

Breeding dispersions and site fidelity of American redstarts (*Setophaga ruticilla*)

R.E. Lemon, S. Perreault, and G.A. Lozano

Abstract: We relate features of the breeding dispersions and site fidelity of American redstarts (*Setophaga ruticilla*) to breeding success and interpret the findings in terms of sexual selection. One-year-old male redstarts show delayed plumage maturation, making male dispersions particularly easy to appreciate. In our study site in New Brunswick, Canada, older males usually arrived early each breeding season and gathered in contiguous territories or neighborhoods, while subadult males arrived later and settled peripherally to the adults. Subadult males constituted about 40% of the male population, on average, yet only 5% of banded nestlings returned to the natal breeding ground. Also, newly adult males, 2 years old or more, constituted about 15% of all males. Nearly 50% of adult males returned, twice the return rate of subadults. Among returns, older males returned more often to the same territory than did those that were subadult the previous year. Regardless of age, returns of males in a subsequent year were predicted more by the duration of their stay on the breeding territory than reproductive success. Males outnumbered females. Females returned less often than their mates, but more often if they had fledged young. Females rarely returned to the same mate or territory, but often returned to the same vicinity. The subadult males seem to represent a special dispersive phase of the life history. The evidence indicates strong competition among males for territories and females, older males being more often successful in both circumstances.

Résumé : Nous examinons ici les relations entre les caractéristiques de la dispersion et de la fidélité au site et le succès de la reproduction chez la Paruline flamboyante (*Setophaga ruticilla*) et nous examinons les résultats en fonction de la sélection sexuelle. La maturation du plumage est tardive chez les mâles de 1 an, ce qui facilite l'observation de la dispersion chez les mâles. Dans notre zone d'étude, au Nouveau-Brunswick, Canada, les mâles plus âgés arrivaient ordinairement tôt à chaque saison de reproduction et se réunissaient dans des territoires ou voisinages contigus, alors que les mâles sub-adultes plus jeunes arrivaient plus tard et s'installaient en périphérie. Les mâles sub-adultes constituaient environ 40% de la population de mâles en moyenne et pourtant, seulement 5% des oisillons bagués revenaient à leur territoire natal. De plus, les nouveaux mâles adultes, de 2 ans ou plus, ne constituaient qu'environ 15% de la population totale de mâles. Près de 50% des adultes revenaient dans la zone de reproduction, deux fois le taux de retour des sub-adultes. Parmi les individus qui revenaient, les mâles adultes revenaient plus souvent au même territoire que les mâles encore sub-adultes l'année précédente. Indépendamment de l'âge, les retours de mâles une année subséquente étaient reliés à la durée de leur séjour en territoire de reproduction qu'à leur succès reproducteur. Les mâles étaient plus nombreux que les femelles. Les femelles revenaient moins souvent au territoire de reproduction que les mâles, mais elles le faisaient plus souvent si elles avaient réussi à rendre leurs oisillons au stade de l'envol. Les femelles revenaient rarement au même partenaire ou au même territoire, mais souvent elles revenaient dans le même voisinage. Le stade sub-adulte chez les mâles semble représenter une phase de dispersion spéciale au cours de la vie. Il semble y avoir une forte compétition chez les mâles pour l'obtention d'un territoire et d'une partenaire; dans les deux cas, ce sont les mâles plus âgés qui ont la plus haute fréquence de réussite.

[Traduit par la Rédaction]

Introduction

Animals often gather in certain geographic areas to facilitate mating and the rearing of young. The spatial patterns, or dispersions, of the potentially breeding individuals are usually nonrandom because of influences from a number of factors, including the distribution and abundance of primary resources such as food, water, and shelter, and competition among individuals for these resources or among themselves as reproductive partners (Baker 1978; Shields 1982; Ford 1989;

Johnson and Gaines 1990; Payne and Payne 1993). Movements between different potential breeding sites are called dispersals: those to the first breeding site are natal dispersals, while later movements between sites are breeding dispersals (Greenwood and Harvey 1982). The tendency to return to the natal or breeding ground is termed site fidelity or philopatry.

The pattern of settlement on the breeding ground and dispersal to and from it are two parts of a common quest, namely reproductive success. So whether to stay and breed at a site or to move on in search of another involves weighing potential costs, present or future (Greenwood 1980; Payne and Payne 1993). Among birds it is common to find that dispersal occurs more often in younger individuals, before investment in acquisition and protection of resources becomes heavy.

