Opportunistic breeding in the Cape spiny mouse (*Acomys subspinosus*)

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The relationship between *Protea humiflora* and its small mammal pollinators was investigated at the fynbos/karoo ecotone in the Riviersonderend Mountains, South Africa. *Acomys subspinosus* occurred in low densities at Jonaskop, with around 3.9 ± 2.0 (mean ± 1 S.D.) individuals/ha (six months of trapping). Low repeat trapping may result from low survivorship or emigration from the area after flowering of *P. humiflora*. Mean mass of *A. subspinosus* was lower than published values due to a high proportion of juveniles in the population, coinciding with *P. humiflora* flowering. Comparison with other published data suggests that *A. subspinosus* is an opportunistic breeder. This contrasts with its geographically nearest congener, *A. spinosissimus*, in which breeding is restricted to the summer months, but is similar to data for other *Acomys* species. Minimum home range areas (≈0.23 ha, minimum overnight distance 39 ± 6 m), were relatively high and may indicate a species surviving on thinly dispersed resources.

Key words: **animal–plant interaction, non–flying mammal pollination, *Protea humiflora*.**

The eight species of *Acomys* have an extremely wide distribution, occurring in arid regions from southern Pakistan through the Middle East and most of Africa to the Cape (Nowak 1991). Two species are recognized within southern Africa, the spiny mouse *A. spinosissimus,* and the Cape spiny mouse *A. subspinosus* (Dippenaar & Rautenbach 1986). *A. subspinosus* has a restricted range (de Graaff 1997) and is described as a true fynbos endemic (Breytenbach 1982). Little is known of the life history, diet or habits of *A. subspinosus,* and this species was included in the 1976/1977 South African Red Data Book as rare, owing to low numbers and a lack of information on its basic biology (Meester 1976). The species is no longer listed since 'its rocky mountainous terrain is unlikely to be degraded' (Smithers 1986).

We carried out a study of the mammal-pollinated *Protea humiflora* (Proteaceae) in the Riviersonderend Mountains of the western Cape, South Africa (Fleming & Nicolson, in press). *A. subspinosus* is a flower visitor and potentially important pollinator of *P. humiflora.* Here we record information on the density and breeding of *A. subspinosus* at Jonaskop (33°55′S, 19°31′E, 630 m) and compare this with published data for the species.

The slope at Jonaskop is north-facing, with exposed rock and heterogeneous vegetation densities, ranging from near-open ground, with little cover, to areas of dense growth of *P. humiflora* bushes, some 1–1.5 m high. The vegetation is typical of the fynbos/karoo ecotone, and is dominated by Asteraceae and Thymelaeaceae/Rhamnaceae; *P. humiflora* was usually the only species of Proteaceae present. We trapped over three nights every month, on the new moon, from June to November 2000, thus comparing winter months, when *P. humiflora* was flowering, with the following spring. Two adjacent grids (50 m apart) of 64 Sherman traps each (10 m apart, baited with peanut butter and oats), yielded a total trapping area of 1.28 ha. Although *P. humiflora* inflorescences were removed over one of these grids, for the purposes of the present study, the grids are not considered separately.

Each captured animal was identified, weighed, measured and individually marked by toe–clipping. Breeding status was recorded: females were recorded as perforate or non-perforate and nipple development was noted. Juveniles were considered *post hoc* as those individuals <17 g on the basis that the smallest sexually active individual

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was 17 g (see also David & Jarvis 1983). Densities were calculated for the minimum number alive; population estimates (e.g. Begon 1979) were not possible due to low recapture rates and violation of the assumption of a closed population.

Acomys subspinosus was caught in low densities at Jonaskop, with the average trapping density over six months being 3.9 ± 2.0 (mean ± 1 S.D.) individuals/ha (Fig. 1A). Densities were both spatially and temporally heterogeneous, highest numbers being encountered during peak flowering of *P. humiflora* in August (Fleming & Nicolson, in press). Densities on the two adjacent grids differed fourfold and were significantly correlated with the availability of inflorescences (Fleming & Nicolson, in press). Of 20 individuals encountered, only seven were trapped over two consecutive months and only two over a longer period, reflecting either low survival or a transient population. No individual marked during a previous study in 1996/7 (I.G. van Tets, unpubl. data) was re-trapped in 2000.

