

# Cyclic dynamics of snowshoe hares on a small island in the Yukon

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**Abstract:** Snowshoe hare (*Lepus americanus*) populations were monitored from 1977 to 2001 on Jacquot Island (5 km<sup>2</sup>) in Kluane Lake, southwestern Yukon, and on nearby mainland sites. Jacquot Island hares averaged twice the density of mainland control populations and, although they show 10-year cycles, fluctuate with much lower amplitude than mainland populations. Three separate intensive studies over 6 years attempted to determine what caused these differences. We tested two hypotheses to explain the dynamics. Reproductive rates of hares were similar on Jacquot Island and the mainland. Adult survival rates were higher on the island in most years, with the exception of years of population decline. Juvenile survival rates from 0 to 30 days of life were much higher on the island than on the mainland except for decline summers. The adult- and juvenile-survival differences between the island and the mainland were explained most consistently by predation. Improved survival on the island is correlated with a reduction in the numbers and types of predators found on Jacquot Island compared with the mainland. In particular, red squirrels were rare on Jacquot Island, arctic ground squirrels were absent, and the larger predators, like lynx and great-horned owls, were sporadic in occurrence on this small island.

**Résumé :** Des populations de lièvres d'amérique (*Lepus americanus*) ont été suivies de 1977 à 2001 sur l'Île Jacquot (5 km<sup>2</sup>) au Lac Kluane (sud-ouest du Yukon), ainsi qu'à des sites sur la terre ferme, à proximité. Les densités de lièvres sur l'Île Jacquot équivalent en moyenne au double de celles des populations témoins sur la terre ferme et, quoique les premières fluctuent selon un cycle de 10 ans, leurs fluctuations sont d'une amplitude de beaucoup inférieure à celles des populations de terre ferme. Les causes de ces différences ont été examinées au cours de trois études intensives différentes s'échelonnant sur 6 ans. Nous avons testé deux hypothèses quant à la dynamique de ces populations. Les taux de reproduction sur l'île Jacquot et sur la terre ferme sont similaires. La plupart des années, le taux de survie des adultes est plus grand sur l'île que sur la terre ferme, sauf durant les années où les populations sont en déclin. Le taux de survie de 0 à 30 jours chez les juvéniles est beaucoup plus grand sur l'île que sur la terre ferme, excepté durant les étés de déclin. C'est l'effet des prédateurs résidants qui explique le mieux les différences de taux de survie entre les lièvres de l'île et ceux de la terre ferme, aussi bien chez les adultes que chez les juvéniles. Le meilleur taux de survie des lièvres sur l'île associé à une guildes de prédateurs plus pauvre en nombres et en espèces que celle des sites la terre ferme. Plus particulièrement, les écureuils roux sont rares sur cette petite île, les spermophiles arctiques y sont absents, et les plus gros prédateurs comme le lynx et le grand-duc ne s'y trouvent que sporadiquement.

## Introduction

Since 1977, snowshoe hare (*Lepus americanus*) populations in the Kluane region of the southwestern Yukon have been studied to determine the causes of the 10-year cycle (Krebs et al. 1986, 1995, 2001). One anomaly discovered by

this research is a population of snowshoe hares on an island in Kluane Lake that does not show the same cyclic dynamics as other hare populations in the area. With 10 years of data, Krebs et al. (1986) and Trostel (1986) suggested that the hare population of Jacquot Island fluctuated much less than mainland populations. Since then we have gathered 15 more years of data on these populations and have attempted to find out why these differences occur. Variation between island and mainland populations, in relatively close proximity, provides a good opportunity to examine the influence of various factors on the snowshoe hare cycle.

We carried out intensive studies of reproduction and survival both on the island and the mainland to isolate any demographic differences that might occur. In particular, we did intensive work on Jacquot Island from 1991 to 1994 (Zimmerling 1993; Jardine 1995), using radiotelemetry of juvenile and adult hares. In this paper we evaluate the role of predation in creating the observed variation in population dynamics between the island and mainland areas. Predation has been the primary proximate cause of mortality in cyclic mainland populations of snowshoe hares that have been monitored by telemetry (Hodges 2000). A number of studies of

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mountain hares (*Lepus timidus*) and brown hares (*Lepus europaeus*) on islands off the coast of Scandinavia have produced strong evidence that predation, or lack of it, is a major factor driving the dynamics of these island populations (Häkkinen and Jokinen 1981; Lindlöf and Lemnell 1981; Marcström et al. 1989).

The objectives of this research were to (i) measure survival rates of adult snowshoe hares in Jacquot Island and mainland study areas, (ii) gain information on the relative numbers of predators in the two areas, (iii) measure survival rates of juvenile hares from 0 to 28 days of age, and (iv) determine the proximate causes of mortality of both adult and juvenile snowshoe hares in the two areas. With the information gained, we examined the validity of the following hypotheses derived from our earlier studies summarized in Krebs et al. (2001):  $H_1$ : predation rates on adult hares differ between the mainland and Jacquot Island areas. Jacquot Island predation could be less predictable than the mainland because ice melt in spring restricts movements of mammalian predators to and from the island. As a result, predator numbers on the island may vary randomly from year to year. In some summers there may be no large mammalian predators, such as coyotes (*Canis latrans*) or lynx (*Lynx canadensis*), on the island.  $H_2$ : early juvenile survival is higher on Jacquot Island than on the mainland. If red squirrel (*Tamiasciurus hudsonicus*) and arctic ground squirrel (*Spermophilus parryii plesius*) population densities are lower on the island, snowshoe hare leverets might survive better during the first month of life in all years.