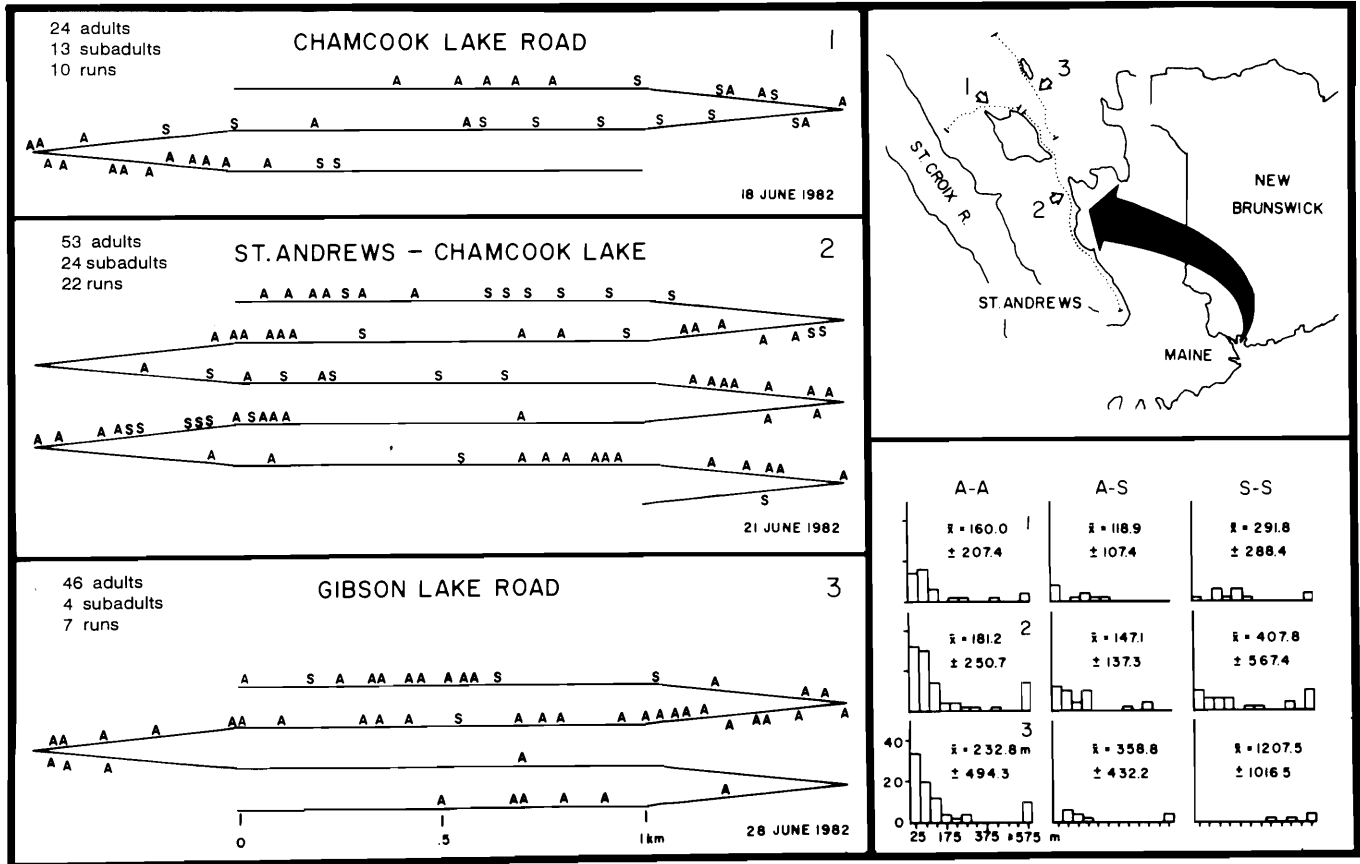
For most migratory passerine birds in north-temperate zones, the breeding grounds incorporate territories defended

Received July 19, 1995. Accepted July 29, 1996.

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Fig. 1. Distributions of male American redstarts of two age-classes (A, adult; S, subadult) on three linear transects near St. Andrews, New Brunswick. The location of each sample is shown on the map, but the details are presented as if each sample were a folded line. Distances to nearest neighbors (mean \pm standard deviation are shown at the lower right).



by individual males, advertised through song, and most often with a single resident female (Lack 1968). In certain species, younger subadult males (= yearling, 1 year old, or second year (SY)) are separated from older adults (= after second year (ASY)) (Hill 1989), as shown by age-related differences in plumage (Rohwer et al. 1980; Lyon and Montgomerie 1986). American redstarts (*Setophaga ruticilla*) show such plumages, and several authors have claimed that different habitats are selected by adult and subadult males (Ficken and Ficken 1967; Howe 1974; Morris and Lemon 1988b; Sherry and Holmes 1988).

As noted, hypotheses concerning dispersal tend to weigh the potential costs and benefits from settlement or dispersion. In this paper we relate details of breeding dispersions of American redstarts and their annual returns to reproductive success. We consider especially the differences among males of different ages, particularly subadult and adult, but also the differences between sexes. We present a simple qualitative model of these aspects in terms of sexual selection.