Our low trapping densities for *A. subspinosus* are still well within the range of published data (Table 1): *A. subspinosus* is simply not a commonly encountered species (Meester 1976). At a second site 10 km west of Jonaskop (at the base of Wolfieskop), only one individual was captured in nine months' trapping. Both sites were north-facing slopes, supporting similar vegetation and with similar amounts of exposed rock, consistent with descriptions of the habitat preference of *A. subspinosus* (Bond *et al.* 1980; Breytenbach 1982; David & Jarvis 1983). A similar patchy distribution has been described by other authors; various explanations have been proposed. Breytenbach (1982) and Bond *et al.* (1980) found increased densities with altitude (although at the sites they studied, altitude was also correlated with plant and rock cover); however, an increase with altitude was not evident in the survey carried out by Nel *et al.* (1980). While Bond *et al.* (1980) found a correlation between the density of *A. subspinosus* and dense phytomass, particularly below 60 cm, we found a correlation with *P. humiflora* fecundity but not density (Fleming & Nicolson, in press); such relationships with vegetation variables may reflect food resource availability. *A. subspinosus* feeds almost exclusively on seeds (91 %, Nel *et al.* 1980; 94 %, Breytenbach 1982), especially ant-dispersed seeds of Restionaceae and Proteaceae with eliasomes (Breytenbach 1982; Bond & Breytenbach 1985). The remainder of the diet

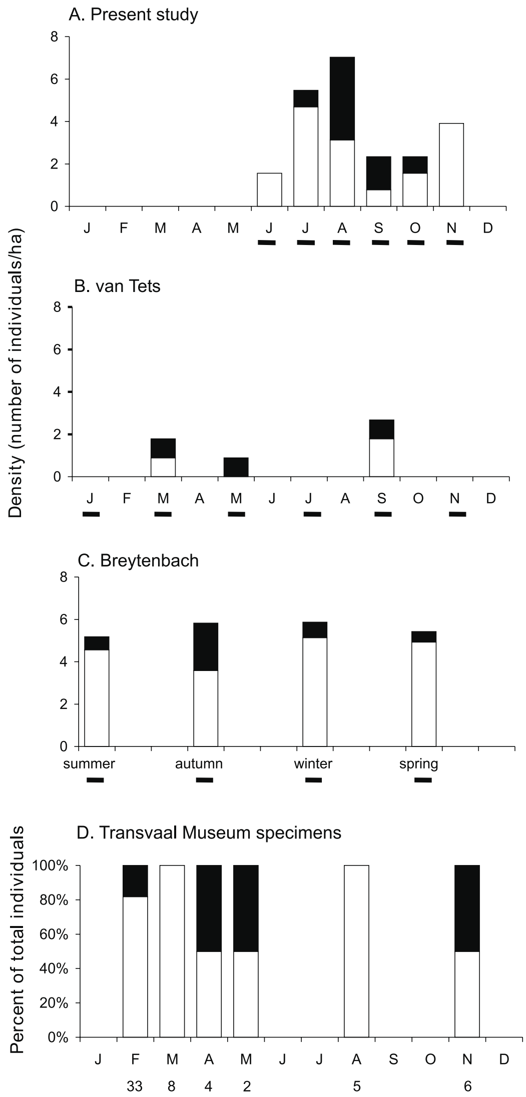

Fig 1. Densities of *Acomys subspinosus* adults (>17 g, white bars) and juveniles (<17 g, black bars) recorded in the present study (**A**), and by van Tets (unpubl. data) at Jonaskop (**B**), and Breytenbach (1982) from the Groot Swartberg (**C**). Black lines under the *x*-axis indicate months for which trapping was carried out; densities given as the number of individuals per hectare calculated from trapping over three nights. (**D**) shows the relative proportion of adult and juvenile Transvaal Museum specimens; values under the *x*-axis are numbers of specimens for which mass values were available.

consists of green plant material (0–5 %) and insects (2–10 %) (Nel *et al.* 1980; Breytenbach 1982). In addition, we found that *A. subspinosus* fed extensively on *P. humiflora* flower products during July and August, pollen grains constituting up to 80 % of scats, and that flower availability had a signifi-

Table 1. *Acomys subspinosus* trapping densities (present study and data from the literature). Densities are numbers of individuals/ha, except for Nel *et al.* (1980), where values are the percentage trap success.