## Methods

### Study area

Jacquot Island is approximately 5 km<sup>2</sup> and is located near the north end of Kluane Lake in southwestern Yukon (61°N, 138°W). The island consists of two separate sections joined by a thin (30 m wide) isthmus. The northern portion of the island (approximately 400 ha) is separated from the mainland by a minimum of 1.5 km. The southern end (approximately 54 ha) is separated from the adjacent mainland by a minimum of 3 km. We assume that Jacquot Island is completely isolated from the migration of hares and terrestrial predators during ice-free months. From late November to late May, ice covers the lake and, during that time, terrestrial animals can move to and from the island.

The understory habitat of Jacquot Island is dominated by shrub willow (*Salix* spp.), with small patches of birch (*Betula glandulosa*) present only at the northern end of the island. White spruce (*Picea glauca*) dominate the canopy, with a few additional groves of balsam poplar (*Populus balsamifera*) and aspen (*Populus tremuloides*). Jacquot Island is relatively hilly, with several treeless windswept hilltops covered with only grasses and low shrubs. The two mainland areas used in this study (Control 1 = Sulphur, Control 2 = Silver Creek) served as unmanipulated control grids for the Kluane Boreal Forest Ecosystem Project. The Silver Creek and Sulphur grids were approximately 40 and 60 km southeast of Jacquot Island, respectively. The understory habitat of the mainland grids is dominated by grey willow (*Salix glauca*) and buffalo berry (*Shepherdia canadensis*). The dominant tree species is

white spruce, with small amounts of balsam poplar also present.

Throughout this study we refer to the mainland Sulphur grid as Mainland 1 and to the Silver Creek grid as Mainland 2. In some instances the two grids have been combined to increase sample size and, in these cases, we refer simply to the mainland.

### Trapping of hares

We monitored hare numbers on two Jacquot Island grids (Jacquot North and Jacquot South) and two mainland grids (Mainland 1 and Mainland 2). Mainland grids were 600 × 600 m, and trapped an effective area of 60 ha. Jacquot North measured 300 × 300 m from 1977 to 1990 and from 1995 to 2001, but was enlarged to 450 × 360 m from 1991 to 1994. Jacquot South was the same size as Jacquot North, except during 1991 to 1994, when it was enlarged to 480 × 300 m. The effective trapping area was 25 ha for the smaller grids and 35 ha for the expanded grids. We used a minimum of 50 live traps on the smaller-sized grids and 84 live traps in the larger areas. Tomahawk live traps were baited with apple and alfalfa and were left locked open between trapping sessions. One trapping session consisted of 2–3 nights of trapping within a 5-day period. Upon capture, each hare was given a numbered ear tag, weighed, sexed, and its right hind-foot measured; the reproductive condition of females was noted as lactating or nonlactating. Population size was estimated with the program CAPTURE (Otis et al. 1978) and the Jolly–Seber full model, as in previous studies (Krebs et al. 1995, 2001).

