There is no reason to suppose that a similar paralysis may not occur in other groups of nightworkers. Indeed, it has been claimed that the incidence of sleep paralysis may be up to 4 times higher in males than in females[16]. Clearly, it would be of interest to study male populations, such as process controllers, pilots or air traffic controllers, who often perform an essentially sedentary task at the low ebb of many of their circadian rhythms, and under relatively sleep-deprived conditions. We are currently planning such a study. If this paralysis is found to occur in these populations, where the cost of a failure to respond can be even higher than that in nursing, it would suggest a strong need to reduce the level of sleep deprivation under which such populations commonly work, and to ensure that no single individual is ever left in sole control. However conscientiously such individuals may force themselves to stay awake, any emergency that arose could trigger a paralysis that prevented them from responding to it.

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Adaptive respiratory variation in 4 chromosomal species of mole rats

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Summary. Oxygen and carbon dioxide pressures were measured in subcutaneous gas pockets of 4 chromosomal species of the *Spalax ehrenbergi* complex. Oxygen pressures of 11.8, 13.6, 16.9, and 17.2 torr and CO_2 pressures of 84.2, 82.9, 80.1, and 64.1 torr were measured for the chromosomal species 2n = 52, 54, 58, and 60, respectively. The differences between the 4 chromosomal species in their subcutaneous gas tension appear to reflect adaptive respiratory variation associated with geographic variation in climate. It underlies an important respiratory physiological correlate of ecological speciation in the extremely hypoxic and hypercapnic subterranean environment.

What are the respiratory physiological correlates of speciation? We explored this problem in the actively speciating complex of subterranean mole rats of the *Spalax ehrenbergi* superspecies in Israel[1,2]. The superspecies consists of 4 chromosomal species, each adapted to a different climatic regime characterized by a combination of humidity and temperature. The distribution of the chromosomal species is correlated with increasing aridity southwards (2n = 52, 54, 58, 60). Fossorial mole rats spend most of their life in the unique underground atmosphere[3] and are highly adapted to living in extreme hypoxic-hypercapnic conditions[4–8]. Consequently, the respiratory physiology of the mole rat deviates considerably from the normal mammalian pattern[5–8]. The extreme hypoxic-hypercapnic subterranean environment selects for respiratory adaptations which maintain an adequate gas exchange.

The mole rat is able to maintain resting and elevated metabolic rates at levels of hypoxia in which the comparably sized white rat cannot keep its normoxic metabolism[4]. Although the mole rat has a normal resting mammalian metabolic rate, its resting heart rate, cardiac output, and ventilation are lower than the values predicted from its body mass[5,7,8]. The reduced convection of both air and blood at rest implies increased extraction of oxygen. The high affinity of the mole rat's hemoglobin ensures oxygen loading at low alveolar P_{O_2}[5], and the low unloading pressure is compensated by short diffusion distances in the tissue[6]. Thus, the low tissue P_{O_2} and high tissue P_{CO_2} (estimated by s.c. gas pockets) of the mole rat are indicative parameters of its adaptation to the subterranean atmosphere[5].

The general respiratory adaptations characterizing the evolution of *Spalax* for its unique subterranean burrow atmosphere must also affect its speciation process. If burrow atmospheres vary geographically due to climatic and soil heterogeneity, respiratory adaptations can be expected to follow suit in the derivatives of speciation. Indeed, in Israel, precipitation is far higher and soil conductivity lower in the north (where 2n = 52 and 54 range) as compared with the central and southern regions (where 2n = 58, and particularly 2n = 60 occur). Here we present evidence supporting the hypothesis that the 4 chromosomal species of *S. ehrenbergi*

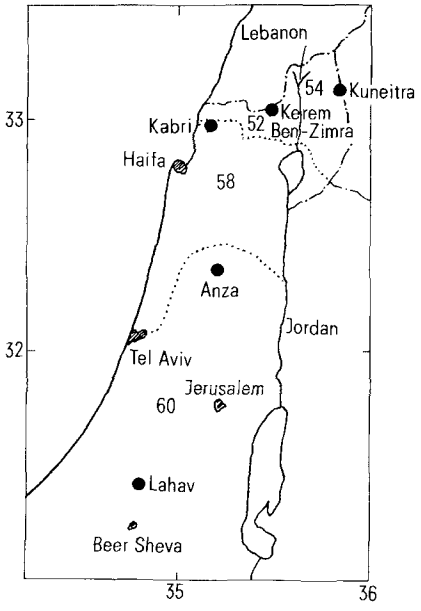

Figure 1. Distribution of 4 chromosomal species of mole rats in Israel (bordered by dotted lines) and the locality of the experimental animals (solid circles).

