where stresses, resulting from slow inflation of the deep rift zone, are high (Fig. 3a). At the time of the shallow intrusion, the rift opened about 2 m (refs 11, 15, 21), an eruptive fissure formed (Fig. 1), and seismicity within this region of the south flank immediately increased by more than a factor of ten (Fig. 2a). The intrusion also resulted in changes in the patterns of stressing and seismic activity (Fig. 3a, b). Relative to the pre-intrusion period, seismic activity shifted away from the rift and more shallow events occurred. These changes are consistent with stresses that we have calculated for the 1983 intrusion (Fig. 3b). That is, the regions of increased and decreased earthquake rates correspond to regions of increased and decreased stress, respectively, resulting from the intrusion.

We believe that the boundary element model of the 1983 intrusion is also a reasonable representation of the stress changes for the 1977 intrusion. Each occurred in the same region[15,20], each resulted in very similar changes in seismicity patterns and rates, and the limited deformation data for the 1977 event are consistent with the more extensive 1983 data set.

Figure 3c gives the distribution of stress changes for the 1983 intrusion obtained from the seismicity data using equation (4). Counts of earthquakes for this calculation are made on a square grid with 0.5-km spacing of centres, over a radius of 1 km. A three-year period, t_1, was used for counts before the event (N_1), and 90 days, t_2, was used for counts following the event (N_2). We use the stressing rate results for the small polygon in Fig. 1 to set $\dot{S}_r = 0.3$ MPa yr^{-1} before intrusion and $\dot{S}_r = 0.15$ MPa yr^{-1} following the intrusion. Additionally, the parameter $A\sigma$ is made depth-dependent by allowing σ to increase with depth by the weight of the overburden less hydrostatic pore-fluid pressure.

For the region of the small polygon (Fig. 1), the boundary element model gives a stress increase of 0.3–0.6 MPa for the 1983 intrusion. This compares well with the seismicity-based stress change of 0.5 MPa obtained for both the 1977 and 1983 intrusion events using equation (3) (Fig. 2b). The pattern and magnitudes of stress changes at the time of the 1983 intrusion obtained from earthquake data using equation (4) (Fig. 3c) are in agreement with the boundary element calculation (Fig. 3b). Regression of the Coulomb stresses from the boundary element model of the intrusion against stresses from equation (4) has a slope of 1.1, and the correlation coefficient is 0.80 (Fig. 4).

In summary, seismicity changes coincide with documented deformation events for the south flank of Kilauea volcano. Inversions of earthquake rates for stress changes based on equation (1) give consistent results that agree with other estimates of stress. An additional internal consistency check of the earthquake rate formulation is provided by the previously described slowing of deformation rates that began around 1981–1983. As noted above, equation (1) predicts an inverse relationship between stressing rate and the time t_a for seismicity to decay to the background rate following a stress step. As the data of Fig. 2a show, the time for seismicity to return to a background rate following the 1983 intrusion is about twice as long as that following the 1977 intrusion; this is consistent with a halving of the stressing rate.

The methods presented here provide a way to use seismicity rate information in earthquake catalogues as a stress meter. This approach is able to resolve both positive and negative stress steps, as well as long-term changes in stressing rate. Because this approach does not depend on previous models of specific structures, it can also provide constraints on the models used to analyse observations of deformation. □

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Concurrent density dependence and independence in populations of arctic ground squirrels

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No population increases without limit. The processes that prevent this can operate in either a density-dependent way (acting with increasing severity to increase mortality rates or decrease reproductive rates as density increases), a density-independent way, or in both ways simultaneously[1–3]. However, ecologists disagree for two main reasons about the relative roles and influences that density-dependent and density-independent processes have in determining population size[4,5]. First, empirical studies showing both processes operating simultaneously are rare[6]. Second, time-series analyses of long-term census data sometimes overestimate dependence[7,8]. By using a density-perturbation experiment[9–12] on arctic ground squirrels, we show concurrent density-dependent and density-independent declines in weaning rates, followed by density-dependent declines in overwinter survival during hibernation. These two processes result in strong, density-dependent convergence of experimentally increased populations to those of control populations that had been at low, stable levels.