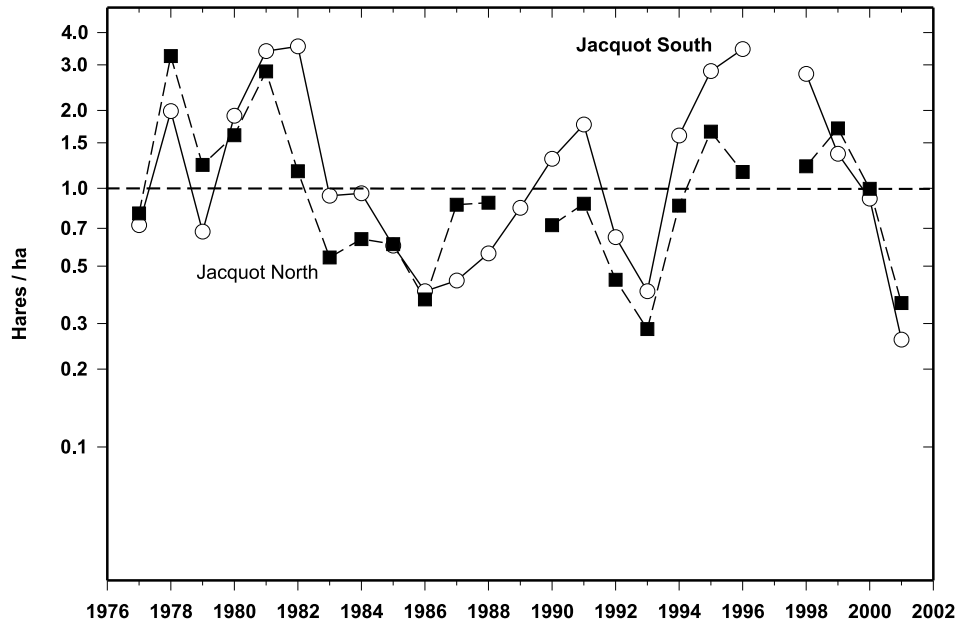
### Survival of hares

During the intensive study periods of 1984–1985 (Trostell 1986) and 1991–1994 (Zimmerling 1993; Jardine 1995), we maintained 15–20 radio collars on adult hares on each grid at all times. Approximately half the collars contained mortality switches and the pulse rate doubled if the collar was not moved within a period of 4 h. All collared hares were located visually every 1–2 days. Survival rates for radio-collared adults were calculated using the Kaplan–Meier method (Pollock et al. 1989a, 1989b). The cause of death of hares was determined at the site of recovery. If predation occurred, the predator involved was identified from feathers, white-wash, scats, or tracks (Krebs et al. 2001, CD-ROM frame 37).

In hares, two to three distinct litter groups are born 35–45 days apart during each summer. Following the procedure outlined by O'Donoghue and Bergman (1992), for each summer from 1991 to 1994 we attempted to capture 10–15 pregnant females for each litter group shortly before parturition on each of the island grids and on Mainland 1. The females were placed in wire-mesh cages (60 × 60 × 120 cm) at their point of capture. The back half of each cage was covered with burlap. The bottom of each cage was lined with moss and spruce branches, and spruce branches were also placed along the sides and woven into the top wire to create a concealed area for the female. Females were fed half an apple and 30–40 willow twigs each morning and evening. Upon parturition, the cage was opened to allow the female to leave.

When the female had departed (usually only 2–3 min), each leveret was tagged with a numbered ear tag, weighed, sexed, and its right hind-foot measured. As many as four

**Fig. 1.** Population-density estimates of snowshoe hare populations on Jacquot North (■) and Jacquot South (○) during spring in the years 1977–2001, Kluane region, Yukon. Hares reached peak numbers on Jacquot Island in 1981–1982, 1991, and 1997–1998. Trends were similar on the two grids with the exception of 1988–1990 and 1996.



leverets from each litter were fitted with a radio transmitter. The transmitters (Biotrack, model SR-1; mass = 2–3 g) were attached directly to the back with Super Glue (The Border Company, Willowdale, Ont., Canada). Fur was removed from a small patch on the back to allow contact with the skin. Transmitters remained attached for 3–4 weeks before falling off. After handling the litter, materials were removed from the maternity cage, placed on the ground, and made into a small “nest” in which the leverets were placed. The maternity cage then was removed from the site to avoid attracting or deterring predators.

Radio-tagged leverets were visually located at 1- to 2-day intervals to determine if they were still alive. If a leveret was found dead, the cause of death was determined in the same way as for adults. Survivorship curves for radio-tagged leverets were calculated by the Kaplan–Meier procedure. Survivorship curves were compared using the log-rank test (Pollock et al. 1989b; Krebs 1999).

#### Relative density of predators

During the summers of 1991 through 1994, each field worker recorded the number of hours in the field each day and the number of each species of predator seen during that time. The total number of hours and the total number of sightings by all workers during each month were compiled and an index of sightings/100 h in the field was calculated. The same procedure was used on both the mainland and island sites, to allow for comparisons of predator sightings between the mainland and island areas. Predator numbers were assessed by these sighting indexes (Hochachka et al. 2000).

Counts of active middens and visual sightings of red squirrels using middens were used to estimate the numbers of red squirrels on each of the Jacquot Island grids from 1991 to 1994. The abundance of arctic ground squirrels was estimated through observation of active burrows. On the mainland, red squirrel and arctic ground squirrel numbers were estimated

through live-trapping and mark–recapture methods by the Kluane Boreal Forest Ecosystem Project (Boonstra et al. 2001). Live-trapping and visual counts at middens or burrows give comparable density estimates for these highly visible squirrels.

#### Understory cover

Understory cover was measured at two heights, 10 and 100 cm above the ground. Cover at 100 cm above the ground should measure the amount of concealment from avian predators that an area offers to hares, while cover at 10 cm should measure the amount of concealment from terrestrial predators.