Methods

We studied American redstarts between 1980 and 1990 at or near St. Andrews, New Brunswick, Canada. To illustrate the local separation of males we used two sets of data. One was based on male locations as determined in three linear transects outside St. Andrews (Fig. 1). In all three transects, males were located by playing tape-recorded songs from a Uher 4000 tape recorder. Two of the tran-

sects were along public roads and locations were recorded relative to the distance determined on a vehicle's odometer. The third sample was along an abandoned railroad, where distance was measured by counting steel rails, each 33 ft (1 ft = 0.3048 m) long. The forests were more continuous than, but otherwise similar to, that at St. Andrews (see below).

The remaining data were obtained from the main study site in St. Andrews, an area of roughly 1 \times 1.5 km bounded in the west by the Huntsman Marine Sciences Centre and in the east by the properties of the Sunbury Shores Arts and Nature Centre. The habitat is patchy, located in a semi-suburban area, and includes a large golf course. The dominant vegetation is a mixture of second-growth conifers (spruce, *Picea* sp.; balsam fir, *Abies* sp.) and hardwoods (maple, *Acer* sp.; birch, *Betula* sp.). Additional details of the study area are given in Morris and Lemon (1988a, 1988b). The two sites at St. Andrews had different geographic perspectives and some extensive differences in floristic detail. The Huntsman site faced west along the St. Croix River and so was often exposed to cold northwesterly winds; from the standpoint of a human observer it was geographically conspicuous. The Sunbury Shores area faced south and was more protected from winds.

Each year the first male was seen on or about 15 May. Mist-netted individuals were marked with three colored plastic bands and a numbered U.S. Fish and Wildlife aluminum band. Using playback of territorial redstart songs, we estimated that we captured over 90% of all males, and percentages of adult males caught were even higher. Males that remained for less than 1 week, especially subadults, were sometimes not captured. Also, a few males escaped from nets and were never captured. Females were captured near nests, and numbered only about 25% of captured males.

Table 1. Clustering of male American redstarts by age-class in 2 years in the Huntsman area, St. Andrews, N.B., as shown by the frequency of nearest neighbors.

Year	A-A	A-S	S-A	S-S	<i>P</i>
1982	12	2	4	12	0.001
1984	10	1	2	5	0.013

Note: In each pair of letters, the first is the age-class of the subject and the second that of his nearest neighbor (A = adult; S = subadult.). *P* values are based on Fisher exact tests, two-tailed.

At St. Andrews, the main study areas were visited at least 3 times weekly. We plotted the locations of the males' territories on maps in order to examine the dispersions and returns and movements from year to year. Territory centers were the geographic centers of the plots. If a male's territory in a subsequent year was either the same or overlapped that of the previous season by 50%, we scored it as the same territory. Otherwise we scored the event as a move to a more distant territory. Real distances moved were measured from the maps, from territory center to territory center.

Reproductive data

We did not have complete data for all years because of competing interests. For total counts of males by age-class we used data from 1982 through 1989. In 1987 we collected eight males, so we did not calculate returns from that year. For reproductive data of males, we confined ourselves to 4 years, 1982, 1984, 1987, 1988. These were years when we actively searched for nests for all males. Because we had fewer banded females from which to garner data, the periods of data collection were somewhat different from those for males, being from 1981 to 1984 and 1988. For the 3 years for which we had the date when males were last seen, the dates sometimes coincided with the departure dates of the observers, 26 July in 1982 and 1984 and 11 July 1988. If they had young, redstarts often deserted their territories, apparently in search of food. In 1982 we put much effort into finding nests late in July, anticipating possible second broods, but found none.

In earlier analyses (Morris and Lemon 1988b; Lemon et al. 1992), we emphasized the success of nests. Because of predation and re-nesting, such an emphasis can give a biased view of the success of individual birds. Here, instead, we used two categorical estimates to calculate male success. The first was simply whether a female was seen in the male's territory. We designated this circumstance as a pairing, although we often had no evidence of any actual sexual relationship between a male and female. Neither the presence of a nest nor its ultimate success affected this particular estimate.

The second and more meaningful measure of success was whether young were actually fledged from a territory, regardless of the number of nests located there. In a few instances we scored as successful cases where nests were not found but where young were observed with the territory owners. Neither measure determined whether the young had actually been sired by the apparent owner.

Results

Dispersions of males by age-class

Male American redstarts often separated their breeding territories by age-class, adult and subadult. This is seen most clearly in two of three linear transects near St. Andrews (Fig. 1). In transects 1 and 2, there were significantly fewer alternating strings of adult and subadult males than expected by chance (Wald-Wolfowitz runs test: route 1, $z = 2.70$,

Table 2. Fledging success of American redstart males that nested in the Huntsman (HMSC) and Sunbury Shores (SS) areas in 1982–1984 and 1987–1988.

