Spatial and temporal trends and effects of population size on the frequency of color phenotypes in the wild red fox (*Vulpes vulpes*)

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Abstract: We analyzed the hypothesized relationships of temporal, spatial, and harvest trends with frequency of red fox (*Vulpes vulpes*) color morphs in 57 Hudson's Bay Company posts over a 20- to 26-year period, but found none of the strong relationships postulated to exist. A meta-analysis of each data set suggested a weak inverse relationship between latitude and frequency of the red morph. Meta-analysis further indicated a weak positive relationship with time and the frequency of the red phase, although this trend was not due to climate change. No relationship was found between harvest size and color phase, or between a 1-year lagged harvest size and color phase, which evaluated the effects of dispersal. The data sets did not allow conclusive determination of the mechanisms behind the trends, but it is postulated that a slight selective advantage is found for the dark morphs at high latitudes, while the temporal increase in frequency of the red phenotype is probably the result of northward dispersal from southern populations.

Résumé : Nous avons procédé à l'analyse de relations hypothétiques entre les tendances temporelles, spatiales et démographiques et la fréquence des différents phénotypes du Renard roux (*Vulpes vulpes*) (couleur) en 57 stations de la Compagnie de la Baie d'Hudson pendant une période de 20–26 ans et nous n'avons trouvé aucun fondement quant à de fortes corrélations. Une méta-analyse de chaque série de données a permis de supposer l'existence d'une faible relation inverse entre la latitude et la fréquence de la forme rousse. La méta-analyse indique également l'existence d'une faible relation positive entre le temps et la fréquence de la forme rousse, mais cette tendance n'était pas attribuable à un changement climatique. Aucune relation n'a été trouvée entre le nombre de renards capturés et la forme, ou entre le nombre de renards capturés l'année précédente et la forme, une mesure des effets de la dispersion. Les séries de données ne permettent pas de tirer des conclusions sur les mécanismes qui conditionnent les tendances, mais nous croyons à l'existence d'un léger avantage sélectif en faveur des individus de forme foncée aux latitudes élevées, alors que l'augmentation du nombre d'individus de forme rousse en fonction du temps résulte probablement de la dispersion vers le nord des populations australes.

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Introduction

Interest in the genetics of coat-color inheritance in the red fox (*Vulpes vulpes*) has spanned this century, owing to the value of its fur. Extensive experimental matings indicated that genetic control of traditional coat colors (red, cross, and black) is based on epistatic interactions of two genes (Iljina 1934; Ashbrook 1937; Kellogg 1941; Nes et al. 1983; Adalsteinsson et al. 1987; Nes et al. 1988; Johnson and Hersteinsson 1993). Investigators have consistently examined spatial and temporal changes based on the three major color phases: red, cross, and black (Cowan 1938; Cross 1941; Haldane 1942; Butler 1945, 1947, 1951; and Calhoun 1950).

Many authors have found various trends in the distribution of the phenotypes in the red fox, but few have tested them statistically. Cowan (1938) reported that the frequency of the dark (cross and black) phenotypes increased with latitude and towards the coastal regions in western Canada. Cross (1941) found that populations in southern Ontario had a higher percentage of the red phase than northern populations. The cross phase showed the opposite trend, having its highest concentration in northern Ontario. The black phase exhibited a similar but weaker pattern of higher frequencies in the north. Butler (1945) showed a decrease in the frequency of the black phase throughout Canada during the 24-year period from 1916 to 1939. A similar temporal trend was found in the Mackenzie River basin during 1860–1930 (Butler 1947). His study also found a decrease in abundance of the silver and cross phases along a north–south gradient. However, both of these papers (Butler 1945, 1947) used highly edited data sets and should be viewed with some degree of circumspection. All of these investigators reached the same conclusions: the frequency of the red phase has been increasing during the past century and dark-phase foxes are more abundant at higher latitudes.

Several mechanisms have been proposed to explain the decreasing frequency of the black and cross phenotypes. Haldane (1942) suggested that selective hunting of black-phase foxes was reducing their numbers. However, Butler (1945) found, through interviews with hunters and trappers, that less than 5% of the foxes taken in the wild were shot. He also indicated that, on average, a silver pelt was worth

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no more than a red pelt by 1945. Butler (1945) also noted that trapping was nonselective as to phenotype. He proposed three alternative explanations for the increase in red-phase foxes. First, their dispersal from the south had swamped northern gene pools, which is analogous to secondary contact. Second, he proposed that differential survival or reproductive success among phenotypes altered phenotypic frequencies. Finally, Butler proposed that criteria for classifying the pelts as to phenotype might have changed over time.

Calhoun (1950) regarded selection, other than hunting, against the black phase during population peaks as the most probable cause of the changing frequencies. Alternatively, he proposed that fox populations survived in refugia during the Wisconsin glaciation, one in Alaska and the other in northeastern Canada. Several areas in the northeast remained ice-free and could have served this purpose, including Anticosti Island, nunataks on the Gaspé Peninsula, and the Torngat mountains (Dyke and Prest 1987). He postulated that the population in the Alaska refugium had a high frequency of the Alaskan black allele, the Canadian black allele predominated in the northeastern Canadian population, and the gene pool in the area south of the ice sheet was dominated by alleles producing the red phase. With glacial retreat, the red phenotype moved northward, swamping the small isolated gene pools. Macpherson (1965), however, argued that none of the northern refugia contained red-phase foxes. He suggested that the present distribution of phenotypes is a result of reestablishment from populations that persisted below the southern terminus of the Wisconsin glaciation. Butler (1945) provided some evidence against the selection theory, while supporting the swamping hypothesis, when he showed that the increase in frequency of the red phenotype may be due to dispersal from surrounding areas, and pointed out that no evidence of differential reproductive success has been found among ranch-bred color phases (Butler 1945). Butler (1947) provided additional support for a swamping effect on the northern gene pools when he showed that the frequencies of the black and cross phenotypes decreased in the northern areas following a population peak. He suggested that this indicated an influx of red-phase foxes dispersing northwards, owing to population pressures. However, these data were not tested statistically. Allen and Sargeant (1993) provide evidence that dispersal of red foxes in North Dakota resulted in an equalization of densities between areas.