In the boreal forest of the southwestern Yukon, populations of arctic ground squirrels (*Spermophilus parryii plesius*) fluctuate by a factor of about three (0.7–2.2 ha^{-1}) in synchrony with the 10-year cycle of snowshoe hares[13]. These squirrel populations are sparser and more dynamic than those in open tundra and meadow habitats, where densities are higher—5.5 ha^{-1} (ref. 14) to 16 ha^{-1} (ref. 15)— and apparently stable[14,16]. Whereas squirrel populations in alpine and arctic habitats are thought to be limited by food availability, suitable burrowing habitat, and spacing behaviour[14,16,17], a large-scale 10-year experimental manipulation of food and predators by the Kluane boreal forest ecosystem project[18] showed that squirrel populations in the boreal forest were limited by an interaction between food and predators[19,20] that acted primarily through changes in reproduction[20]. By design, the Kluane project examined limitation (processes that changed the average or equilibrium population density[10]), and was unsuitable for determining population processes that operate in a density-dependent manner.

At the completion of the Kluane project in spring 1996, densities of ground squirrels in four control areas averaged 1.6 ± 0.15 ha^{-1}; exclusion of predators increased the density of one population to 3.3 ha^{-1}; food addition increased the density of squirrels in two other populations to 5.9 and 11.6 ha^{-1}; and predator exclusion combined with food addition increased the density of one population to 30.1 ha^{-1} (ref. 20). After the predator-exclusion fences were removed and food addition ended, it took two years for densities of ground squirrels in the experimental sites to converge to those on the control sites (Fig. 1) in a strong density-dependent manner (Fig. 2). The strength of density-dependent population growth rate may be overestimated by regressing rates of population growth on population density[8] when sampling variance is ignored, particularly in time-series analyses. However, variance in estimates of population size (Fig. 1) were nominal owing to the high trappability of arctic ground squirrels (77–95%)[19]. In contrast to the time-series approach, our experiment avoids problems associated with: (1) temporal autocorrelation of sequential data; (2) insufficiencies of annual data in detecting density-dependent processes that act on timescales shorter than a year (ref. 21); and (3) lack of ability to detect the mechanisms of density dependence.

To identify the mechanisms determining density dependence in ground squirrel populations, we monitored reproduction (presence of lactation, weaning success and litter size), emigration and survival (active season survival by radio-telemetry and winter hibernation survival from trapping records) for two years after the cessation of the experimental treatments in all populations (see Methods). We also continued to supplement the food of two high-density populations (Food A, B) (Fig. 1). Two variables were strongly and significantly density dependent (Table 1): the proportion of females weaning a litter (Fig. 3a), and the proportion of females surviving winter hibernation (Fig 3b). Together, both variables explained 90% of the variation in the annual rate of population change ($n = 11$, $p < 0.001$) as experimental densities converged towards control densities. Partial correlations indicated that overwinter survival accounted for 79% of the variance in annual rates of population change after differences were adjusted for changes in weaning rate. When population changes were adjusted for differences in overwinter survival, weaning rate accounted for 23% of the variance in annual rates of population change. The proportion of females lactating was weakly density dependent, but both summer survival and litter size were density independent (Table 1). Emigration of adults did not contribute to the decline of the experimental populations as none of the females fitted with radio-collars (1996, $n = 79$; 1997, $n = 51$) emigrated despite the high densities and lack of food resources on some sites. Juvenile males disperse independently of population density and resources[22]. In contrast, juvenile females remain near the natal area under a wide range of population densities and only disperse from food-supplemented populations at summer densities of 60 ha^{-1} (ref. 22). Such situations never occurred after the treatments were removed because juveniles were unlikely to be weaned at densities above 12 ha^{-1} in the absence of supplemental food (Fig. 3a).

Food resources were the primary factor determining the proportion of females weaning a litter. High-density populations that continued to receive supplementary food (Food A, B) had high weaning rates (82–89%) compared with unfed high-density populations which displaced them above the density-dependent relationships of unsupplemented populations (Fig. 3a). However, increased
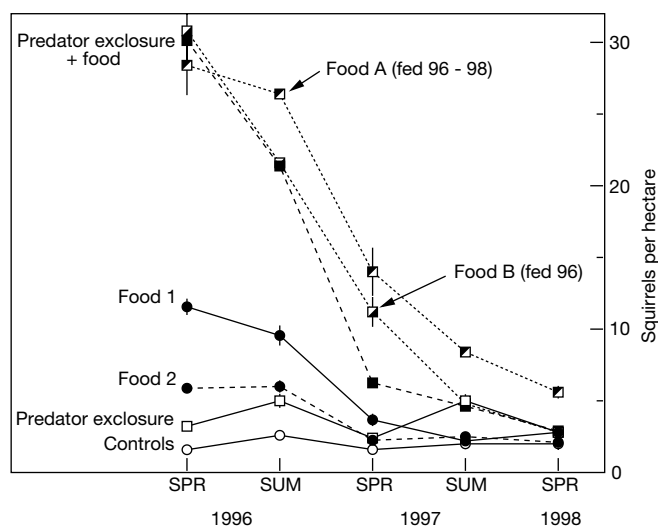