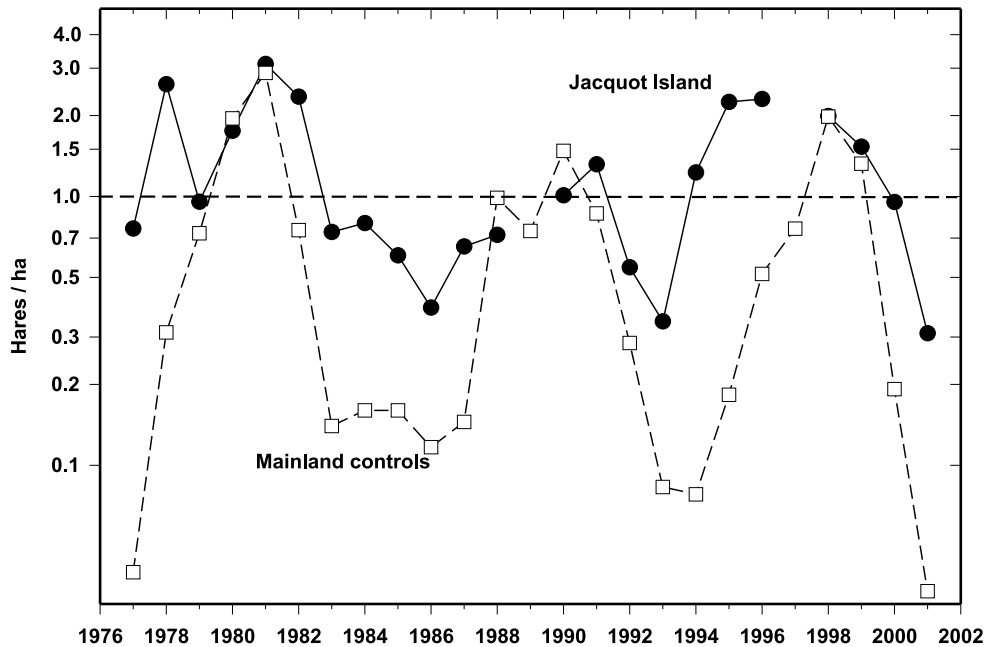
We used a relative index to determine the density of understory cover. In each study area, 30 locations were randomly picked. Measurements were made with a sighting stick, 1 m long and 2 cm wide. In the middle of the stick, 25 black and orange alternating stripes (each 1 cm wide) were painted side by side. At each location, the sighting stick was held horizontally at 10 and 100 cm above the ground. An observer stood 5 m away and observed the number of stripes that were blocked from view by vegetation or woody debris. The eye level of the observer was the same as the height of the sighting stick. Four measurements, in the cardinal directions, were done at each location. At each study area the mean number of obstructed bars was calculated from the 120 observations. A site with no understory would have an index of 0, while a site with a complete understory would score a maximum of 25.

## Results

#### Population densities

The densities of snowshoe hares fluctuated in a similar pattern on Jacquot North and Jacquot South from 1977 to 2001 (Fig. 1). The correlation between density estimates for

**Fig. 2.** Hare population density changes for mainland control sites (□) and Jacquot Island grids (values are the average of Jacquot North and Jacquot South (●)) during spring in the years 1977–2001. While peak densities tend to coincide, hares are not as sparse during the low phase of the hare cycle on Jacquot Island.



the two grids was 0.60 over this period ( $n = 25$ ). Some differences were evident around 1989 and 1996, when there were unfortunate lapses in the trapping record. Hares numbers were high on Jacquot Island in 1981–1982, 1991, and 1996–1998. Maximum spring densities were about 3 hares/ha on Jacquot North and 3.5 hares/ha on Jacquot South. Minimum densities were about 0.3 hares/ha on both island grids.

Mainland hare populations reached peak numbers in 1981, 1989–1990, and 1998 (Krebs et al. 2001), so the overall cyclic trends have been broadly similar on the island and the mainland for the past 25 years. Figure 2 illustrates the trends in hare densities for the island and mainland populations. Maximum spring densities on the mainland hare grids were 2.9 hares/ha and minimum densities about 0.02 hares/ha. The most striking difference between the island and mainland hare populations occurred during the cyclic low phase. Hare densities on the island averaged 0.57/ha in 8 years of low numbers, while on the mainland in the same years, the average hare density was 0.11/ha, a fivefold difference. The most striking difference between these two areas occurred in 1993. The average population density on Jacquot Island increased 3.5-fold from 0.4 hares/ha in spring 1993 to 1.4 hares/ha in spring 1994. At the same time, hares on the mainland showed little change from the low density of 0.08 hares/ha.

There is no indication that the maximal rate of increase during phases of population growth is different between the island and the mainland sites (about a 3- to 4-fold increase in density from spring to spring). But when populations are declining, the declines appear to be more severe at the mainland sites. In 10 years of population decline spread over the 25 years of data, hares on mainland grids declined an average of 57% per year, whereas hares on island sites declined an average of 44% per year.

On average over 25 years, the island hare populations

were about twice as dense (1.3/ha) as those of the mainland hares (0.7/ha) and showed less variance in density (CV for island population densities 0.7, for mainland 1.1). Given these differences in density changes between the island and the mainland, we next asked whether reproductive rates and survival rates differed between island and mainland hares.

**Survival of adult hares**

In general, survival rates differed little among the different sites on Jacquot Island, so we combined radiotelemetry data from the island to compare it with mainland survival data. Table 1 shows that, with the exception of 1992, adult hares on Jacquot Island survived slightly better than their counterparts on the mainland. In 1984–1985, 1991, and 1994, summer 28-day survival rates were significantly higher on Jacquot Island grids than on mainland grids by 5–22% (log-rank test,  $P < 0.01$ ; Table 1). The largest change in survival trend we measured was between summer 1991 and summer 1992, when adult hare survival on the island dropped and adult hare survival rates on the mainland grids increased substantially. On average, an adult hare on Jacquot Island had a 9% better chance of surviving a 28-day period (0.90) than a mainland hare (0.81). This survival differential amounts to an annual expectation of 25% survival on the island versus 6% on the mainland for these particular years.