A survey of the literature indicates that foxes have the ability to rapidly colonize areas and disperse great distances, as is required for swamping to occur. Colonization rates for the red fox averaged 22 km per year on Baffin Island (Macpherson 1964). Several studies of dispersal by juveniles show that distances range from 2 to 200 km per year (Lloyd 1975; Storm et al. 1976; and Englund 1970). The mean dispersal distance of juveniles in Ontario was 30 km for males but only 8 km for females (Voigt and Macdonald 1984). Zimen (1984) found that in Germany and France the majority of males dispersed between 17 and 500 km, long-range movements being directed by topography and forest distribution. Hersteinsson and Macdonald (1982), radio-tracking red foxes in England, showed that the males tended to disperse within the first year, while some vixens joined the social groups in their natal territory. They failed to track the dispersal distance of juveniles, however. In addition to the capacity for dispersal over

Table 1. Predicted relations between variables and the models that could produce the observed distribution of phenotypic frequencies.

Model	Harvest size	Time	Temp.	Latitude
Swamping dispersal	Yes	Yes	No	Yes
Diffusion dispersal	No	Yes	No	Yes
Selection	No	No	Yes/no	Yes

long distances, the generalist diet of the red fox, which includes chamois (*Rupicapra rupicapra*), earthworms (*Lumbricus terrestris*), fruits, berries, tubers, rodents (Macdonald 1980), and hare (*Lepus americanus*) (Major and Sherbourne 1987), may increase survival probabilities during the dispersal phase.

There are three objectives to this paper. The first is to test the hypothesis that the frequency of the red phase has increased through time (Haldane 1942; Butler 1945, 1947; and Calhoun 1950). We expand on the temporal-shift hypothesis by examining the relationship between climate and phenotypic frequency to determine if climate change could be responsible for any observed trends. Second, we examine whether the relationship between latitude and phenotypic frequency hypothesized by Cross (1941), Butler (1945, 1947), and Calhoun (1950) exists. Third, we evaluate the relationship between population size, as indexed by harvest size, and the frequency of the red phase (Butler 1945, 1947; and Calhoun 1950). We also try to identify which mechanism, swamping or selection, is responsible for any observed patterns. We further break the swamping hypothesis into two different mechanisms, population-driven dispersal (swamping dispersal) or passive diffusion (diffusion dispersal). If dispersal is driven by population pressure, we would expect to see a significant relationship between harvest size and phenotypic frequency, as well as significant effects with respect to time and latitude (Table 1). Passive diffusion occurs simply because there are more red-phase foxes than alternative color morphs, especially in southern populations (Table 1). If this is the case, we should see a significant effect of time and latitude on phenotypic frequencies. If selection is controlling the phenotypic relationships, latitude and (or) temperature should be the only significant component (Table 1).

Materials and methods

The color-morph data were taken from the pelt-count records of 58 Hudson's Bay Company posts in Manitoba ($n = 13$), Ontario ($n = 25$), and Quebec ($n = 20$). The time series for the Ontario posts included harvest data from 1915 to 1935, while the Manitoba and Quebec time series ran from 1915 to 1941. All years are biological years, which correspond, for example, to the period between June 1, 1915, and May 31, 1916. While we would have liked to analyze longer time series, this was the extent of the retrievable data. The records included numbers of furs in each of four categories, red, smoky red (or gold), cross (including Alaskan, or gold, cross, and blended, or silver, cross), and black − silver (including substandard silver, Alaska silver, sub-Alaska silver, and blended, or double, silver). In this paper we defined red-phase foxes to include the true red phase and smoky red. The other phenotypes were lumped together by the Hudson's Bay Company as described above. Even if some pelts were misidentified, this should not affect our results, owing to the large sample sizes.