	HMSC		SS	
	Fledged young	Did not fledge young	Fledged young	Did not fledge young
1982–1984	15	20	20	22
1987–1988	1	9	5	15

$P = 0.0034$; route 2, $z = 2.69$, $P = 0.0036$). These estimates of significance are conservative, having been corrected for continuity, in spite of reasonable sample sizes (Siegel 1956). Distances between nearest subadult neighbors were usually much greater than between nearest adult neighbors (Fig. 1). Adult males were usually closer nearest neighbors than were subadults. The third sample failed to yield significance because it contained too few subadults.

Similar separations of males occurred at St. Andrews, especially in certain areas and years (Fig. 2). In 9 years, the Sunbury Shores area always had a preponderance of adult males, but in the Huntsman area this occurred in only 4 years, the difference between the two sites being significant (Fisher exact test, two-tailed, $P = 0.029$). The difference between the two areas was particularly striking in 1988. Within the Huntsman area during 1982 and 1984, the separation by age-class was also evident from the distributions of nearest neighbors (Table 1).

Significant floristic differences have been described for the Huntsman and Sunbury Shores areas (Morris and Lemon 1988b), therefore it seemed possible that older males selected areas guaranteeing higher reproductive success. However, we found no significant differences in fledging success of birds that nested in the two areas (Table 2). Because fledging success of males by age-class in 1982–1984 was much higher than in 1987–1988 (Fisher exact test, two-tailed, $P = 0.016$), we treated the data for each pair of years separately (1982–1984, $P = 0.82$; 1987–1988, $P = 0.64$).

Composition and recruitment of the male breeding population

As Figs. 1 and 2 show, dispersions of males by age can be influenced by features of recruitment and population size. The population of males at St. Andrews declined significantly from the peak years of 1982 and 1984 to 1989 (Spearman $r_s = -0.95$, $P < 0.01$) (Fig. 3). The declines applied both to males returning from a previous year and to newly recruited males. There were more recruits than returns in every year.

Male recruits to the study area were of three types: (1) subadults that had hatched in the same area the previous year; (2) subadults that had hatched elsewhere; and (3) adult males aged 2 or more years not previously resident in the area. Members of group 1 were relatively few (see "Returns of nestlings" below) and had little impact on totals. Subadults were otherwise the most common group of males in 7 of 8 years, constituting roughly 20–50% of all males (Fig. 4); returning adult males, 3 years old or more, ranked first once and second 5 times in 8 years. Among adult males (Fig. 5), new adults ranked second 3 times and third 4 times.

Fig. 2. Dispersions of male American redstarts in 4 years at the Huntsman (HMSC) and Sunbury Shores (SS) sites at St. Andrews. Symbols represent approximate territorial centers held by males.