We have fewer data on radiotelemetry survival rates over the winter period for Jacquot Island. During the winter of 1984–1985, survival on Jacquot Island was 0.84/28 days (95% confidence limits (CL) 0.81–0.87), while hares on the mainland survived at a 28-day rate of 0.78 (95% CL 0.72–0.84). The suggestion is that winter survival on the island was slightly better than it was on the mainland in this year. During the low-density winter of 1993–1994, live-trapping data indicated an 83% survival over 8 months on the island versus a 13% survival rate of radio-collared hares on the

**Table 1.** Survival rates (28 day) of radio-collared adult snowshoe hares, *Lepus americanus*, (with 95% confidence limits (CL)) in Jacquot Island and mainland study areas, Kluane region, Yukon Territory, in the summers of 1984–1985 and 1991–1994.

	Jacquot Island			Mainland		
	Survival rate	95% CL	<i>n</i>	Survival rate <sup>a</sup>	95% CL	<i>n</i>
Summer 1984–1985	0.93	0.89–0.95	137	0.87	0.82–0.91	108
Summer 1991	0.87	0.82–0.92	101	0.65 <sup>b</sup>	0.55–0.75	53
Summer 1992	0.81	0.61–0.90	42	0.83	0.61–0.96	30
Summer 1993	0.90	0.83–0.96	23	0.85	0.68–0.94	12
Summer 1994	1.00	1.00–1.00	32	0.90	0.85–0.95	42

**Note:** *n* is the number of individual radio-collared snowshoe hares.

<sup>a</sup>Significant difference between years for mainland, with 1991 lower than all other years ( $P < 0.05$ ).

<sup>b</sup>Mainland survival rate significantly lower than Jacquot Island in 1984–1985, 1991, and 1994 ( $P < 0.001$ ).

**Table 2.** Proximate causes of mortality of radio-collared adult snowshoe hares on Jacquot Island and the mainland during the summer months in 1991–1995.

Mortality factor	Percent mortality							
	Summer 1991		Summer 1992		Summer 1993		Summer 1994	
	Jacquot Island	Mainland	Jacquot Island	Mainland	Jacquot Island	Mainland	Jacquot Island	Mainland
Lynx	0	5	36	9	0	0	0	8
Coyote	29	38	14	0	0	0	0	0
Unknown mammal	0	10	14	27	17	17	0	0
Goshawk	12	0	0	27	0	0	0	15
Great-horned owl	6	0	0	0	0	0	0	0
Unknown bird	12	5	7	0	0	17	0	0
Unknown predator	29	43	21	27	67	17	0	31
Unknown	12	0	7	9	17	50	0	46
Total dead ( <i>n</i> )	17	21	14	11	6	6	0	13

**Note:** Values are percentages except for sample size (total dead).

mainland over the same 8 months. Again survival rates were more favorable on the island.

No clear differences were detected in proximate causes of mortality of adult hares between the island and mainland populations, but differences between years in the two areas were apparent (Table 2). In a typical year, lynx sign was relatively rare on Jacquot Island. In 1991, 1993, and 1994, no lynx predation was observed on the island but, in 1992 (the 1 year a lynx was known to live on the island), lynx predation was the largest cause of mortality. In 1991, both goshawks (*Accipiter gentilis*) and great-horned owls (*Bubo virginianus*) were involved in predation on the island. In 1992 through 1994, no predation by either of these avian predators was observed on the island. On the mainland, both lynx and coyotes are major mammalian hare predators, as are great-horned owls and goshawks (Hodges et al. 2001). The main conclusions shown in Table 2 are that predators are the main cause of death on the island, as they are on the mainland, and that the exact predators causing the losses of adult hares on the island vary greatly from year to year.

#### Juvenile survival on Jacquot Island

Low population densities on both the island and the mainland limited the number of leverets that could be radio-

tagged in 1992 and 1993. On Jacquot Island in 1991, 105 leverets were radio-tagged from the first and second litters. In 1992, only 12 leverets could be radio-tagged and, in 1993, only 25 leverets were radio-tagged. In 1994, hares became more abundant and 94 leverets were radio-tagged. Similar sample-size problems occurred on the mainland (Table 3).

Juveniles on Jacquot Island always had better survival rates than their mainland counterparts, except for 1992 when survival was low everywhere (Table 3). Figure 3 illustrates the high survival of Jacquot Island juveniles in 1994, a year of large sample sizes on both sites. The pattern of juvenile survival changes on Jacquot Island from 1991 to 1994 matched that of the mainland, with poorer survival in 1991 and 1992 and improved survival in 1993 and 1994 when the island population began a strong recovery. Over these 4 years, a juvenile on Jacquot Island had, on average, a 50% chance of surviving its first 4 weeks of life, while a juvenile on the mainland had, on average, only a 26% chance. The best predictor of population growth rate for our detailed studies on the island and the mainland from 1991 to 1994 is the leveret survival rate ( $r = 0.84$ ,  $n = 7$ ; Fig. 4).