Our analysis of these historical data requires three major assump-

Fig. 1. Locations of Manitoba posts constituting the four latitudinal transects MAN1, MAN2, MAN3, and MAN4.
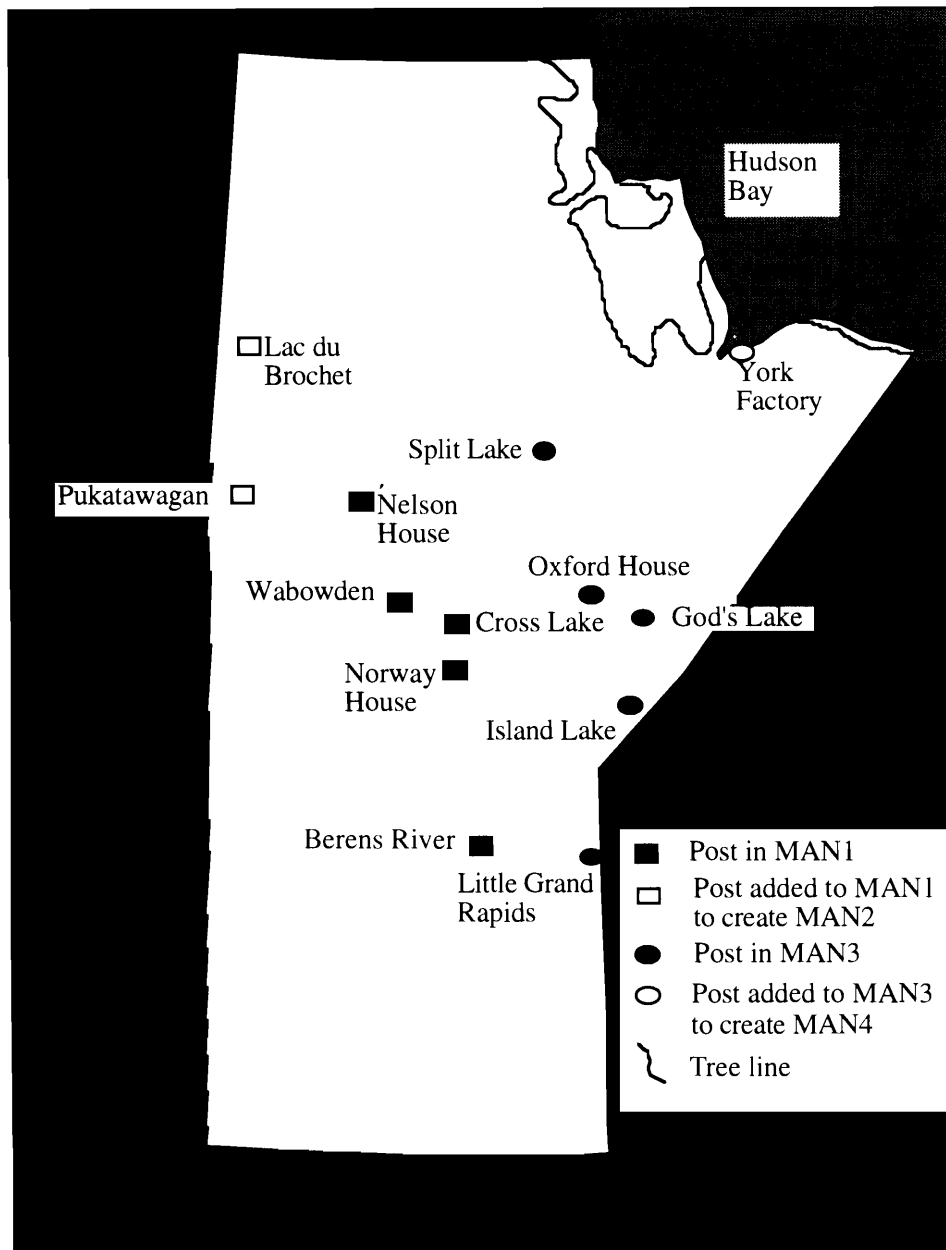
tions: that there was no selective trapping, that trapping effort was constant, and that harvest records provide a measure of population size. The first assumption is dealt with in the Introduction. A constant trapping effort is assumed, as Moran (1953) and Arditi (1979, 1989) found that weather conditions had no significant effect on effort. The third assumption, as well as the first two, are common throughout the literature (e.g., Elton 1942; Keith 1963; Gilpin 1973; Bulmer 1974, 1975; and Finerty 1979, 1980).

All data were analyzed as logit-transformed frequencies of the red phenotype (F_{red}). The logit transformation, defined as $\ln(p/1 - p)$, scales the frequency range from (0,1) to ($-\infty$, ∞). Since it is not possible to take the natural log of 0, data points corresponding to the absence of the red phenotype ($p = 0$) were not evaluated. This manipulation involved the exclusion of only 4 of 1612 data points. In a similar manner, the data point (1/0) is undefined, so the greatest frequency less than 100% for each province was used. Trends were

examined only for the red-phase foxes because they were the commonest, thus minimizing the number of zero data points.

To determine if there was a temporal trend in F_{red}, data were evaluated using linear regression (Harris 1986; Gerrodette 1987; and Titus et al. 1989). Each population was evaluated for the duration of its time series. The slope of these regressions, F_{red} against time (TIME), indicates the direction and intensity of change in F_{red}. A provincial-level analysis was also performed by summing the populations from all posts for each year and regressing the values of F_{red} against the summed harvest size. Any temporal trend could be the result of climate change during the period of investigation. We examined the degree to which climate change could have influenced phenotypic frequencies by regressing F_{red} for each post against the average temperature across Canada (TEMP) for the corresponding year.

The relationship between latitude (LAT) and F_{red} was examined using linear regression on a series of north—south posts constituting

