

Mammal population cycles: evidence for intrinsic differences during snowshoe hare cycles

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Abstract: Some mammals in high northern latitudes show regular population cycles. In snowshoe hares (*Lepus americanus*), these occur every 9–10 years. One hypothesis proposes extrinsic causes such as food shortage or predation. The other proposes intrinsic causes through different morphs that alternate between different phases of the cycle. The morphs should differ in behaviour or physiology. This hypothesis predicts that animal lineages bred from high and low phases of the population cycle should differ in reproduction and survivorship. In a 16-year breeding program, lineages of purebred high-phase female hares had reduced reproductive rates relative to those of purebred low-phase females, resulting in extinction of high-phase lineages. Reproductive output declined with age in high- but not low-phase animals. These lineages also differed in longevity and senescence. These results are consistent with the intrinsic hypothesis and suggest a mechanism for alternating population densities that could work synergistically with extrinsic causes like predation and food shortage.

Résumé : Les populations de certains mammifères des latitudes nordiques subissent des cycles réguliers. Ceux du lièvre d'Amérique (*Lepus americanus*) reviennent tous les 9–10 ans. Une hypothèse veut que les cycles soient déclenchés par des facteurs extrinsèques, comme la famine ou la prédation. L'autre hypothèse veut que ce soient des facteurs intrinsèques par lesquels différentes formes d'une espèce alternent d'une phase à l'autre du cycle. Selon cette hypothèse, les formes différencieraient par leur physiologie et leur comportement et les lignées animales obtenues de l'élevage de phases de densité élevée et de phases de densité faible du cycle de la population devraient avoir une reproduction et une survie différentes. Au cours d'un programme d'élevage d'une durée de 16 ans, les lignées pures obtenues de femelles de phase élevée avaient des taux de reproduction faibles relativement à ceux des lignées pures issues des femelles de phase basse, résultant en l'extinction des lignées de phase élevée. Le rendement reproductif diminue avec l'âge chez les animaux de phase élevée, mais pas chez les animaux de phase basse. Ces lignées diffèrent aussi par leur longévité et leur sénescence. Nos résultats sont compatibles avec l'hypothèse des facteurs intrinsèques comme déclencheurs des cycles et semblent indiquer l'existence d'un mécanisme de fluctuation des densités de la population qui pourrait agir en synergie avec les facteurs extrinsèques, tels que la prédation et la famine.

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Introduction

Population cycles in mammals and birds are unusual in nature and are found largely in high northern latitudes (Keith 1963; Finerty 1980; Sinclair and Gosline 1997; Krebs et al. 2001a). Hypotheses for the causes of these cycles fall into two groups. "Extrinsic" causes such as changes in food supply, predation, and weather have received much attention recently (Erlinge et al. 1983; Sinclair et al. 1993; Krebs et al. 1995, 2001b). In contrast, "intrinsic" causes related to differences in the animals themselves have received much less attention because of the difficulty in obtaining such evidence.

We define intrinsic to mean features of the animal that can be passed through generations either by genotypic or by maternal processes. Chitty (1960, 1967) proposed that there might be two morphs in a population that would differ in their sensitivity to the effects of density and crowding. Such differences would be reflected in behaviour, physiology, or genotype (Christian 1961; Mihok and Boonstra 1992; Chitty 1996; Boonstra et al. 1998) and would result in different sensitivity to external mortality factors. These morphs could alternate in frequency so that birth rate, mortality, and population density would also alternate, hence, a cycle of numbers could develop. One morph could predominate at high and declining densities (high phase), the other at low and increasing densities (low phase) during cycles of northern mammals. There is now evidence that density cycles are related to genetic differences in social and mating behaviour of lizards (Sinervo et al. 2000, 2001; Bjørnstad 2001). Intrinsic mechanisms are relevant to the theory of population regulation because they determine how a population responds to the external environment, in particular because delayed responses produce population cycles.

Snowshoe hare (*Lepus americanus* Erxleben) populations of northern Canada have become the classic example of long-term persistent cycles. Snowshoe hares have a 10-year cycle in numbers, evidence for which extends back to the

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early 1800s based on the fur returns of the Hudson Bay Company (MacLulich 1937; Elton and Nicholson 1942) and more recent documentation (Marshall 1954; Cary and Keith 1979; Smith 1983; Krebs et al. 1986, 1995, 2001a); its signature is detected even earlier in tree rings (Sinclair et al. 1993).