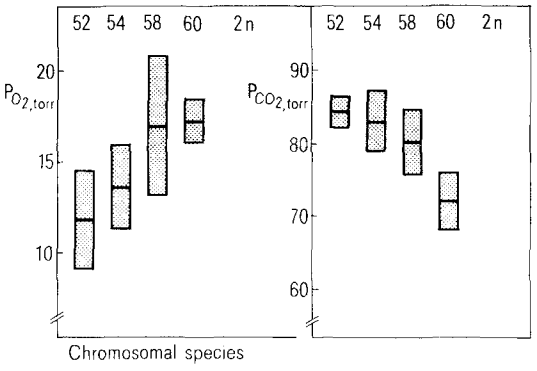

Figure 2. P_{O_2} and P_{CO_2} in s.c. gas pockets; mean and SEM (bars) for the 4 chromosomal species of mole rat.

in Israel vary geographically in their respiratory adaptations in accord with their climatic origins. Respiratory physiology appears to be correlated with ecological speciation in the subterranean niche.

Materials and methods. The 34 experimental animals were adult female and male mole rats from 4 chromosomal species (see table and figure 1) that had been kept in standard laboratory conditions of 20 °C and 60% relative humanity for more than 9 months.

A week before testing, we injected 30 ml air under the skin of a mole rat's back, and this s.c. gas pocket was renewed with another 10 ml of air 4 days before testing. The kinetics of gas changes in s.c. gas pockets of mole rats and of rats are very similar: they reach 90% of equilibrium within 6 h, almost level at 12 h, and arrive at complete equilibrium at 4 days[5,9]. During the week of equilibration of gas tension between the s.c. pocket and the tissue, the animals were kept in the same laboratory at room temperature. Gas samples from the s.c. pockets were analyzed in duplicate for O_2 and CO_2 with Microscholander gas analyzer.

Results. S.c. gas pressures of the 4 chromosomal species are plotted in figure 2. No difference could be demonstrated between the two 2n = 60 populations, P_{CO_2} of 68.4 ± 10.9 SD and 55.1 ± 13.4 SD torr and P_{O_2} of 16.7 ± 4.1 SD and 18.4 ± 2.2 SD torr for Lahav and Anza populations, respectively. Therefore, values of both groups were combined in figure 2. The results indicate that subcutaneous P_{O_2} increases 11.8, 13.6, 16.9, and 17.2 torr and s.c. P_{CO_2} decreases 84.2, 82.9, 80.1, and 64.1 torr with the chromosomal species 2n = 52, 54, 58, and 60, respectively. Only the difference of P_{O_2} and P_{CO_2} between 2n = 52 and 2n = 60 was significant (t-test, $p < 0.025$ and $p < 0.005$, respectively), but the southward tendency is clearly seen from 2n = 52 through 2n = 54, 58-60.

Discussion. The hypothesis put forward in this study suggests that a southwardly decreasing environmental cline of hypoxic-hypercapnic conditions occurs in the burrow atmosphere of mole rats. Three interacting factors combine to decrease clinally hypoxic-hypercapnic burrow conditions in Israel. First and foremost is the amount of annual rainfall, which is concentrated in wintertime and decreases southwards within the *S. ehrenbergi* complex from about 1400 mm in the northern range of *Spalax* on Mount Hermon to 100 mm yearly mean in the northern Negev. The higher level of rainfall in the northern regions (where 2n = 52 and 54 range) clogs the air pores in the soil[3] and causes frequent floods and free-standing water for weeks, particularly during the winter breeding season in January and February[11]. Secondly, soil texture also affects gas exchange with the external atmosphere[3]. Such an exchange is favorable in light as compared with heavy soils. In general, heavy soils predominate in northern Israel (particularly terra rossa and dark clay soils), whereas lighter soils (sands, sandy loams, and steppic soils) increase southwards. Thirdly, mean annual temperature increases southwards in Israel. Low ambient temperature enhances the hypoxic-hypercapnic conditions through an elevation of the mole rat's metabolic rate which is more marked in individuals from farther north. The 3-factor combination of rainfall, soil texture, and temperature suggests the hypoxic-hypercapnic cline in the geographic order corresponding to the ranges of 52, 54, 58, and 60, as was indeed found here and is demonstrated in figure 2. The increased soil permeability to gases in the mole rat's habitat, in the order 2n = 52 to 2n = 60, allows for high inspired P_{O_2} (and low $P_{I_{CO_2}}$) in the burrow atmosphere. The possible high loading P_{O_2} of the blood allows for high unloading pressure; thus, the tissue gas tensions of the species 2n = 60 approach the normal mammalian interspecific constant tissue gas tensions ($P_{O_2} = 40$, $P_{CO_2} = 45$ for the white rat)[10].

The chromosomal species tested and their ecogeographical background

Chromosomal species (2n)	Population	Sample size (N)	Weight (g) mean ± SD	Mean annual precipitation (mm)	Elevation (m)	Temperature mean (°C) February	August
52	Kerem Ben-Zimra	7	164 ± 30	700	800	7.1	23.8
54	Kuneitra	10	156 ± 36	820	940	3.1	29.5
58	Kabri	8	146 ± 36	600	150	9.2	25.0
60	Anza	3	177 ± 39	451	400	12.4	27.6
60	Lahav	6	131 ± 19	300	400	11.6	26.0

Despite the high precipitation in Kuneitra, the climate there is more continental and therefore more arid than Kerem Ben-Zimra's climate.

