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POPULATION TURNOVER IN A MONOGAMOUS ANTELOPE (*MADOQUA KIRKI*) IN NAMIBIA

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Only a few of the 75 species of African bovids live in monogamous reproductive groups. These include the Neotragini (subfamily Antilopinae—klipspringer, steenbok, suni, oribi, and dikdik), the Cephalophinae (diukers), and one representative of the Reduncinae (southern reedbeek) (Wittenberger and Tilson, 1980). Monogamy in antelope is correlated with sexual monomorphism, male parental aid, specialized vocalizations, and male defense of multipurpose territories containing scarce browse (Dubost, 1980; Dunbar and Dunbar, 1980; Jarman, 1974; Kleiman, 1977; Ralls, 1976; Tilson and Norton, 1981; Wittenberger and Tilson, 1980). Despite numerous field observations of social groupings of these small and typically wary species (reviewed in Leuthold, 1977), details at the population level are scarce (Hendricks, 1975). Here we report on annual turnover rate in a population of Damara dikdik (*Madoqua kirki*) in South West Africa/Namibia. We also describe features of their social and spacing behavior, with comparison to East African populations.

A dikdik population was censused from a vehicle during 13 consecutive days in October and November 1976 at Blubokkie Drive, 6 km S Namutoni, Etosha National Park, South West Africa/Namibia. Two years later a second census at the same site was made during 12 days in December, 1978. The area is typical dikdik habitat (see Boshe, 1984); a mosaic of woodland thicket with an 8-14-m high canopy, open glades with a well developed shrub understory up to 2 m, and little or no grass. Dominant shrubs and typical plants at Namutoni included *Spirostachys africana*, *Terminalia psuntoides*, *Colophospermum* sp., *Grewia* sp., and *Acacia* sp. (after Tinley, 1969).

Observations began at sunrise (mean time = 0610 h; local standard time) and continued until sunset (mean time = 1915 h), excluding midday intervals (1230-1500 h) when dikdik were usually resting under shrubs.

Population censuses were considered complete when no new individuals were encountered for 3 consecutive days; this occurred during the two study periods on the eighth and seventh day, respectively. Behavioral notes were based on 182 h of discontinuous observations, ranging from momentary sightings to 3.2 h of continuous observations.

We identified 13 adult pairs and 3 solitary adult female dikdiks by natural cuts and notches along edges of ears, and for some males, by horn shape (Fig. 1). Of the 29 adults of both sexes, 27 (93%) had distinctive ear patterns which remained evident in the survivors (see also Hendricks, 1975). Two undistinguishable adults (males 1 and 15) were always encountered sufficiently far apart from one another (about 2 km) to prevent any confusion. Individual recognition among immature offspring was not precise; two males were identifiable, two other males and one female were not.

We determined dikdik ranges by reliance on the following. Reference locations and movements of in-