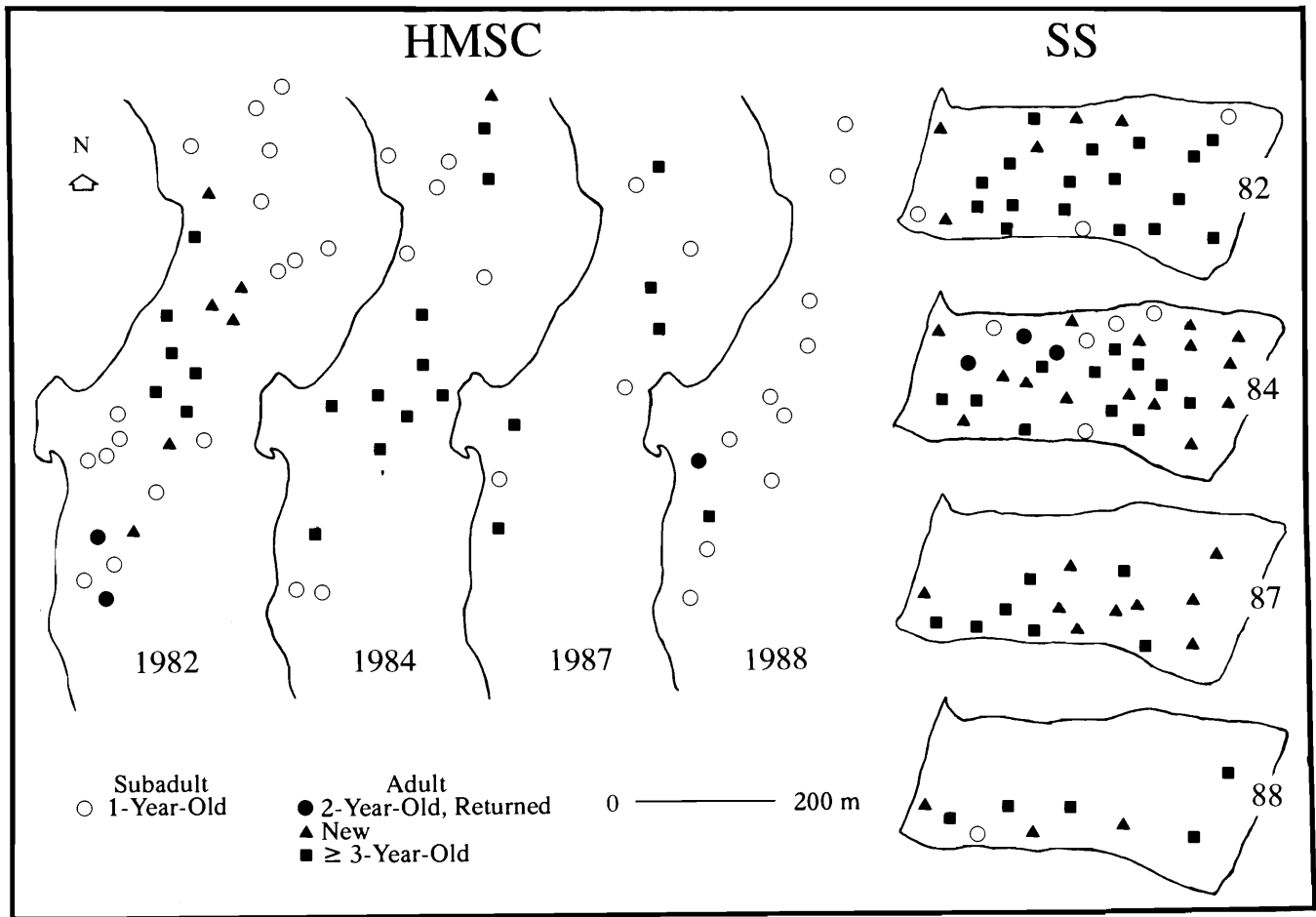


Fig. 3. Total population of potentially breeding male American redstarts at St. Andrews between 1982 and 1989, divided into returned and recruited males.

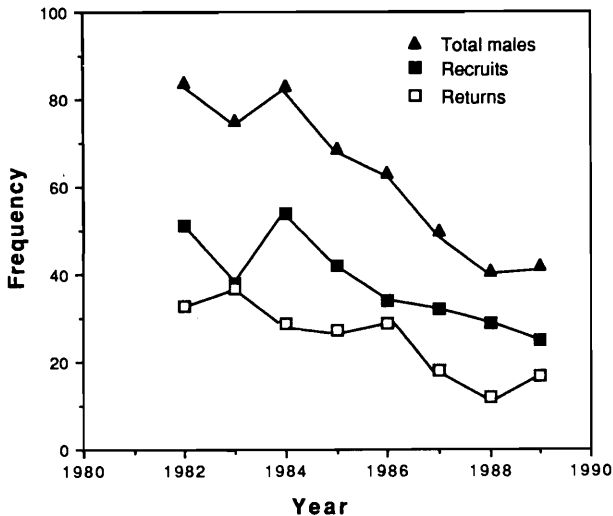
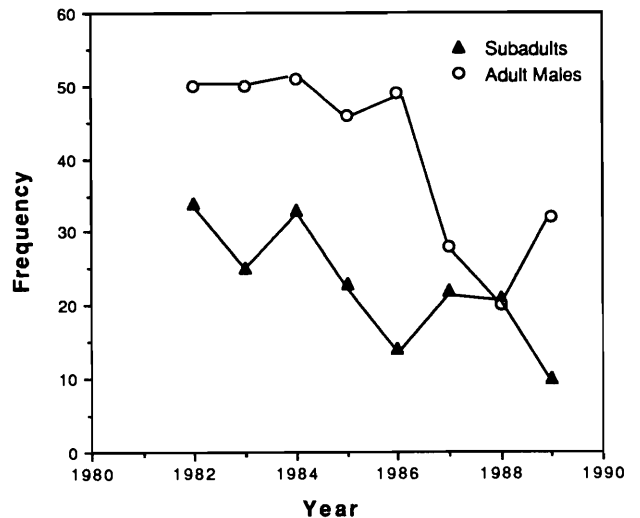


Fig. 4. Numbers of adult and subadult male American redstarts on the study site at St. Andrews between 1982 and 1989. Subadults were 1 year old; adults were 2 years old or more.



Although varying considerably, annual returns from one year to the next were generally much lower for subadult males (26%) than for adults (44%) (Wilcoxon $T = 2.03$,

$P = 0.042$, one-tailed) (Fig. 6). Similarly, pooled returns of adult males between 1981 and 1988 were significantly higher than those of subadults (Fisher exact test, two-tailed, $P =$

Fig. 5. Breakdown of the adult male population shown in Fig. 4. New adults were new to the study area; returned adults had been present the year before as adults; returned ex-subadults had been present as subadults the year before.