The standardization of the laboratory environment, their relatively long time in captivity, and the relatively similar body weights suggest that the difference in s.c. gas tension between the 4 chromosomal species is intrinsic and has a genetic basis in accord with the climatic selection of the species ranges. It is remarkable that significant differences were found between the 4 chromosomal species in their swimming ability in the following decreasing order: $2n=52$, $54>58>60$[12]. This result seems to support the hypothesis that differential swimming ability of individuals among the chromosomal species may be associated with the extent and level of flooding and free-standing water, since, as indicated earlier, $2n=52$ and 54 range in high-precipitation regimes, whereas $2n=58$ and 60 are from areas characterized by lower precipitation. The geographic variation in the swimming ability of the chromosomal species displays a pattern parallel to that in the differential respiratory adaptations described here. Furthermore, both phenomena may be explained by the very same climatic-edaphic model described earlier. Both the selection for better swimming ability and the ability to withstand extreme hypoxic-hypercapnic conditions characterizing the $2n=52$ and 54 chromosomal species may be due to climatic selection.

The chromosomal speciation of *S. ehrenbergi* in Israel has several adaptive physiological correlates, including metabolism[13], thermoregulation[14], and nonshivering thermogenesis NST[15]. The progressive change of s.c. gas tension discovered in this study represents another important parameter in the aforementioned adaptive physiologic syndrome, thereby reinforcing the physiological correlates of ecological speciation through chromosomal rearrangements in the *S. ehrenbergi* complex.

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Biological effects of singlet delta oxygen on respiratory tract epithelium[1]

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Summary. Exposure of hamster tracheal organ cultures to gas phase singlet delta oxygen, $^1O_2$, at atmospheric pressure produced significant alterations in the mucociliary epithelium resulting in changes in ciliary activity and cellular morphology.

Singlet delta oxygen is recognized as a potential oxidant in polluted atmospheres[2]. The health related effects of $^1O_2$ have not been reported due to the lack of adequate atmospheric generation methods. A laboratory apparatus for the gas phase generation of $^1O_2$ at 1 atmosphere has recently been described[3]. Chemical studies indicate that $^1O_2$ is sufficiently long lived to be a predisposing factor in respiratory tract disease. Since tracheal epithelium is a target tissue for the induction of acute toxicity by oxidant gases, experiments were conducted to evaluate the short term effects of $^1O_2$ on hamster tracheal organ culture.

Materials and methods. The $^1O_2$ generator consisted of a 13 mm outer diameter × 20 cm water-jacketed, Pyrex flow tube lined with a thin film of rose bengal which was prepared by evaporation from a methanol solution of the dye. A mixture of 95% N_2:5% O_2 was passed through the flow tube at 8 l/min while the dye film was exposed to strong visible radiation from four 1000 W projection lamps (G.E. Model DPT) enclosed in an air-cooled reflector. The exit gas was passed directly into a cube shaped exposure chamber (1′ × 1′ × 1′) from the top and down onto culture dishes supported on a rack in the middle of the chamber.

The concentration of the gas phase $^1O_2$ entering the chamber was monitored for each run by the intensity of the 1.27 micron emission[4], using a 'chopped' germanium diode detector system with sensitivity of 0.0025 ppm. The mean gas phase $^1O_2$ concentration for all experiments at the normal operating conditions was 0.121 ± 0.005 ppm.

Organ cultures were prepared from tracheas of 4–6-week-old male Syrian golden hamsters by previously described methods[5]. Tracheas were initially cultured for 24 h, allowing explants time to adjust to external environment before treatment. Culture dishes containing tracheal ring explants in L-15 medium were exposed to $^1O_2$ in a controlled atmosphere chamber (Bellco Glass Inc., Vineland, NJ). The chamber was placed on a rocker platform that rocked 10 cycles per min, allowing the tracheal rings contact with both $^1O_2$ and culture medium. Ring explants were exposed for 2 h to $^1O_2$ from the top of the controlled atmosphere chamber. The evaporation loss was compensated for by the periodic (once an hour) addition of medium to the dishes. The effects of $^1O_2$ on cilia beating frequency and cytology[5] were assessed immediately after the 2-h exposure, and rings processed for histology.

Results and discussion. The data presented in the table show that a concentration of 0.121 ppm singlet oxygen causes a significant decrease in cilia beating frequency and significantly greater cytological alterations than in control exposures. The gas entering the exposure chamber in the control exposures was identical to that used in the $^1O_2$ exposures except no $^1O_2$ was present in the gas (N_2/O_2, 95%/5%). In the singlet oxygen