Fig. 2. Locations of Ontario posts constituting the latitudinal transect ONT.
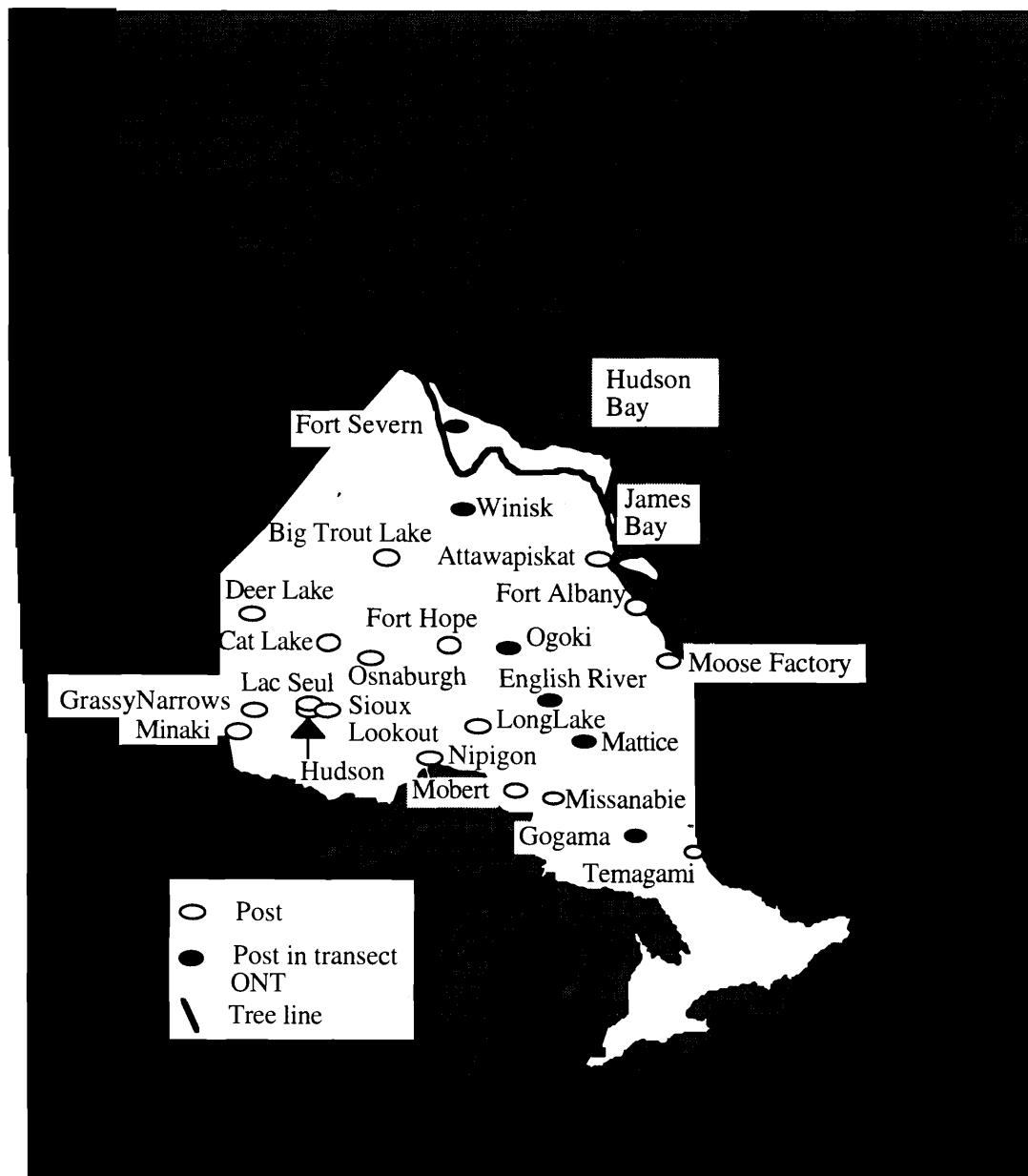

a latitudinal transect. Latitude was deemed a suitable substitute for climate change, as temperature, mean annual number of days with snow cover, and average yearly snow fall paralleled latitudinal shifts through much of the study range (Department of Mines and Technical Surveys 1957). Using latitude to approximate climatic variables also allows incorporation of several different variables such as those listed above. The posts were chosen by determining the nearest northern neighbor within a 250-km band centered around the initial post. In Manitoba, this produced one transect (MAN1) consisting of Berens River, Norway House, Cross Lake, Wabowden, and Nelson House (Fig. 1). The two most westerly posts (Lac du Brochet and Pukatawagan) were added to MAN1 to produce the second transect, MAN2. The third transect, MAN3, consisted of Little Grand Rapids, Island Lake, God's Lake, Oxford House, and Split Lake. The northernmost post in the east (York Factory) was added to MAN3, producing the fourth transect, MAN4. The Ontario transect (ONT) consisted of Gogama, Mattice, English River, Ogoki, Winisk, and Fort Severn (Fig. 2). Two Quebec transects were created.

QUE1 originated at Grand Lac and included Senneterre, Woswanaby, Nemaska, Fort Rupert, Eastmain, Fort George, and Great Whale River (Fig. 3). The second Quebec transect (QUE2) included the northernmost population, Wolstenholme, to QUE1. A regression $(F_{red} = \text{LAT})$ for each transect was run for each year in the time series. A latitudinal effect over time was also evaluated by regressing the sum of each post's harvest over time against F_{red}.

To determine the relationship between F_{red} and harvest size (N_t), we regressed F_{red} against the ln-transformed population size for each post. These analyses were then repeated with a 1-year time lag (N_{t-1}) to evaluate delays due to maturation and dispersal of juveniles. Population size and lagged population size were also examined at the post–year level by utilizing each year of each post (post–year) as a separate data point. All reported r^2 values are adjusted values.

A post hoc meta-analysis was performed on the data sets to identify weak trends in the data. Meta-analysis examines patterns in the results of data sets regardless of the significance of the individual