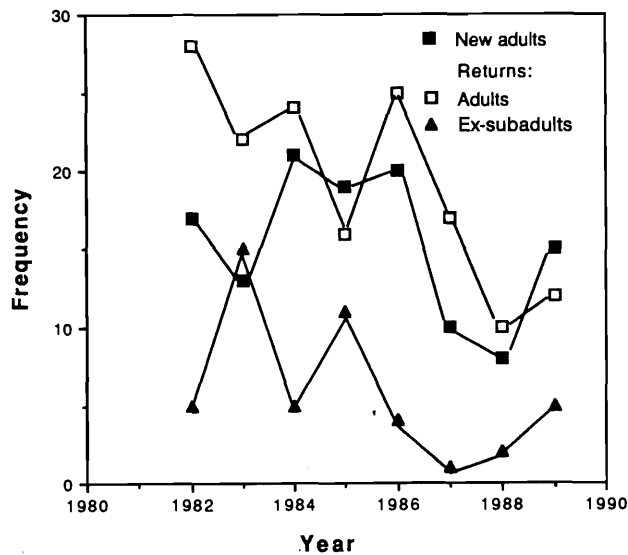
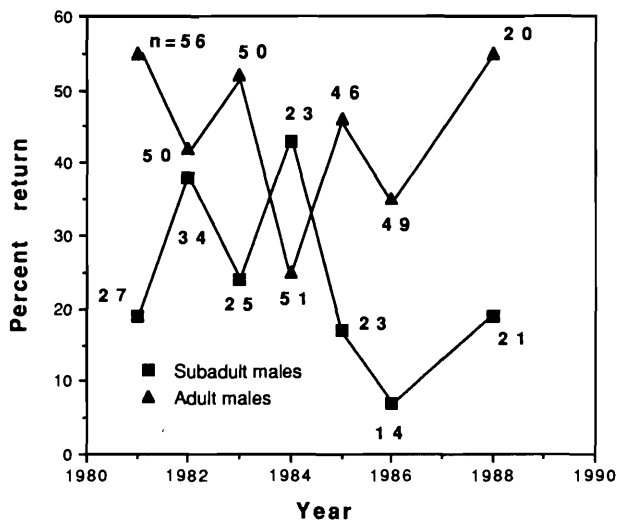


Fig. 6. Relative returns of subadult and adult male American redstarts to the breeding ground at St. Andrews from one year to the next. Data are percentages of returns from the year preceding the return, based on samples of the stated sizes (*n*).

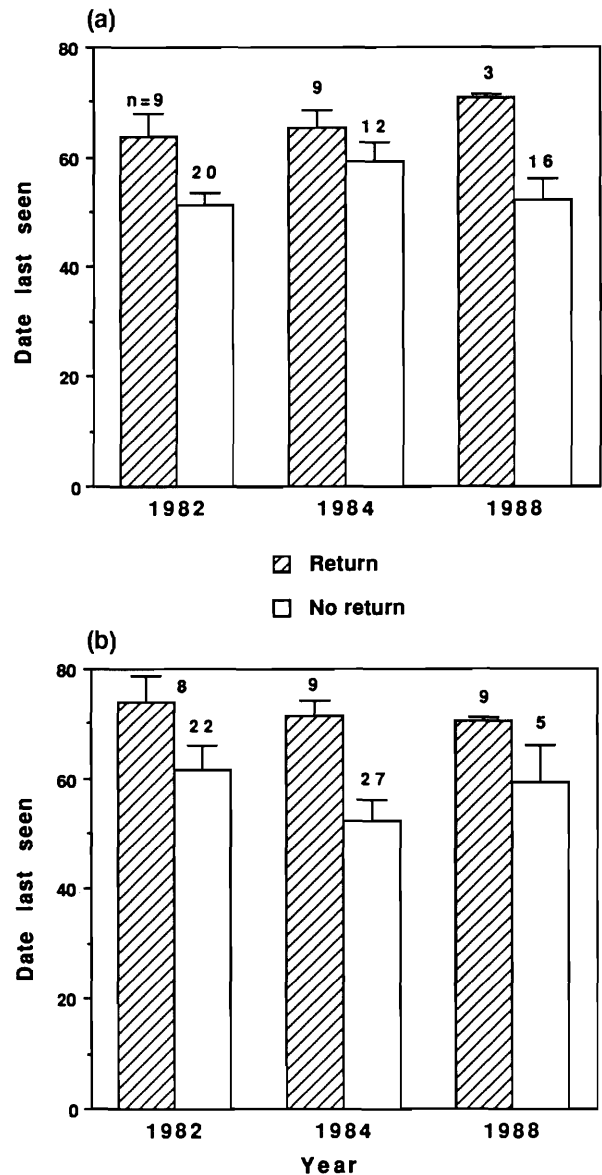


0.00018). From 1981 through 1985, relatively high and low returns of adults alternated with opposing low and high returns of subadults (Fig. 6). New and older adults returned in the same proportions. No males were seen after an intervening year of apparent absence.

Predicting annual returns of males

Separating the males by age-class, we examined whether success in attracting a female or fledging of young were predictors of return (Table 3). Only fledging by adult males in 1982 predicted a subsequent return (Fisher exact probability test, two-tailed, $P = 0.0097$).