Figure 1 Convergence of arctic ground squirrel population densities after the removal of the experimental treatments of the Kluane project[18] in spring 1996. Food addition (Food A, B) without predator exclusion slowed the rate of population decline, so that by 1998 spring densities (Food A) were still three times that of controls. Vertical error bars represent 1 s.e. of the population estimate for all experimental populations and 1 s.e. of the mean population estimate from four control populations. Points that appear without error bars have measures of error that are smaller than the symbol.
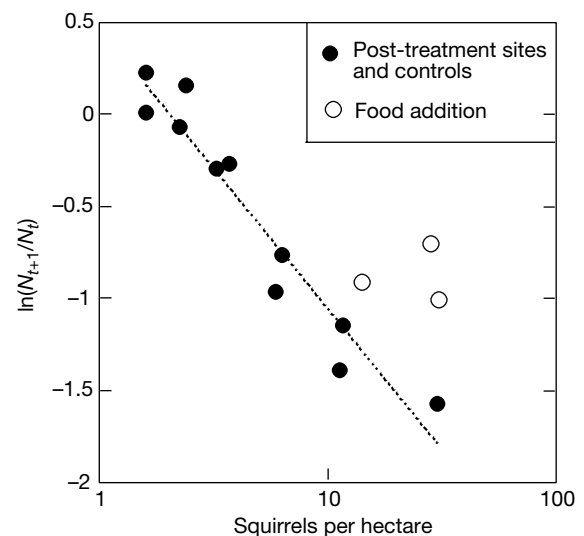

Figure 2 Density-dependent rates of population change of arctic ground squirrels after the experimental treatments of the Kluane project[18] were removed in spring 1996. Here $\ln(N_{t+1}/N_t)$ is the rate of population change (N_{t+1} is the population size in the spring of year $t+1$; N_t is the population size in the spring of year t). Data are shown for controls and for the former experimental treatments. The equation of the dashed line is: rate of change = $-1.5[\log(\text{density})] + 0.5$, with $r^2 = 0.93$, $P < 0.001$. Data from sites where food was added were not included in the regression, but demonstrate that rates of increase were positively influenced by added food.

reproduction reduced, but did not prevent, the decline of the fed high-density populations (Fig. 1) compared with unfed high-density populations (Fig. 2). Fed high-density populations had higher overwinter survival (47–58%) than unfed high-density populations (11–20%), which again displaced them above the density-dependent relationships of unsupplemented populations (Fig. 3b). However, the food that we were supplying seemed to play a smaller role in determining overwinter survival than in determining weaning rate, because fed high-density populations had lower overwinter survival than unfed, low-density populations (60–95%) (Fig. 3b). The decline of the fed high-density populations was not accounted for by reduced summer survival as summer survival was very high (100% in 1996 and 86% in 1997), but was almost entirely attributable to poor overwinter survival. The food that we were providing was nutritionally optimized for the metabolic needs of rabbits, and may have lacked sufficient quantities of dietary components—possibly essential fatty acids—that are essential to hibernating mammals for reducing energy expenditure during hibernation[23]. Together, the rabbit food that we supplied and the natural food was insufficient to maintain high overwinter survival in extremely dense ground squirrel populations.