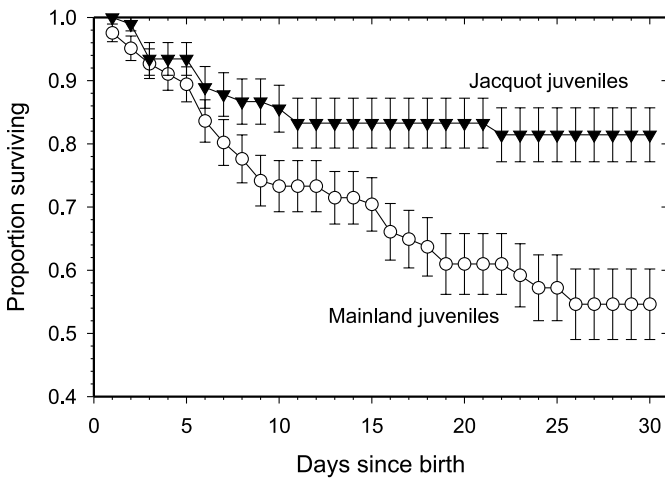
For most hare litters the highest mortality occurred within the first 5 days of life. During this time leverets were most

**Table 3.** Average survival rates of juvenile hares during the first 28 days of life for the Jacquot Island and mainland grids from 1991 to 1994.

	Jacquot Island			Mainland		
	Survival rate	95% CL	<i>n</i>	Survival rate	95% CL	<i>n</i>
Summer 1991	0.54	0.44–0.64	105	0.10	0.03–0.24	39
Summer 1992	0.27	0.06–0.61	12	0.33	0.10–0.65	13
Summer 1993	1.00	0.86–1.00	25	?	—	—
Summer 1994	0.83	0.75–0.90	94	0.55	0.44–0.66	123

**Note:** Data from all three litter groups over each year were pooled to increase sample sizes. No data were available for 1993 for the mainland, because of sparse populations.

**Fig. 3.** Kaplan–Meier survivorship curves for snowshoe hare juveniles from Jacquot Island and the mainland in 1994. A total of 94 leverets were followed on Jacquot Island and 123 on the mainland. Error bars are 1 SE.



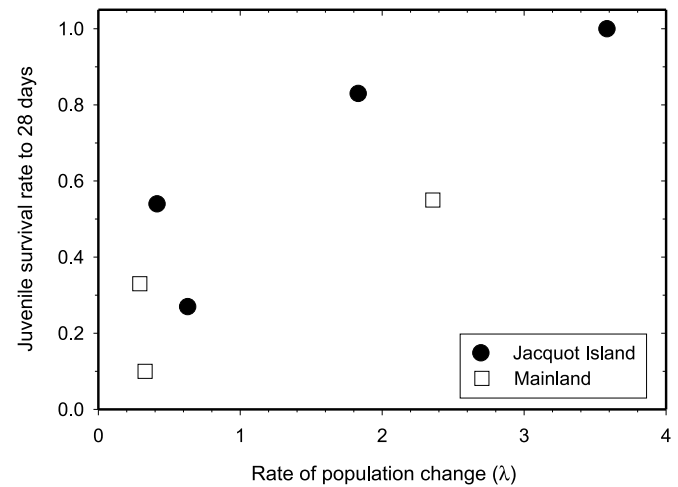
often found together, close to the place of release from the maternity cage. Most leverets began to separate and find individual hiding spots between 5 and 7 days of age, and survival improved greatly as they became more mobile (Gillis 1998). In 1991 and 1992, nearly a quarter of the leverets died from exposure within 5 days of birth. In most instances entire litters died in a single day. These losses resulted from severe snow or rainstorms that soaked the small leverets and caused hypothermia (Zimmerling 1993).

Coyote predation was a major cause of mortality on Jacquot North in all years. All predation attributed to coyotes occurred in the first 5 days of life and consisted of all siblings of a single litter disappearing on the same day. Coyotes apparently were able to find young leverets when they were still hiding together and unable to move rapidly. Red squirrel predation was a significant mortality factor for all litters on all grids. Red squirrels typically hauled leverets to their nests in trees, where their remains and radio could be found. Red squirrels were responsible for the death of 19% of radio-tagged leverets on Mainland 1, 25% on Jacquot North, and 50% on Jacquot South in 1991, when we had the best data on the causes of death for leverets.

**Predator numbers**

Sightings of all predators differed between years and among areas (Table 4). Coyote abundance was similar on the island

**Fig. 4.** The relationship between the rate of population change ( $\lambda = \frac{N_{t+1}}{N_t}$ ) and the survival rate of juveniles in their first 28 days of life for hares on Jacquot Island and the mainland (1991–1994 data). Survival is measured in year *t* and the rate of population change from spring *t* to spring *t* + 1.



and the mainland. Lynx sign was never found on Jacquot Island except during the summer of 1992, when a lynx was sighted several times each month. All the avian predators of hares were much less common on Jacquot Island than they were on the mainland, with the single exception of great-horned owls in 1992. In particular, when hare numbers were increasing rapidly in 1993 and 1994, predator sightings on Jacquot Island were very near zero.