Fig. 7. Dates last seen (mean + SE) for subadult (a) and adult males (b) that returned or did not return the subsequent year.



Instead, date last seen on the breeding ground was a better predictor of return to the same area by both yearling and adult males in the 3 years for which we had data (Table 4). Those that were seen later were more likely to return (Fig. 7). On average, subadult males were last seen earlier than were adults in 1982, but otherwise not. We had no estimate of mortality by age, but most disappearances of males were either soon after arrival, especially for subadults, or in mid-July. So we assume mortality to have been almost negligible while the birds were in our area.

Between-year territorial changes made by returning males

Subadult and adult males often separated by age, and the areas used one year by each age group were often reused by the same age group the following season. Therefore, one might predict that among males returning to the same breeding ground, former subadult males should move to new terri-

Table 3. Numbers of returning male American redstarts from the stated year to the next, depending on whether they had mated or fledged young.

	Returned				Not returned			
	Mated	Not mated	Fledged young	Did not fledge young	Mated	Not mated	Fledged young	Did not fledge young
Adults								
1982	19	2	13	8	24	5	7	22
1984	10	3	4	9	29	9	11	27
1988	11	0	2	9	9	0	4	5
Subadults								
1982	8	5	3	10	10	12	2	20
1984	6	3	1	8	8	5	1	12
1988	3	1	1	3	9	8	1	16

Note: Only for "adults, 1982, fledged young" was the return of more birds significantly predicted.

Table 4. Summary of a Type III sum of squares analysis of covariance of male age (subadult or adult) and date last seen as predictors of return the following season (see Fig. 6).

Year	Effect	df	F	P
1982	Age	1	1.66	0.212
	Date last seen	1	21.48	0.0001
	Age × date	1	2.53	0.115
1984	Age	1	0.859	0.859
	Date last seen	1	3.87	0.053
	Age × date	1	0.24	0.626
1988	Age	1	0.07	0.786
	Date last seen	1	5.38	0.0259
	Age × date	1	0.28	0.599

teries to join established groups of adult males. To test these predictions, we scored males in two groups: those that returned to the same territory or one contiguous with it, and those that settled on a more distant territory. Because the number of returns was relatively small, especially of subadults, we combined the data from 3 years.

Males that were subadults the previous season returned significantly less often to their previous territory than did males already adult (15 former subadults returned and 11 settled farther away; 39 adults returned and 6 settled farther away) (Fisher exact test, two-tailed, $P = 0.009$). Even so, over half the former subadults returned to the previously held territory or to an adjacent one. In both age groups, no measure of reproductive success was a significant predictor of territory change. Even the rare adult moves sometimes followed successful seasons. We found no differences in frequencies of return to the different areas of our study site.

Another appropriate measure of change in location is simply the distance between territory centers from one year to the next. Such data can be related to the Poisson distribution to assess whether the second territory was selected independently of the first. Annual returns were so treated for subadult and adult males between 1980 and 1989, excluding 1987 (Fig. 8). The shortest interval, 0–50 m, includes most

returns to the same territory. The poor fit to the Poisson distribution resulted from too many males returning to the territory of the previous season. A few males may have returned to areas adjacent to the prime study areas or at much greater distances. We banded birds at two sites 1.5 and 3 km from the study area but found no birds previously banded at either.