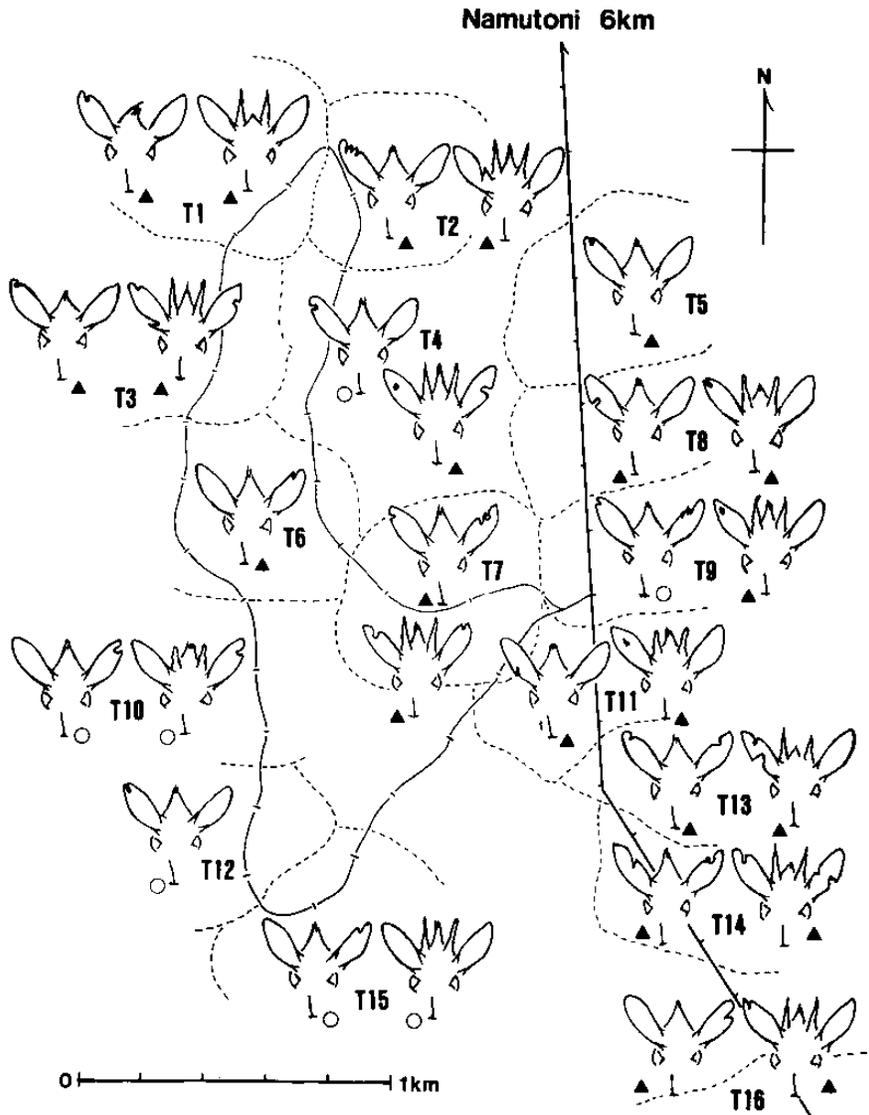


FIG. 1.—The study area in Etosha National Park, SWA Namibia, showing approximate home range/territory boundaries. Dikdik with closed triangles disappeared between censusing periods. Females that lost their mate, then regained a new one, are identified by open circles. Adult pairs 10 and 15 stayed together and were at the same site 25 months later. Male dikdik have horns; females do not.

dividuals were noted in relation to stone cairns placed every 100 m along the edge of 7.3 km of gravel road. On average, each group was sighted 3.2 times per day, some for extended periods of time and others only briefly. These data were transferred to a 1:5,000 map drawn from an aerial photograph and projecting lines indicated the directions, distances, and times of movement for individuals or groups. Lines connecting the outermost observation points represented home range/territorial boundaries (Fig. 1). Because of our limited observations we do not distinguish between the spatial concepts of home range or territory; the term territory is used here in agreement with other observers (Boshe, 1984; Hendricks and Hendricks, 1971; Tinley, 1969). For only three dikdik was range size at Namutoni ascertained with any certainty (2, 4, and 7) in 1976; the mean area of these ranges was about 10 ha (range = 7.5–12 ha).

By contrast, Tinley (1969) reported an average size of 0.3 ha for 21 dikdik territories in the same area.

TABLE 1.—Size and frequency of occurrence of *Madoqua kirki* social units upon initial observations compared to prolonged observation (>15 min; n = 195).

Individuals/group	Initial observation		Prolonged observation	
	n	%	n	%
1	101	51.8	33	16.9
2	68	34.9	96	49.2
3	14	7.2	56	28.7
4	3	1.5	10	5.1
5	4	2.1	0	0
6	1	0.5	0	0
7	3	1.5	0	0
8	0	0	0	0
9	1	0.5	0	0

Territories of East African dikdik reportedly range from an average of 0.05 ha (Boshe, 1984), 2 ha (Simonetta, 1966), 7.5 ha (Hendricks and Hendricks, 1971), 8 ha (Hendricks, 1975) to 10 ha (Walther, 1972). Boshe's (1984) study of habitat manipulation attributed variability of dikdik territory size to shrub density. Shrub reduction totalling 40% or more of dikdik territorial space resulted in territory abandonment or boundary extension to compensate for reduced resources.

Three social units, including solitary dikdiks, were observed: (1) mated adult pairs with or without offspring; (2) unmated resident females; and (3) transient solitary individuals of both sexes. Adult pairs were considered mated if they were observed foraging or resting together. The status of pairs was often not immediately clear because dikdik do not always forage in close proximity to each other, but they always rested together during midday (see below). Among 13 identified groups, nine (69%) were comprised of an adult pair only, three (23%) included an adult pair and a single immature juvenile, and one pair (8%) had two offspring, a juvenile and a presumably immature subadult. On the average these family groups included 2.4 ± 0.7 individuals.