Fig. 3. Locations of Quebec posts constituting the two latitudinal transects QUE1 and QUE2.
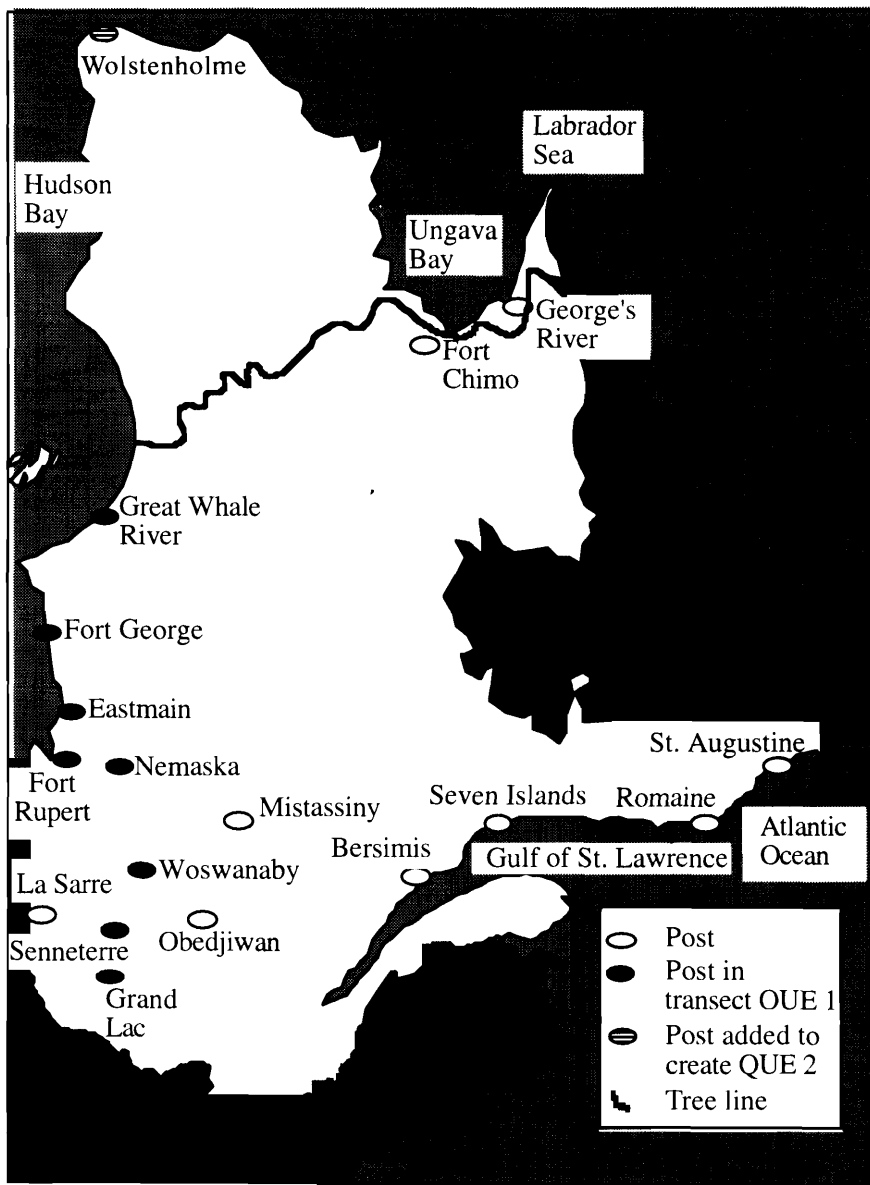
tests, creating an independent data set based on the results of the previous analyses, weighted by the sample sizes (Hedges and Olkin 1985; Gurevitch et al. 1992; Fernandez-Duque and Valeggia 1994). A nonrandom pattern in the results of the regression analysis can be found by looking at the ratio of the positive to negative slopes of the regression analyses. A significant deviation from the expected 1:1 ratio would indicate that there is a weak trend of increasing or decreasing frequency of the red phenotype. Chi-squared analysis was performed on the results of each set of regressions for each province.

Results

Linear regression: F_{red} = TIME

Regression of F_{red} = TIME for the Manitoba time series showed a significant positive slope ($p < 0.05$) at 4 of the 14 posts; Nelson House, Oxford House, Split Lake, and York Factory (Table 2). The nine other populations (Berens River, Cross

Lake, God's Lake, Island Lake, Lac du Brochet, Little Grand Rapids, Norway House, Pukatawagan, and Wabowden) exhibited nonsignificant ($p > 0.05$) slopes. Examination of the combined data sets from Manitoba showed no relationship ($p = 0.07$). Meta-analysis indicated a significantly greater number of positive slopes ($\chi^2 = 6.23$, $p = 0.01$) than expected by chance (Table 2).

Regression of F_{red} = TIME was significantly positive ($p < 0.05$) for 10 Ontario posts (Cat Lake, Fort Hope, Hudson, Long Lake, Moose Factory, Nipigon House, Osnaburgh, Sioux Lookout, Temagami, and Big Trout Lake). The 16 other populations had nonsignificant ($p > 0.05$) slopes (Table 3). Analysis at the provincial level showed a significant positive slope ($\beta = 0.0162$, $r^2 = 0.4896$, $p = 0.0004$). A significant skew ($\chi^2 = 4.84$, $p = 0.03$) towards a positive slope was found for Ontario in the meta-analysis (Table 3).

F_{red} = TIME regressions produced significantly positive

Table 2. Results of regressions of the frequency of red-phase foxes for Manitoba populations, using the variables TIME, TEMP, N_t, and N_{t-1} as main effects.

Post	TIME	TEMP	N_t	N_{t-1}
Berens River	+	+	+	+
Cross Lake	+	+	+	+
God's Lake	+	+*	+	+
Island Lake	+	+	−*	−*
Lac du Brochet	−	−	−	+
Little Grand Rapids	+	+	−	−
Nelson House	+*	+	+*	+*
Norway House	+	−	+	+
Oxford House	+*	−	+	+*
Pukatawagan	+	−	+	+*
Split Lake	+*	+	+*	+
Wabowden	−	−	+	−
York Factory	+*	−	+	+*
Num +	11	7	10	10
Num −	2	6	3	3
χ^2 (df = 1)	6.231	0.08	3.769	3.769
p	0.013	>0.9	0.052	0.052

Note: The variables are described in the text. +, positive nonsignificant slope; −, negative nonsignificant slope; *, significant slope ($p < 0.05$) of the indicated sign; Num +, total number of positive slopes; Num −, total number of negative slopes.

($p < 0.05$) slopes for three populations in Quebec (Bersimis, Fort George, and St. Augustine) and a significant negative slope for one (George's River). The 15 remaining posts showed nonsignificant slopes (Table 4). No relationship was indicated at the provincial level ($p = 0.26$) for Quebec. No deviation ($\chi^2 = 3.20$, $p = 0.07$) from a 1:1 ratio of positive to negative slopes was found in Quebec (Table 4).