Intrinsic differences in morphs should be detectable in purebred lines. Each morph should differ in some character such as reproduction, longevity, or survivorship that affects demography. We predict that animals bred from the high phase of a cycle should have lower reproduction or survival relative to animals bred from the low phase (Krebs 1978). Until recently, such a test has been difficult to carry out (Millar 1983; Mihok and Boonstra 1992). However, a breeding experiment over 16 years (1980–1995) using snowshoe hares from the Yukon, Canada, has provided data relevant to these predictions.

Materials and methods

Snowshoe hares from the high and low phases of the 10-year cycle were obtained during the long-term population study of the 10-year cycle at Kluane, Yukon, Canada (Krebs et al. 1995, 2001b). Hares were captured in live traps and shipped by air to the Animal Care Facility at the University of British Columbia, Vancouver. During the nonbreeding period (September–January), animals from the same lineage were kept in groups of 5 or 6 in large outdoor pens (5 × 15 m) covered for protection from predators and extremes of climate. Pens were made of chainlink fencing and hardware mesh covered on the outside with burlap cloth to shield animals from disturbance. These pens included grass and shrubs and covered boxes that were used for resting and hiding. Food was standard medicated rabbit chow for protection from internal parasites.

From February to August (the breeding season), female–male pairs were isolated in separate pens with concrete walls (5 × 5 m) until mating was observed or pregnancy was detected by abdominal palpation. The male was then returned to its communal pen. Females were isolated until they gave birth. Within 24 h of giving birth, the female was introduced to another male in a separate pen for several hours during the day. She was then returned to her nursery pen containing her babies. This procedure was repeated for 3 days to allow her to conceive again (because hares are most receptive in the immediate postpartum days). This mating protocol did not interfere with nursing of young because suckling occurred once a day for 3–5 min in the evening between 1900 and 2300 (A.R.E. Sinclair, unpublished observations), and mothers were returned well in advance of this period. Juveniles were weaned naturally when the mother gave birth to the next litter 35 days later. At this point, juveniles were transferred to a large pen where they lived communally with other juveniles of the same lineage. All animals were treated the same and treatment conformed to the requirements of the Canadian Council on Animal Care.

Low- and high-phase animals were kept separate. Visual, auditory, and olfactory communication between them was possible during the nonbreeding period but not during the breeding period. Because all births and deaths were recorded, longevity was known for all animals born in the colony. Ani-

mals brought from the field were not used in the analysis of longevity because their date of birth was not known. Annual reproductive output for females in the wild was obtained from radio-collared females (Stefan 1998; Stefan and Krebs 2001) to compare with data from the captive animals.

The first high-phase group was obtained in the winter of 1979–1980 during the peak in wild population numbers. A second high-phase colony was established in 1990 during the subsequent peak. The first low-phase colony was established in the 1985–1986 winter when the wild population was at its low point in numbers. A second low-phase lineage was established in 1994 during the next low phase in the wild population.

Results

Population trend and reproduction

Both high-phase colonies declined to extinction, the first in 6 years and the second in 3 years. In contrast, the first low-phase colony persisted for 10 years until it was disbanded in early 1996. During this time it overlapped in time the second high-phase colony that went extinct, although the conditions for the two colonies were identical. The second low-phase lineage was established in 1994 and persisted to 1996 when the colony was disbanded.

Both lineages of high-phase animals declined rapidly in reproductive capacity (young born per female per year) (Fig. 1). In contrast, the two low-phase lineages maintained their annual reproductive capacity, with the first lineage doing so while the natural population went through a complete cycle of numbers. The regression of reproduction on year (for data using individual animals) for the first high phase has a slope of -2.81 ($n = 25$) and that for first low phase has a slope of 0.01 ($n = 39$), the two slopes being significantly different ($t = 3.39$, $n = 64$, $P < 0.005$).

The two high-phase lineages overlapped with the low-phase lineage during 1985–1987 and 1991–1993, and despite identical treatment, the two phases continued to differ in reproductive output (Fig. 2). The reproduction in pure lineages of low-phase females was significantly higher than those for two high-phase lineages in both periods when lineages overlapped (t test, $P < 0.05$).