Arctic ground squirrels and red squirrels are both important predators of juvenile hares on the mainland (O’Donoghue 1994). Arctic ground squirrels were never observed on Jacquot Island, although they are abundant on the mainland (Boonstra et al. 2001). Red squirrels occur on Jacquot Island but at much lower densities than on the mainland. Densities of red squirrels did not vary between years. On Jacquot Island, estimated densities of red squirrels in spring in 1991–1994 were 0.20–0.30/ha. On the mainland, densities of red squirrels in spring ranged from 1.53 to 2.33/ha over the years 1991–1994 (Boonstra et al. 2001). Red squirrels were 5–10 times more abundant on the mainland than on the island.

**Understorey cover**

Habitats with a dense understorey are preferred by snowshoe hares (Wolff 1980). The amount of understorey vegetation

**Table 4.** Sighting indexes (sightings/100 h in the field) for predators on the Jacquot Island and mainland grids during the summers of 1991–1994.

	Jacquot Island				Mainland			
	1991	1992	1993	1994	1991	1992	1993	1994
Coyote	0.18	0.08	0.14	0.0	0.28	0.06	0.13	0.23
Lynx	0.0	0.81	0.0	0.0	0.31	0.13	0.14	0.0
Great-horned owl	0.13	0.23	0.0	0.0	0.35	0.06	0.07	0.02
Goshawk	0.78	0.0	0.0	0.0	3.05	1.00	0.91	0.42
Red-tailed hawk	0.88	0.0	0.0	0.50	2.85	2.40	2.52	2.01
Marsh hawk	0.80	0.85	0.0	0.06	1.20	2.38	1.02	0.96
Total no. of hours in the field	2244	2396	1425	1592	8662	8441	8966	5004

in an area affects the ability of hares to avoid predation. If hares tend to survive better on Jacquot Island, this may be the result of systemic habitat differences.

We measured understory cover at two heights, 10 and 100 cm above the ground. Both study areas on Jacquot Island had denser low-level cover than the mainland study areas (Table 5) and were as dense in high-level cover as the more dense Mainland 1. Much of the low cover on Jacquot Island consisted of low shrubs and downed woody debris from an old fire. These study areas were most difficult for humans to traverse and, we presume, more difficult for predators to search. Zimmerling (1993) showed that there was less low cover at locations of hare kills by predators on Jacquot Island than at random sites in the same area, and Trostel (1986) found that mortality rates were lower in the areas on Jacquot Island that had the densest cover.

## Discussion

Population density changes on Jacquot North and Jacquot South were similar and, consequently, we assume that we sampled the demography of the whole island population of snowshoe hares. Population trends on the island followed the long-term hare cycle on the mainland, with the major difference that hare densities in the low phase were much lower on the mainland than they ever were on the island. The island population was buffered so that, on average over 25 years, the island hare populations were about twice as dense as the mainland hare populations and showed less variance in density.

Hare population densities on Jacquot Island might be higher because of higher reproductive rates or higher survival rates. From an exhaustive analysis of the reproductive parameters of Jacquot Island hares, Trostel (1986) and Jardine (1995) concluded that these differed not at all from those of mainland hares. Hare reproductive rates fluctuate dramatically over the 10-year cycle (Cary and Keith 1979; Stefan and Krebs 2001) but changes occur in a similar way on the island and the mainland. Thus, survival differences must underlie the demographic patterns of the island population.

Summer survival of adults on Jacquot Island is almost always higher than that of adults on the mainland, with the exception of years of population decline (e.g., 1992). A similar pattern was found in the survival of leverets from birth to 30 days. We have fewer data on overwinter survival. Trostel (1986) found that overwinter survival was better on Jacquot Island than on the mainland, and Jardine (1995) reported

**Table 5.** Mean ( $\pm$ SE) understory cover density on the Jacquot Island and mainland grids at 10 and 100 cm above the ground.

Study area	Cover density at a height of	
	10 cm	100 cm
Jacquot Island North	17.8 $\pm$ 1.1	12.7 $\pm$ 1.3
Jacquot Island South	23.1 $\pm$ 0.7	13.8 $\pm$ 1.2
Mainland 1	5.4 $\pm$ 0.9	8.3 $\pm$ 1.4 <sup>a</sup>
Mainland 2	10.8 $\pm$ 1.1	13.8 $\pm$ 1.3

**Note:** With the index used, the densest possible cover would score 25 and the least dense cover would score 0. Sample size is 30 in all cases. At a height of 10 cm, all areas are significantly different.

<sup>a</sup>Significantly lower than the other three areas.

similar findings with a small sample size. There has been no indication that overwinter survival is any worse on Jacquot Island than on the mainland in any given year. The dense understory cover on Jacquot Island (Table 5) could be one factor involved in reducing predation rates on the island. We conclude that island hare populations maintain higher average densities than mainland hare populations because of improved juvenile and adult survival among island hares.