Four unmated adult females were observed. Three females were repeatedly encountered within specific areas. One additional individual, a transient, was observed on 3 of 13 days crossing the contiguous territories of three identified groups. Regular use of discernable paths and specific dunging and resting sites by the three solitary females suggested they were residents that had lost their mates (see below). No offspring accompanied them, but conspicuously developed teats indicated the females were parous. By contrast, the one transient female was considered nulliparous. Eleven other observations were of solitary males that could not be individually identified. They may have been subadults of the resident adult pair or transients. They were never observed in the company of other dikdiks.

A comparison of the possible groupings of all dikdiks sighted on initial encounters with observations lasting 15 min or longer were significantly different ($\chi^2 = 96.5$, $d.f. = 7$, $P < 0.05$; Table 1). Initial observations gave solitary individuals as the most frequent social class (52%). After 15 min this value dropped to 17%; usually because the male was observed to catch up with the female. Conversely, adult pairs and their offspring accounted for 42% of all initial observations, but increased to 83% after 15 min, also due to the male joining the female and offspring. Spatial separation while foraging is not unusual for small animals that use crypsis to avoid predators (Jarman, 1974). There were nine observations of social groups numbering five or more individuals. These groups separated into two or three groups within the 15 min criteria (Table 1), suggesting that they were temporary aggregations of neighboring groups upon common boundaries, a behavior common to dikdik (Hendricks and Hendricks, 1971; Tinley, 1969).

Twenty-five months later the dikdik population consisted of nine paired adults, five with an accompanying offspring, and one solitary adult female. Of the paired animals, only two were still together and residing in the same home range/territory. Three other adult females who were with new mates also remained in the same home range/territory (see below). Thus, 11 of 13 (85%) males and 11 of 16 (69%) females were lost, which is not a significant departure from equal-sexed mortality (Fisher's exact test). The calculated annual turnover rate of 36% (72%/2 years) for the Namutoni adult dikdik population was significantly greater than the 21% rate calculated for a population of the same species inhabiting rocky inselbergs in the Serengeti National Park, Tanzania ($\chi^2 = 7.56$, $d.f. = 1$, $P < 0.01$; Hendricks, 1975).

Available evidence suggests that dikdik disappearances can be attributed to mortality rather than emigration and re-establishment in alternate habitat. We censused outlying regions 1 km peripheral to our study area regularly and never relocated individuals that had disappeared. Furthermore, small monogamous

antelope typically show a high degree of site fidelity that extends through the lifetime of individually paired adults (Dubost, 1980; Hendricks, 1975; Tilson, 1980) and may even extend to successive generations. Secondly, the Namutoni area of Etosha National Park supports a diverse and dense population of possible dikdik predators, including caracal (*Felis caracal*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), and jackals (*Canis mesomelas*). Thirdly, nomadism or migration by dikdik has never been reported.

Dikdik are reported to demarcate their territories by: (1) scent-marking throughout their space; (2) dunging at specific sites along boundaries; (3) assuming optical intimidation postures when in the presence of neighboring conspecifics; and (4) chasing intruders (Boshe, 1984; Hendricks and Hendricks, 1971). At Namutoni, scent marking, or the deposition of glandular secretions from preorbital glands, was performed throughout the family's territory, along feeding routes, and at dunging sites upon the territory periphery, as described for East African populations. Hendricks and Hendricks (1971) reported that an adult male scent-marked 19 times in 45 min along 400 m. For comparison, we recorded 21 scent-marking events in 28 min along 275 m for one male and 18 scent-marks in 32 min along 300 m for another. A scent-marking behavior not previously reported was that when the female of the pair was scent marking she was always followed by the male at varying distances (range: 1–20 m). Regardless of how far behind (which we assume was beyond vision of one another), the male always scent-marked over the substrates marked by the female; never missing one and not marking any not marked by the female. This behavior pattern is typical of other monogamous Neotragini that we have observed elsewhere in Southwestern Africa, including klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), and duiker (*Sylvoicapra grimmia*).

We conclude that disappearance of adults in a population of dikdik in South West Africa/Namibia was not preferentially biased towards either sex. The annual turnover rate of 36% was higher than turnover rates of 25% reported for East African populations. Mean territory sizes were larger in South West than in East Africa. Defense of space was essentially identical in both populations, with only trivial differences noted, despite the geographical isolation of these populations since the Pleistocene (Bigalke, 1968).

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