Effects of age

As would be expected, lifetime reproduction was positively related to longevity in both high- and low-phase animals (for high phase, regression slope of lifetime reproduction on longevity = 0.423 , $n = 27$, $P < 0.002$; for low phase, regression slope = 0.496 , $n = 25$, $P < 0.0001$).

The differences in reproductive trends between high- and low-phase animals in our breeding experiment were due largely to a decline in reproduction with the age of the high-phase females (regression of annual reproduction with age in high phase = -0.176 , $n = 26$, $P = 0.019$). In contrast, low-phase animals maintained their reproductive capacity into old age (Fig. 3).

Genetic components

The genetic heritability of a trait is indicated by a positive relationship between a trait in daughters and that in their mothers. For total lifetime reproduction, there was no relation-

Fig. 1. Mean annual production (no. of leverets/female per year (\pm SE)) of snowshoe hares (*Lepus americanus*) from Yukon, Canada, bred from two high-phase lineages (●, ■) and two low-phase lineages (○, □). Reproduction of both high-phase lineages declined, whereas that of the low-phase did not decline (see text for details). The snowshoe hare density (no./km²) in Yukon, from where the stocks were obtained, is shown by the broken line with solid triangles.

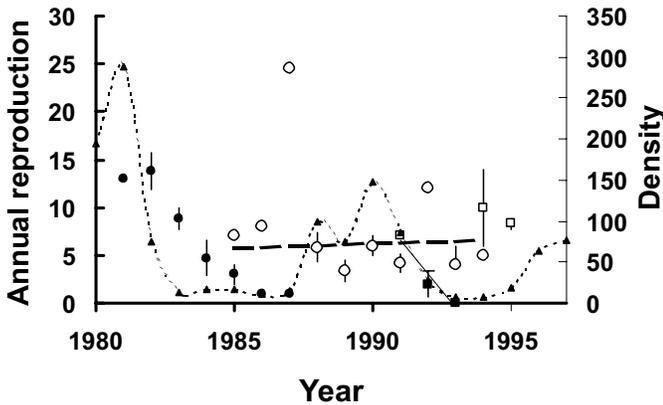
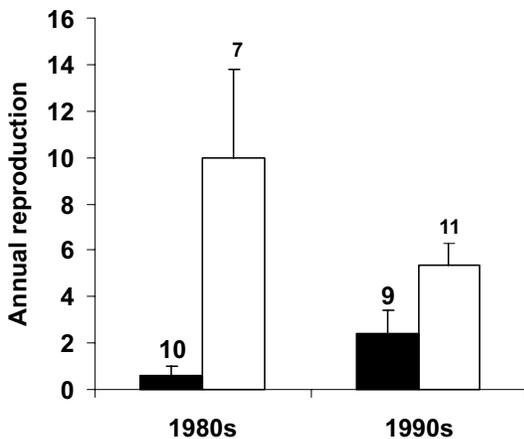


Fig. 2. Mean annual reproduction in pure lineages of low-phase females (open bar) was significantly higher than those for two high-phase lineages (solid bar) in both periods when lineages overlapped (1980s = 1985–1987, 1990s = 1991–1993). Vertical lines above bars are 1 SE; numbers above each bar are sample sizes of females.



ship between mothers and daughters in either phase (combined slope of daughters on mothers = -0.088 , $r^2 = 0.007$), and a similar result was obtained for survival of juveniles to weaning (regression slope = -0.372 , $r^2 = 0.07$). For mean annual reproduction, there was no relationship in low-phase animals (slope = 0.103 , $r^2 = 0.01$) and a weak negative relationship for high-phase animals (slope = -0.236 , $r^2 = 0.09$). Thus, no positive relationships were observed; therefore, we detected no genetic effects within phase lineages.

In contrast, there was a significant negative relationship between longevity of the mother and that of the daughter in low-phase animals (Fig. 4). The regression for low-phase animals had a slope of -0.657 ($n = 20$, $P < 0.005$). In addition, this slope differed ($t = 3.23$, $n = 30$, $P < 0.01$) from that for high-phase animals, which was 0.313 ($n = 10$).

Fig. 3. Mean annual reproduction declined with age in high-phase (solid bar) but not in low-phase female hares (open bar) in pure lineage colonies. Vertical lines above bars are 1 SE.