Author	Location	Trap sessions (nights)	Site	Density/ha
Present study	Riviersonderend Mountains	6 (×3 days), 6 months	Jonaskop	3.8 ± 2.1
van Tets (unpubl. data)	Riviersonderend Mountains	6 (×3 days), 12 months	Jonaskop	0.9 ± 1.1
David & Jarvis (1983)	Rooiberg, Ladismith	2 (×3 days) March & November	3 of their 4 sites*	2.5 ± 1.7
van Hensbergen (1992)	Swartboskloof	22 (×4 days), 24 months	Control grid, pre fire	2.8 ± 2.4
Breytenbach (1982)	Groot Swartburg	6 (×3 days), 18 months	8 habitats	5.1 ± 2.1
Bond *et al.* (1980)	Swartberg Mountains	1 (×4 days), December	8 sites, various altitudes	3.5 ± 5.4
	Baviaanskloof Mountains	1 (×4 days), January	7 sites, various altitudes	13.7 ± 17.1
Nel *et al.* (1980)**	Kammanassie Mountains	1 (×10 days), February	NW, 7 habitats	0.2 ±0.4%
			SE, 16 habitats	0.8 ± 1.6%

*Density calculated for sites where *A. subspinosus* was present.
**Collected 58 individuals in 14 728 trap nights but did not indicate trapping areas.

cant affect on trapping densities (Fleming & Nicolson, in press).

The very low repeat trapping of *A. subspinosus* (only two individuals over more than two months) was slightly lower than the survivorship shown by Breytenbach (1982). Low survival or re-trapability may reflect death or emigration, possibly due to temporally variable food resources, with dispersal or increased mortality of the population after *P. humiflora* flowering.

Males and females were of similar average mass, being 18.0 ± 3.5 g (n = 9) for females and 17.4 ± 4.7 g (n = 11) for males (t-test, NS, overall average 17.7 ± 4.1 g). These body masses were substantially below those reported elsewhere, with significant numbers of juveniles (<17 g). Our average compared with values of 20 g for males (17–23 g, n = 9) and 22 g for females (20–25 g, n = 17) (de Graaff 1981) and 21.2 ± 2.2 g (n = 76, both sexes, Breytenbach 1982), while Transvaal Museum specimens yield values of 19.6 ± 3.8 g (n = 58, both sexes).

Perforate females were encountered during June and July trapping, and females with developed nipples were encountered from July onwards. Males demonstrated little scrotal development, subsequently breeding condition of males was not readily determined. Juveniles were trapped from July through to October (Fig. 1A).

These data indicated that *Acomys subspinosus* was breeding during the winter of 2000 at Jonaskop, coinciding with the flowering of *P. humiflora* (Fleming & Nicolson, in press). However, van Tets (unpubl. data), trapping also at Jonaskop in 1996/7, recorded juveniles in March and May (Fig. 1B), while Breytenbach (1982) recorded similar numbers of pregnant females over all seasons, with peak juvenile numbers during autumn (Fig. 1C). These breeding data are also reflected in a lack of seasonal pattern in mass class distributions (Transvaal Museum data; Breytenbach, 1982) and a reasonably stable sex ratio, near equity (Fig. 2). Finally, Nel *et al.* (1980) recorded no breeding for 58 individuals captured in February (by contrast they noted breeding for *Rhabdomys, Aethomys, Saccostomus, Praomys* and *Graphiurus*). Taken together, these data suggest that breeding of *A. subspinosus* is probably opportunistic, depending on resource availability, and certainly is not restricted to summer as stated previously (de Graaff 1997).

Opportunistic breeding in *A. subspinosus* contrasts with the distinctly summer (October to April) breeding pattern noted for its geographically nearest congener, *A. spinosissimus* (Smithers

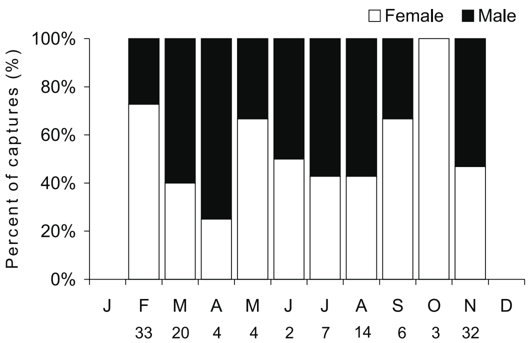

Fig. 2. Monthly variation in sex ratio of *Acomys subspinosus.* Data pooled from the present study, van Tets (unpubl. data), David & Jarvis (1983) and Transvaal Museum specimens. Numbers under the *x*-axis are total numbers of individuals for each month.