Linear regression: F_{red} = TEMP

A significant positive slope ($p < 0.05$) was only found for the regression of F_{red} on TEMP at God's Lake in Manitoba. No significant negative slopes were found (all $p > 0.05$), nor was a significant relationship found at the provincial level ($p > 0.05$; Table 2). Meta-analysis indicated no significant deviation from an expected 1:1 ratio of slopes ($\chi^2 = 0.08$, $p > 0.9$).

None of the 26 Ontario posts had a significant regression (all $p > 0.05$) when the relationship between F_{red} and temperature was examined (Table 3). The provincial-level analysis also failed to show a significant relationship between F_{red} and TEMP ($p > 0.05$). No significant deviation from a 1:1 ratio of the slopes was found for Ontario ($\chi^2 = 2.46$, $p = 0.14$)

Fort Rupert was the only post in Quebec that had a significant negative regression ($p < 0.05$). No other regressions were found to be significant in the province, nor was the provincial level analysis significant (all $p > 0.05$; Table 4). Meta-analysis showed that there were significantly more negative slopes than expected ($\chi^2 = 12.8$, $p < 0.001$).

Linear regression: F_{red} = LAT

The latitudinal regressions of F_{red} on TIME for MAN1 identified 2 years (1917 and 1918) out of 24 with a positive signifi-

Table 3. Results of regressions of the frequency of red-phase foxes for Ontario populations, using the variables TIME, TEMP, N_t, and N_{t-1} as main effects.

Post	TIME	TEMP	N_t	N_{t-1}
Attawapiskat	−	−	−	+
Big Trout Lake	+*	+	+*	+
Cat Lake	+*	+	+*	+*
Deer Lake	+	+	+	+
English River	−	+	+	−
Fort Albany	−	+	−	−*
Fort Hope	+*	−	+	−
Fort Severn	−	−	−	+
Gogama	−	−	−	−*
Grassy Narrows	+	+	−	−
Hudson	+*	−	+	+
Lac Seul	+	+	−*	−*
Long Lake	+*	−	+*	+
Mattice	+	+	−	+
Minaki	−	+	+	−
Missanabie	+	+	−	+
Mobert	−	−	−	−
Moose Factory	+*	+	−*	−*
Nipigon	+	+	−	−
Nipigon House	+*	−	+*	+
Ogoki	+	+	+	+
Osnaburgh	+*	+	−	−
Sioux Lookout	+*	+	+	+
Temagami	+*	+	+	−
Winisk	+	+	−	−
Num +	18	17	12	12
Num −	7	9	13	13
χ^2 (df = 1)	4.84	2.46	0.04	0.04
p	0.03	0.14	0.84	0.84

Note: The variables are discussed in the text. +, positive nonsignificant slope; −, negative nonsignificant slope; *, significant slope ($p < 0.05$); Num +, total number of positive slopes; Num −, total number of negative slopes.

cant slope ($p < 0.05$); all other slopes were nonsignificant (Table 5). When the western posts were added, creating MAN2, all slopes were nonsignificant ($p > 0.05$) except that for 1920, which had a significant positive slope. MAN3 had six significantly negative slopes ($p < 0.05$): 1915, 1918, 1922, 1923, 1928, and 1938. Including York Factory reduced the number of significant negative slopes ($p < 0.05$) to two: 1918 and 1938. When the total through time was used for each Manitoba transect, no significant slopes were found ($p > 0.05$). Meta-analysis (Table 5) indicated that MAN1 differed significantly from a 1:1 slope ratio ($\chi^2 = 5.54$, $p = 0.02$). MAN2 did not show a significant deviation from a 1:1 slope ratio ($\chi^2 = 2.46$, $p = 0.12$). MAN3 and MAN4 both showed a significant excess of negative slopes when examined by meta-analysis ($\chi^2 = 15.38$, $p = 0.0001$, and $\chi^2 = 7.54$, $p = 0.0006$, respectively).

The transect ONT had four significant negative slopes (Table 5): 1916, 1927, 1929, 1932. Other years showed no significant slopes. The summation, through time, of the transect posts failed to produce a significant slope ($p = 0.16$). Meta-analysis of the slope frequencies indicated a signifi-

Table 4. Results of regressions of the frequency of red-phase foxes for Quebec populations, using the variables TIME, TEMP, N_t, and N_{t-1} as main effects.

Post	TIME	TEMP	N_t	N_{t-1}
Bersimis	+*	−	+	+
Eastmain	+	−	−*	−**
Fort Chimo	+	−	+	−
Fort George	+*	−	+	+
Fort McKenzie	+	+	+	+
Fort Rupert	−	−*	+	−
George's River	−*	+	−	−
Great Whale River	+	−	+	−
Grand Lac	+	−	−	−
La Sarrae	+	−	−	−
Mistassiny	−	−	−	+
Nemaska	+	−	−	−
Obedjiwan	+	−	−	−*
Pointe Bleue	−**	− ,	−	−
Romaine	+	−	−	+
Senneterre	+	−	−	+
Seven Islands	+	−	−	+
St. Augustine	+*	−	+	+
Wolstenholme	−	−	−	−
Woswanaby	−	−	−**	−
Num +	14	2	8	8
Num −	6	18	12	12
χ^2 (df = 1)	4.26	12.8	0.800	0.800
p	0.074	<0.001	0.371	0.371

Note: The variables are discussed in the text. +, positive nonsignificant slope; −, negative nonsignificant slope; *, significant slope ($p < 0.05$); **, significant slope ($p < 0.01$); Num +, total number of positive slopes; Num −, total number of negative slopes.

cantly greater number of negative slopes ($\chi^2 = 9.80$, $p = 0.002$; Table 5).