Predation is the immediate cause of death for almost all snowshoe hares (Keith 1990; Hodges 2000; Hodges et al. 2001). Our first hypothesis is that predation rates on both adult and juvenile hares differ systematically between island and mainland sites. With the exception of lynx and great-horned owls on the island, predator numbers declined greatly from 1991 to 1992. A single lynx was present on Jacquot Island during the summer of 1992 and this lynx was a major proximate cause of mortality on the island in 1992 (Table 2). We speculate that the lynx was probably responsible for the decrease in survival rates among adult hares on Jacquot Island in 1992. Although coyotes have been present on the island in most years, they were apparently absent in 1994. From 1991 to 1994, mammalian predators declined to low numbers in the mainland study areas (Boutin et al. 1995). The major difference seemed to be that, while predators declined to very low numbers on mainland sites during the low phase of the hare cycle, they typically declined to zero on the island. All these data are consistent with our first hypothesis, viz. that predation rates differ between the mainland and Jacquot Island.

In previous studies in Scandinavia, the number and type (generalist or specialist) of predators preying on hares were

implicated as the main factor determining the dynamics of hare populations. Lindlöf and Lemnell (1981) compared a high-density island population of mountain hares with an adjacent mainland population and found that the major difference between the two areas was the lack of a mammalian predator, red fox (*Vulpes vulpes*), on the island. Angerbjörn (1989) reported similar results for mountain hares on islands off Sweden.

During winter, mammalian predators such as lynx or coyotes may travel to Jacquot Island. If hare numbers on Jacquot Island are high relative to mainland areas, then predators may stay on the island during the winter and spring. Once the ice on Kluane Lake melts at the end of May, mammalian predators could be trapped on the island until the following winter. If hare numbers on Jacquot Island are low during the winter relative to mainland areas, then predators would possibly abandon the island and, thus, no large mammalian predators would inhabit the island during the following summer. In addition to these factors, there is a stochastic factor: whether mammalian predators visit Jacquot Island by chance in any particular winter. In some winters we were able to track individual mammalian predators across the lake ice to Jacquot Island and pick up their tracks again as they left to go back to the mainland. During the 25 years of study, no lynx ever appeared to breed on Jacquot Island, although coyotes have reproduced there in some years.

Only one small mammalian predator of juvenile hares, the red squirrel, is known to inhabit Jacquot Island, and its population densities on the island are only one-fifth those on mainland sites. The absence of arctic ground squirrels on Jacquot Island constitutes a major difference between the island and the mainland. Both ground squirrels and red squirrels are significant predators of juvenile snowshoe hares on the mainland (O'Donoghue 1994).

We can confirm only an association between high leveret survival rates on Jacquot Island and low densities of red squirrels and the absence of ground squirrels. These data support our second hypothesis, viz. that predators of juvenile hares are at lower densities on Jacquot Island than on the mainland and, as a result, early leveret survival (0–28 days) is higher on the island. Red squirrel predation on leverets varied from year to year on both the mainland and the island (Jardine 1995) and we do not have an understanding of what causes this variability. Consequently we cannot assume high leveret survival rates on the island to be solely an effect of low red squirrel predation.

One unexpected finding from this study was the impact of inclement weather on leveret survival. Exposure affected the survival of leverets in both the island and mainland study areas, and approximately one-third of the leverets died of exposure in 1991 and 1992, years of cyclic decline. Since both the island and the mainland were affected by these losses, they do not explain the differences between the two populations. We do not know if our choice of nest sites affected the risk of mortality due to exposure for leverets. Females that give birth naturally may be more discriminating in their choice of parturition site; however, care was taken to choose sites that would protect the leverets from normal rains.

Reduced recruitment at the peak and decline phases of the hare cycle is a major contributing cause to the population decline (Meslow and Keith 1968; Keith and Windberg 1978;

Krebs et al. 1986; Keith 1990). Our data support the conclusion that recruitment in hare populations is determined by the survival of leverets during the first few weeks of life. Haydon et al. (1999) showed that juvenile survival was the major contributor to snowshoe hare population growth rates, which agrees with our data. On Jacquot Island, leverets experienced on average higher survival rates, possibly owing to reduced predator numbers. As a result, the Jacquot Island population did not experience the same levels of reduced recruitment that were observed on the mainland and thus densities did not fall as low as on the mainland (Fig. 2).

Food shortage is one alternative hypothesis that could explain the difference in dynamics between the island and mainland hare populations. We previously rejected the immediate role of food shortage in generating population changes among Jacquot Island hares based on a food-addition experiment that showed no impact (Krebs et al. 1986). We saw little evidence of severe browsing on Jacquot Island when hare populations were dense and have tentatively concluded that the impact of food supplies on hare demography on Jacquot Island are at best indirect rather than direct via starvation.

We conclude that differences in population dynamics between Jacquot Island and mainland hare populations are correlated with differences in predation rates on both adult and juvenile snowshoe hares. A rigorous quantitative assessment of the relative contributions of these two types of predation remains to be done. In the larger picture of snowshoe hare population cycles, this study underlines the critical importance of predation as a major cause of population trends.

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