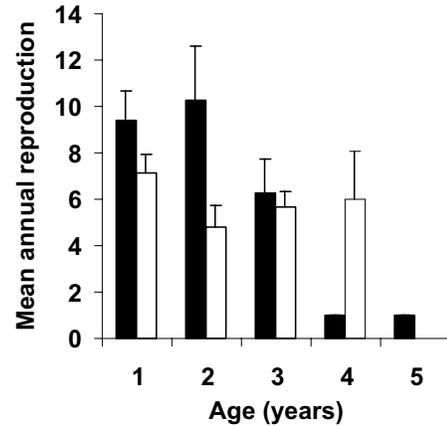
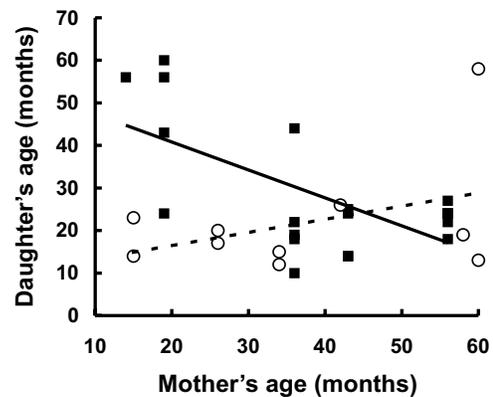


Fig. 4. The longevity of daughters was negatively related to that of mothers in low-phase (■) animals but not in high-phase (○) animals. All individuals were born and raised in the laboratory colony.



Discussion

We predicted that colonies bred from animals derived from different phases of the population cycle should differ in reproduction and survival characteristics when kept under identical conditions. Two colonies of high-phase and two of low-phase animals showed intrinsic differences in reproduction associated with female longevity and senescence in the animals, and these were maintained over several generations. As a result the high-phase colonies declined to extinction, whereas the low-phase colonies were able to maintain themselves until the experiment was terminated. These results corroborate our predictions. They are consistent with the idea that there could be intrinsic differences in animals at different phases of the hare cycle that produce different sensitivity to food shortage, predation, and weather. Thus, populations could alternate between different density levels by responding differently to external causes of mortality.

The negative relationship between longevity of the mother and that of the daughter in low-phase animals (Fig. 4) points to a possible maternal effect passed from mother to daughter (Falconer 1981; Lande and Price 1989; Arnold 1995). Such

an effect has been documented experimentally in mice (Falconer 1960, 1963) and has been suggested from other field studies (Millar 1983; Mihok and Boonstra 1992). Lifetime reproduction is positively related to longevity in both high- and low-phase animals. These relationships suggest the mechanism that long-lived mothers produce more offspring but may invest less in each (perhaps through lower lactation per young born) so that these offspring have shorter lives. These offspring may be weaker and more prone to starvation and predation in wild populations. The passage of these phenotypic effects between generations within phases appears to be different between the high- and low-phase lineages, but it is not yet clear how this occurs. We could not test for genetic differences between phases because samples for molecular analysis of genotype were not available. Thus, these phase differences in demography could be due to either different genetic makeup or phenotypic effects.

Our evidence on intrinsic differences was obtained by chance during a breeding programme for another purpose, and hence the conditions of the experiment were not ideal. Although simultaneous replicate colonies were not maintained, we did have sequential replicates. In addition, high-phase and low-phase colonies existed simultaneously and this overlap was replicated. These overlaps in time suggest that differences in the colonies were not due to differences in laboratory conditions. However, we recognize that the lack of overlap of the two lineages throughout the study allows the possibility that environmental effects could have played a part through maternal or grandmaternal transmission. Observed differences in years of overlap could represent a response by one group of females to earlier conditions that were not experienced by the other group. Maternal transmission should be examined in future breeding experiments.

The reproductive values in the colonies reflected those for the wild population in the Yukon, where high-phase animals (1990–1992) produced on average 8.9 young/female per year and low-phase animals (1994–1996) produced over 15.5 young/female per year (Stefan 1998; Stefan and Krebs 2001). Thus, our high- and low-cycle lineages showed reproductive values similar to the peak and low points of field populations in present and previous field studies (Cary and Keith 1979).

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