Transect QUE1 showed significant negative slopes in 1916, 1917, 1926, 1928, 1932, 1934, 1935, 1939, and 1940 ($p < 0.05$). The remaining years all had nonsignificant slopes (Table 4). When the northernmost post (Wolstenholme) was included in the regression (QUE2), one significant positive slope (1921) was produced. Slopes were negative for 5 years (1925, 1933, 1938, 1939, 1940) ($p < 0.05$), and nonsignificant for the other 20 years. Neither QUE1 nor QUE2 produced a significant slope ($p = 0.33$ and $p = 0.08$, respectively) when the total for the red phenotype through time was examined. Both Quebec transects showed a deviation from the expected 1:1 slope ratio (Table 5; $\chi^2 = 18.62$, $p < 0.0001$, and $\chi^2 = 12.46$, $p = 0.0004$, respectively).

Linear regression: $F_{red} = N_t$

The regressions ($F_{red} = N_t$) in Manitoba showed that the Island Lake time series had a significant negative slope ($p < 0.05$), while Nelson House and Split Lake both showed significant positive slopes ($p < 0.05$). The 10 remaining populations exhibited nonsignificant slopes ($p > 0.05$; Table 2). Analysis of post−years for Manitoba produced a nonsignificant ($p > 0.05$) slope. Meta-analysis (Table 2) indicated a marginally significant pattern of excess positive slopes ($\chi^2 = 3.76$, $p = 0.052$).

In Ontario, the regression of F_{red} on N_t produced two significant negative slopes, Lac Seul and Moose Factory ($p < 0.05$). Four posts (Cat Lake, Long Lake, Nipigon House, and Big Trout Lake) had significant positive slopes ($p < 0.05$). Nineteen populations exhibited nonsignificant slopes (Table 3). A significant negative slope ($\beta = -0.17$, $r^2 = 0.08$, $p = 0.0001$) was found when individual post−years were used. No deviation ($\chi^2 = 0.04$, $p = 0.85$) was found from a 1:1 slope ratio (Table 3).

The regression of F_{red} on N_t in Quebec had only two significantly negative slopes (Eastmain and Woswanaby; $p < 0.05$). The remaining 18 populations exhibited nonsignificant slopes (Table 4). Analysis at the post−year level showed a significant negative slope ($\beta = -0.26$, $r^2 = 0.10$, $p = 0.0001$). However, meta-analysis indicated no deviation ($\chi^2 = 0.80$, $p = 0.37$) from the expected slope ratio (Table 4).

Linear regression: $F_{red} = N_{t-1}$

Analyzing the same data but incorporating a 1-year lag ($F_{red} = N_{t-1}$) produced similar results in Manitoba: 3 significant ($p < 0.05$) positive slopes (Nelson House, Oxford House, Pukatawagan), 1 significant ($p < 0.05$) negative slope (Island Lake), and 10 nonsignificant slopes (Table 2). A significant positive slope ($\beta = 0.36$, $r^2 = 0.13$, $p = 0.0001$) was found when the data was examined at the post−year level. A marginally significant trend was found in the slope ratio ($\chi^2 = 3.76$, $p = 0.052$), with an excess of positive slopes (Table 2).

Ontario had one significant ($p < 0.05$) positive slope (Cat Lake). Fort Albany, Gogama, Lac Seul, and Moose Factory had significant ($p < 0.05$) negative slopes. The 20 other populations produced no significant slopes (Table 3). Individual post−years yielded a significantly negative slope ($\beta = -0.17$, $r^2 = 0.08$, $p = 0.0001$). No significant trend ($\chi^2 = 0.04$, $p = 0.84$) was found in the slope ratio for Ontario (Table 3).

The regression of F_{red} against population size at time $t - 1$ (N_{t-1}) for the Quebec posts had two significant negative slopes ($p < 0.05$), Eastmain and Obijuan. The 18 remaining populations all exhibited nonsignificant slopes (Table 4). No significant pattern ($\chi^2 = 0.80$, $p = 0.37$) was found in the slope ratio (Table 4). At the post−year level, however, a significant negative slope ($\beta = -0.23$, $r^2 = 0.09$, $p = 0.0001$) was found between lagged population size and the frequency of the red phenotypes.

Discussion

None of the Manitoba transects showed consistently significant relationships between the frequency of the red phenotypes and latitude (Table 5), providing no support for the existence of strong latitudinal trends. However, meta-analysis indicated that a majority of the slopes of three transects differed significantly from the expected 1:1 ratio, suggesting a weak trend of decreasing frequency of the red phenotype with latitude. MAN2 was the only transect for which a significance trend was not found in the meta-analysis (Table 5). Several climatic variables change north of Wabowden: the growing season is reduced, the mean annual number of degree-days over 42°F is 500 fewer, and the vegetation changes from boreal forest to the subarctic forest − tundra transition zone (Department of Mines and Technical Surveys 1957). This suggests that the northwestern posts should not be included in the transect

Table 5. Summary of regression of the frequency of red-phase foxes against latitude for the transects in each province.

Year	MAN1	MAN2	MAN3	MAN4	ONT	QUE1	QUE2
1915	−	−	−*	−	nd	−	−
1916	−	−	+	+	−*	−**	+
1917	−*	−	−	−	−	−*	−
1918	+*	+	−*	−*	−	−	−
1919	−	+	−	−	+	−	−
1920	+	+*	−	−	+	−	−
1921	−	−	−	−	−	−	+*
1922	−	−	−*	−	−	−	. +
1923	−	+	−*	−*	−	−	−
1924	−	−	−	−	−	−	−
1925	+	+	−	−	−	−	−*
1926	−	−	−	−	−	−*	−
1927	+	−	−	−	−*	−	−
1928	−	−	−*	−	−	−*	−*
1929	−	− ,	−	+	−*	−	+
1930	−	−	−	−	−	−	−
1931	+	−	−	−	−	−	−
1932	−	+	+	+	−*	−*	−
1933	−	+	−	+	−	−	−*
1934	−	+	−	−	+	−*	−
1935	−	−	−	−	−	−*	−
1936	+	−	+	+	nd	+	−
1937	+	−	−	−	nd	−	−
1938	−	+	−*	−*	nd	+	−*
1939	−	−	−	−	nd	−*	−*
1940	−	−	−	−	nd	−*	−*
Num +	7	9	3	6	3	2	4
Num −	19	17	23	20	17	24	22
χ^2 (df = 1)	5.539	2.462	15.385	7.539	9.800	18.615	12.462
p	0.0186	0.1167	0.0001	0.006	0.0017	0.0001	0.004