1971, Botswana; Sheppe 1973, Zambia; Smithers & Wilson 1979, Zimbabwe). However, aseasonal as well as conflicting seasonal data have been presented for other *Acomys* species (Nowak 1991), suggesting the possibility of opportunistic breeding, with timing dependent on resource availability. The possibility of opportunistic breeding has been proposed for *A. cahirinus,* with breeding commencing a few months after the first rains of the season (Hanney 1965, Malawi; Happold 1966, Sudan). In Kenya, despite an extremely seasonal environment, Neal (1983) found no breeding seasonality for *A. percivali* and *A. wilsoni,* while Hubbard (1972) reported summer breeding in *A. wilsoni,* but winter breeding in *A. hystrella* from Tanzania. These somewhat conflicting patterns seem to support the statement that 'under good conditions, *Acomys* probably breed over the greater part of the year' (Kingdon 1974).

Minimum home range area was estimated as the area of the polygon joining furthermost trap captures for three females that were trapped four or more times. Minimum home range sizes were 0.11, 0.22 and 0.35 ha and showed substantial overlap, while a minimum distance of 39.2 ± 5.6 m (max. 55 m, n = 6) was covered overnight. These data suggest that, despite their diminutive size, *A. subspinosus* cover an area slightly greater than female *Aethomys namaquensis,* a substantially larger animal (47.5 ± 14.9 g, n = 66) in the same habitat (Fleming, Nicolson and van Tets, unpubl. data). Breytenbach (1982) similarly found that *A. subspinosus,* although one of the smallest species he encountered, had the largest home range area estimates. *A. subspinosus* ranges are similar to estimates for the rock mouse, *Petromyscus collinus* (18.3 g, 0.27 ha) in the Namib Desert (estimated from area between points of capture; Withers 1979). These relatively large home range sizes of *A. subspinosus* may reflect opportunistic use of sparsely spread resources, in particular the nectar and pollen available in *P. humiflora* inflorescences at Jonaskop.

Acomys subspinosus contributes significantly to the pollination of *P. humiflora,* and, in turn, gains the food resources that enable winter breeding. In addition to being a potential pollinator for a number of plant species (Wiens *et al.* 1983; Johnson *et al.* 2001), *A. subspinosus* also has a role in seed predation and hoarding in the fynbos (Bond & Breytenbach 1985; Vlok 1995), potentially contributing to the evolution of myrmechochory as a mechanism to evade rodent seed predation (Midgley *et al.*, in press). Its role as an opportunist feeder suggests that individual welfare and breeding of this scarce little animal may be linked with other transient fynbos plant resources.

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Group displays in pale-winged starlings

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Cliff-nesting pale-winged starlings (*Onychognathus nabouroup*) gather on the cliff tops to perform Group Displays which include both aggressive and courtship elements: Hopping, Wing Stretching, Wing Drooping, Wing Flicking, Staring, Head Forward Threat and Butterfly Fluttering. These displays occur throughout the year, most frequently in the late afternoon. We suggest that this behaviour may be important in pair formation, and in establishing dominance relationships between birds breeding at the same site.

Key words: aggression, social behaviour, roosting.

Pale-winged starlings (*Onychognathus nabouroup*) are locally common in the arid regions of southwestern Africa, where they nest and roost on rocky outcrops. They can be found in flocks throughout the year, but nest in monogamous pairs, with only the parents attending the nestlings. Unlike most other members of the genus *Onychognathus,* there is no sexual dimorphism in plumage (Feare & Craig 1998). Adult birds are glossy black with an orange iris (brown in juveniles), and the inner webs of the primary remiges are creamy white, forming a pale wing patch in flight. Following a comprehensive review of the biology of the starling family, this is the only species of African starling in which group displays have been recorded as a regular part of their behavioural repertoire (Feare & Craig 1998).

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We observed pale-winged starlings on a farm east of Cradock, South Africa (32°17′S, 26°01′E) on 23 visits from 1983–1987. Here the birds roosted and nested on a series of cliffs along a narrow river valley. Pairs appeared to roost throughout the year in the clefts where they nested, and even in the non-breeding season birds returned to the cliff at intervals during the day. The number roosting at the study site ranged from 12–30 birds. At this 30 m high cliff, two or three observers carried out dawn to dusk watches on successive days, using 10 × 40 binoculars and a ×20–40 telescope, from a vantage point that offered a clear view of the entire cliff. Total observation time was 328 hours; during observations we attempted to monitor all bird activity on the cliff, and did not use focal animal techniques. Most visits were in spring (8) or summer (8), with fewer observations in autumn (4) and winter (3). Only two colour-ringed birds, both females, were consistently present.