Weaning rate showed strong density dependence, operating concurrently with density independence, when compared among years. Weaning rate maintained the same strength in density dependence over the two years (one-way analysis of covariance (ANCOVA): year $\times$ density, $F = 0.17$, d.f. $= 1$, $P = 0.90$), but females in 1997 were approximately 30% less likely to wean their litters independent of population density than were females in 1996 (one-way ANCOVA: $F = 57$, d.f. $= 1$, $P < 0.001$) (Fig. 3a). This indicates that changes in some regional environmental factor from 1996 to 1997 reduced weaning equally among all of the sites independently of population density, and offset the density-dependent relationship in 1997 below that in 1996. The density-independent effect was not caused by a change in food resources because the food addition site (Food A) also declined in weaning rate (7%) from 1996 to 1997, despite a 55% reduction in population density that should have increased weaning rate in 1997. Data from the Burwash Landing meteorological station (50 km from the study site) show that snow depth in the winter of 1995/96 was 36% greater than the 30-year average, whereas that in 1996/97 was about 30% lower. The greater snow depth in 1996 than 1997 should have maintained warmer soil temperatures during the winter[24] thereby reducing the energy expenditure of hibernating ground squirrels[25]. Body condition of female squirrels, which is a strong predictor of reproductive success[26], was greater on all sites during the spring of 1996 than in spring 1997[27]. We conclude that winter snow conditions acted as a density-independent factor that altered reproduction in ground squirrels equally among all populations in the presence of strong density dependence.

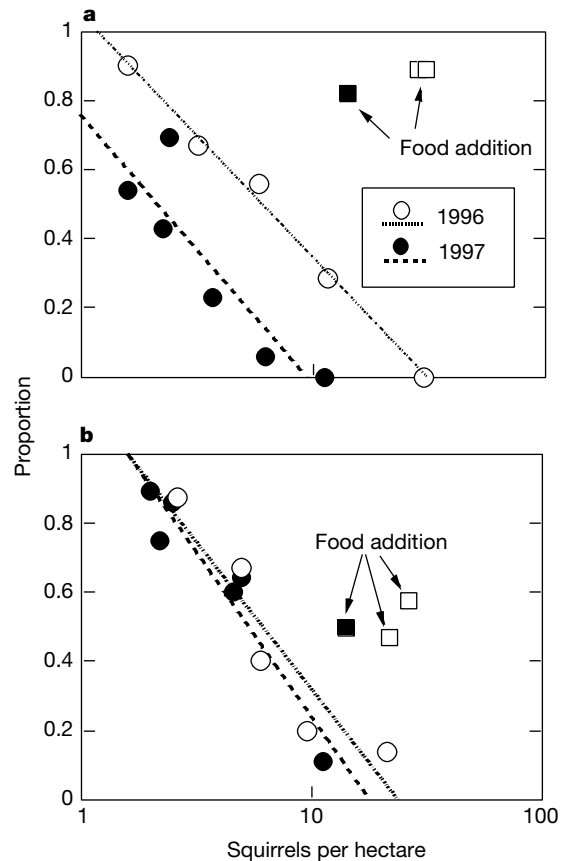The strength of density dependence in overwinter survival, as

Figure 3 Mechanisms of population regulation in arctic ground squirrels. The figure shows density-dependence plots of the proportion of females weaning a litter (**a**) and the proportion of adult females surviving winter hibernation (**b**). Data are shown for controls and for former experimental treatments of the Kluane project[18] after the treatments were removed during spring 1996. The density-dependent relationship in weaning rate in 1997 was offset from that in 1996 such that all squirrels in 1997 had a further 30% reduction in the probability of weaning a litter independent of population density; this demonstrates concurrent density dependence and independence.

Table 1 Regression statistics

Variable	Linear regression					Sample size of squirrels per site *						
	Year	Equation	r^2	N	P†	C	P-PE	P-F1	P-F2	P-PE+F	+FA	+FB†
Lactating	1996	$-0.32x + 1.25$	0.70	5	0.076	22	24	44	25	80	47	39
	1997	$-0.88x + 1.50$	0.55	6	0.092	16	16	17	9	28	16	11
Weaning	1996	$-0.94x + 1.48$	0.97	5	< 0.003	10	9	9	7	15	9	9
	1997	$-1.11x + 1.16$	0.89	6	< 0.005	9	9	9	7	16	6	10
Litter size	1996	$-0.38x + 2.89$	0.19	4	0.57	9	13	6	6	0	28	15
	1997	$-1.57x + 3.21$	0.11	4	0.68	6	7	4	4	0	5	0
Summer survival	1996	$0.07x + 1.11$	0.01	5	0.87	10	9	11	11	15	11	12
	1997	$0.49x + 0.88$	0.06	5	0.70	10	8	8	10	8	7	0
Overwinter survival	1996	$-0.95x + 1.54$	0.88	5	0.019	21	34	53	31	131	32	36
	1997	$-1.08x + 1.08$	0.91	6	< 0.004	19	22	12	7	25	9	8