Note: Chi-squared analysis indicates significant departure from an expected 1:1 ratio of positive to negative slopes in all cases except MAN2. nd, no data; +, positive slope; −, negative slope; *, significant slope ($p < 0.05$); **, significant slope ($p < 0.01$); Num +, total number of positive slopes; Num −, total number of negative slopes.

because of variation in climate. The overall pattern indicates that a weak relationship exists between latitude and phenotypic frequency in Manitoba, and that the pattern is stronger in the central and eastern portion of the province, as shown by the greater number of significant slopes in MAN1, MAN3, and MAN4.

Based on the low number of significant slopes in the transects ONT, QUE1, and QUE2, as well as the nonsignificant provincial analyses in all cases, no strong latitudinal trend exists in these provinces. However, meta-analysis did reveal an inverse latitudinal trend (Table 5) in all three transects.

An inverse relationship between latitude and frequency of the red phenotype supports the swamping, diffusion, and selection hypotheses. If the Canadian allele predominated in northeastern refugia, as Calhoun (1950) hypothesized, secondary contact with populations south of the ice front would establish a cline (Endler 1973). Northward progression of the red phase, mixing with southward dispersal of the black morph, would have produced a latitudinal gradient. Because secondary contact could have occurred over 7000 years ago, continued maintenance of such a cline is not expected unless selection acted to preserve the latitudinal gradient in pheno-

typic frequencies. Thus, the observed latitudinal gradient may be a residue of the postglacial mixing and (or) weak latitudinal selection (Table 1).

The lack of significant temporal regressions casts doubt on the existence of the strong temporal trends in phenotypic frequencies proposed by Haldane (1942), Cross (1941), Butler (1945, 1947, 1951), and Calhoun (1950). However, meta-analysis indicated that a majority of the slopes were positive in Manitoba (Table 2) and Ontario (Table 3) but not in Quebec (Table 4). Analysis at the provincial level further supports the hypothesis that a small increase in frequency of the red phenotype occurred through time. This argues that the phenotypic frequencies in Manitoba and Ontario could be controlled by selection, diffusion, or swamping, but rules out swamping as a mechanism in Quebec (Table 1). Additionally, the significant results with respect to time, and nonsignificant results with regard to temperature, indicate that the positive trend in F_{red} is not based on changing climate in Manitoba and Ontario. While this further supports diffusion or swamping as a factor in the changing frequencies, it does not eliminate other selective forces from consideration.

We suggest two reasons for the weak relationship of

phenotypic frequency with latitude and time. First, there is convincing evidence that the northward extension of the red fox's range coincided with the recent period of warming that began in eastern Canada about 1890 (Hersteinsson and Macdonald 1992). Because our time series began in 1915, more than two decades later, we may have evaluated fox populations with phenotypic ratios already adjusted by selection. Second, the rate of warming, and thus its effects on plant productivity and prey species, increase with latitude (Hersteinsson and Macdonald 1992). Hence, a warming trend would have less effect on phenotypic frequencies within the latitudinal range sampled here (47−57°N) than on those of colonizing populations at higher latitudes. Both points are supported by the nonsignificant relationship between temperature and phenotypic frequency (Tables 2, 3, 4).

There is conflicting evidence regarding density-dependent dispersal in red foxes. We found that each of the five colonizations of Baffin Island occurring during the period under consideration (Macpherson 1964) coincided with a peak in harvest in Quebec ($\chi^2 = 20$, $p < 0.001$). This suggests that population pressures are associated with dispersal. Other researchers, however, found either no relationship between population size and dispersal probability (Allen and Sargeant 1993) or that dispersal distance is inversely related to density (Lloyd 1980; Harris 1981; Trewhella et al. 1988). None of these studies examined colonization events, however, so it is possible that different mechanisms drive dispersal and colonization.

Meta-analysis revealed no significant relationship between frequency of the red phenotype and harvest in Ontario (Table 3) and Quebec (Table 4), although phenotypic frequency in Manitoba was marginally significant for both N_t and N_{t-1} (Table 2), refuting Butler's (1947) hypothesis of a positive relationship between phenotypic composition and population size. The negative slopes for the provincial analysis in Ontario and Quebec suggest that the opposite may be true: the frequency of the red phenotype decreases as harvest size increases. We conclude that swamping was not a determining factor in producing the observed phenotypic ratios in Ontario and Quebec (Table 1), and probably not in Manitoba.

These results argue against any strong trends, or selective forces, altering phenotypic frequencies of the red fox in relation to time, latitude, or population size, although there are weak patterns in phenotypic frequency with respect to time and latitude. We suggest that both mechanisms, selection and diffusion, are necessary to produce the observed results. The significant relationship between time and phenotypic frequency suggests passive northward diffusion dispersal of the red phase from the more densely populated southern areas in Manitoba and Ontario. The Quebec population failed to show a similar relationship, a circumstance expected if this population has reached a stable equilibrium since the glacial retreat. The Quebec population would be the first one expected to reach equilibrium, since this was the first area in which contact between refugial populations was established (Dyke and Prest 1987). The significant latitudinal relationship in all three provinces, however, suggests the occurrence of weak selection. This leads us to posit that both mechanisms (diffusion and selection) influenced the populations in Ontario and Manitoba, while selection alone produced the latitudinal trend in Quebec during this time period.

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