of bats in the pollination of the flowers on which they frequently observed nonflying mammals foraging for nectar. In tropical regions, the differential effectiveness of bats and nonflying mammals in pollinating flowers visited by both groups was discussed by Sussman and Raven (1978), but detailed analyses are needed. In Australia and south temperate Africa a similar problem exists, but it involves birds and nonflying mammals in the former, and insects and nonflying mammals in the latter. Janson et al. (1981) emphasized that many flowers growing in their study area are morphologically similar to those regularly visited and presumably pollinated by nonflying mammals, yet those flowers are ignored by these animals. Thus physiological characteristics, such as odor and nectar must share equal importance with floral structure in identifying floral classes.

Janson et al. (1981) suitably amended the list of structural features proposed by Rourke and Wiens (1977) to include characteristics of the Combretaceae and Bombacaceae they studied. Most notably, the stigma-nectar distance is increased to accomodate the larger visitors, and the flowers are short-lived. Some flowers lack an odor, but probably possess visual cues that may serve to attract the diurnal primates and procyonids that possibly lack the well-developed olfactory senses of rodents. This dichotomy of characters among nonflying mammal-pollinated flowers is not unexpected. Wiens and Rourke (1978) suggested the category might be composed of subgroups. Interestingly, Porsch (1934) originally suggested one class of flowers adapted for mammal pollination, including chiropterophily as a subgroup—a suggestion worth reconsidering. The flowers of *Blakea* (Melastomataceae) (Lumer, 1980) differ in a number of respects from those of Bombacaceae, Combretaceae, Myrtaceae, and Proteaceae, although *Mabea* (Euphorbiaceae) (Steiner, 1981) appears to have no features departing radically from those mentioned by Rourke and Wiens (1977) and Janson et al. (1981). The floral features of *Blakea* need further analysis in this regard, particularly in relation to odor and nectar characteristics. As information accumulates, more additions and modifications to the proposed syndrome will probably be necessary.

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