Reproduction and survival processes were analysed for density dependence by linear regression. All proportional data were arcsine transformed and densities were log-transformed before regression. Sample sizes given are the number of squirrels on each site that were used to calculate each variable before regression. Sites 'Food A' and 'Food B' were not included in the regression when food supplemented.
* Sites are abbreviated as follows: control (C), post-predator exclosure (P-PE), post-food 1 (P-F1), post-food 2 (P-F2), post-predator exclosure + food (P-PE+F), food addition A (+FA), and food addition B (+FB).
† Adjusted by the Bonferroni method for multiple tests of significance.
‡ not food-supplemented in 1997.

indicated by the regression coefficient, remained similar between years (one-way ANCOVA: year × density, $F = 0.251$, d.f. = 1, $P = 0.63$) as was the rate of overwinter survival when the effects of density were removed (one-way ANCOVA: $F = 0.032$, d.f. = 1, $P = 0.86$) (Fig. 3b). Therefore, overwinter survival maintained a constant relationship with density regardless of the changes in winter conditions that operated on weaning rate in a density-independent manner.

Though populations rarely, if ever, maintain or achieve an equilibrium density because of fluctuations in population growth induced by stochastic events[3,10], this does not imply that density-dependence is unimportant or does not exist. Processes that operate in a density-dependent manner return a population towards an equilibrium density and are regulating[10]. Experimental density manipulations are the strongest and most robust approach to teasing apart the relative roles of density-dependent and density-independent determination of population density[9,11,12]. Our study demonstrates the power of this approach by showing how different density-dependent processes can operate to sequentially regulate population density in the presence of density-independent processes. Despite environmental differences between years that altered reproduction in a density-independent manner, density-dependent declines in reproduction remained constant between years and thus served as a dampening force against stochastic changes in reproduction. However, density-dependent weaning rate had a more limited role in regulating arctic ground squirrel populations than did a second and sequential density-dependent process, overwinter survival. During our study, density-dependent overwinter survival dominated density-independent changes in weaning rate resulting in strong density-dependent rates of population change—a necessary condition of population regulation[2]. □

Methods

Spring and summer mark–recapture population estimates of arctic ground squirrels were conducted on areas of 8–10 ha from spring 1996 to spring 1998 within each of four control areas and within the following four former experimental areas of the Kluane project (1987–1996) described in detail elsewhere[18,20]: two food-addition areas (36 ha), a predator-exclusion area (1 km²), and a food-addition area (36 ha) enclosed within a predator-exclusion area (1 km²). All fences were dismantled and food addition was discontinued in spring 1996 with the exception of two 2.5-ha areas (Food A, B) within the former predator-exclusion area with food-addition site where we continued weekly food supplementation by hand to all burrow sites during 1996; 20 kg of rabbit food per ha. Food B was not supplemented after 1996 but was monitored as ground squirrel densities on that site converged with those on the other sites. Population estimates and their standard errors were calculated using a closed population mark–recapture heterogeneity model (jack-knife) from program CAPTURE[28]. Weaning success was calculated as the proportion of all females that had litters appearing above ground. Litter size was determined by intensive live-trapping at the natal burrow at the time when young appeared above ground. Dispersal and summer survival was based on radiotelemetry of adult females. Overwinter survival was calculated from trapping records as the proportion of individuals captured in spring that were present in the population before hibernation in the previous year. The details of our procedures for weaning success, litter size, dispersal and survival are described elsewhere[20,22].

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Variation in the reversibility of evolution

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How reversible is adaptive evolution[1–6]? Studies of microbes give mixed answers to this question[6–11]. Reverse evolution has been little studied in sexual populations[12–14], even though the population genetics of sexual populations may be quite different. In the present study, 25 diverged replicated populations of *Drosophila melanogaster* are returned to a common ancestral environment for 50 generations. Here we show that reverse evolution back to the ancestral state occurs, but is not universal, instead depending on previous evolutionary history and the character studied. Hybrid populations showed no greater tendency to undergo successful reverse evolution, suggesting that insufficient genetic variation was not the factor limiting reverse evolution. Adaptive reverse evolution is a contingent process which occurs with only 50 generations of sexual reproduction.

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