Returns of nestlings

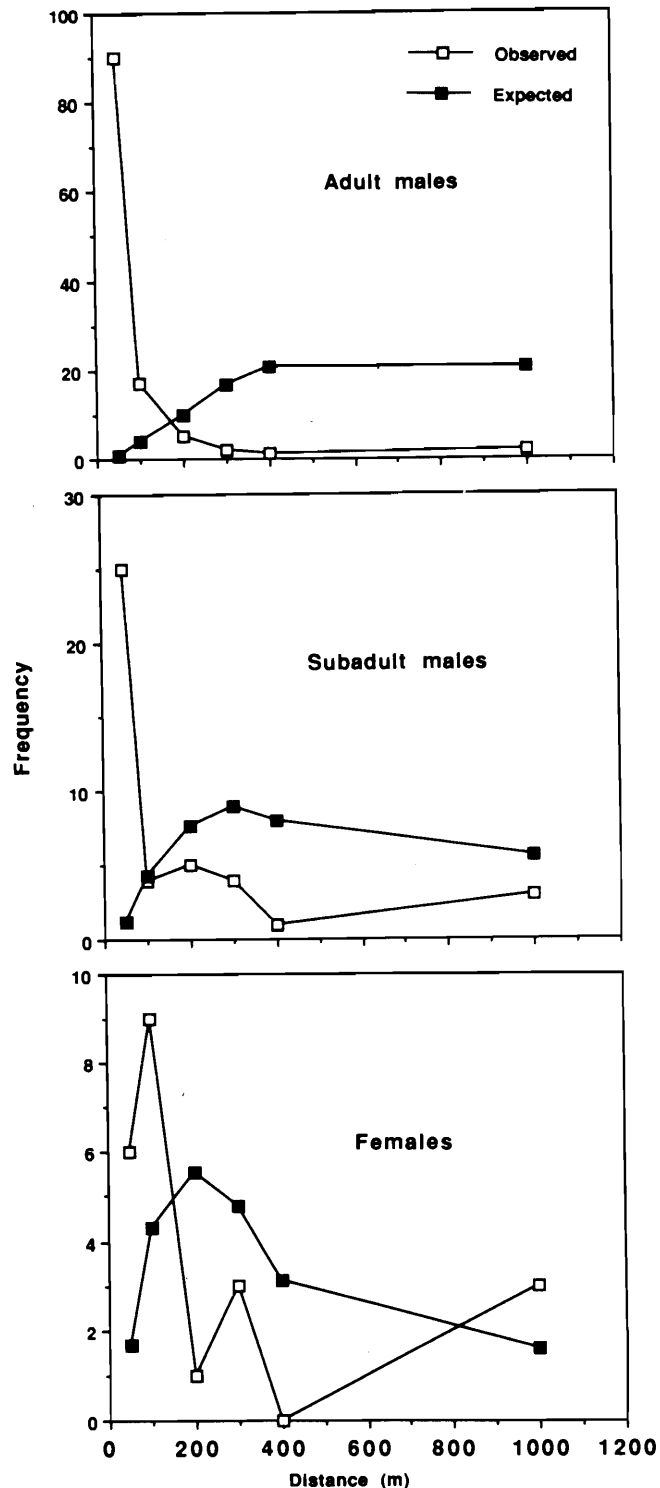
Of 172 nestlings banded between 1980 and 1988, nine (5%) returned to the study site, 5 males and 4 females. Two banded yearling males could not be caught and may have been additional to those mentioned. Of the five males, three stayed briefly as subadults and were not seen again, while two had mates on territories 0.5 km from their natal nests. Three females resided approximately 300 m from their natal nests; none paired with a father.

Returns of adult females

From 1980 to 1988, we banded 112 adult females in territories of identified males. Of these, 16 returned in one or more immediately succeeding seasons, yielding a total of 24 actual returns, or only 24 of 119 (21%) possible returns. One female was noted to return 4 times, 4 twice, and 11 only once. Of the 24 female returns, 22 were assigned to known males. Of these 22 females, 5 returned to the same territory, 8 to a contiguous territory, and 3 to no farther than two territories from the original. So 16 females (73%) returned to the immediate vicinity of the first territory or actually to it. Six females moved between 400 m and 1 km from the original territory (Fig. 8). One female nested as an apparently bigamous mate of adult male 541 in 1981. She subsequently nested with four different males, three of which were adults; the first two nests were on successively contiguous but different territories. In her fourth year she moved 400 m to pair with a subadult, only to return in the fifth year to her original territory. We recorded successful broods in her first 2 years only.

The breeding success of females was a strong predictor of their return to the study site: of females that fledged young, 16 returned and 36 did not; after failing to fledge, 8 returned and 59 did not (Fisher exact test, two-tailed, $P = 0.020$).

Fig. 8. Comparison of the actual distances moved from the original territory in one year to a territory in the following year, and those expected by chance in the Poisson distribution. Results are from two age-classes of males and from females. Distances less than 50 m were usually to the same territory or to one contiguous with it.



The annual samples were small, so for this analysis data from all years were combined. We could not meaningfully record dates when females were last seen, as was done with males.

Females returned significantly less often than their mates.

Adult male mates yielded 32 returns and 58 nonreturns (36%), whereas their female mates yielded 19 returns versus 71 nonreturns (21%) (Fisher exact test, two-tailed, $P = 0.047$). Of subadult male mates, 14 returned (51%) and 13 did not, whereas 4 of their female mates returned (15%) and 23 did not ($P = 0.008$). The returns of the two age groups of males in this data set were not significantly different ($P = 0.177$), nor were returns of their respective female mates ($P = 0.588$). The probability of both members of a pair returning to the same breeding ground was 0.08. Therefore, returns to the same territory were even less probable. There were only eight occasions when both mates from the previous season returned, and on only two of these did they remate; both rematings involved male 225 and female 330 in 1984 and 1985 on the same territory. The female had mated with a different male previously on a contiguous territory.

The movements of returning females fitted the Poisson distribution better than did those of males (Fig. 8). Although some females returned to the original territory or its vicinity, the settlement pattern was closer to random.

Discussion

Dispersions of males

The dispersions of the males were clearly nonrandom, which is consistent with claims made elsewhere (see the Introduction). Later arrival of the younger males is important in separating them from older ones (Morris and Lemon 1988b). There may also be some direct exclusion of younger males by the older ones (Sherry and Holmes 1989). Yearlings are often found in the absence of adult neighbors, suggesting that they may not recognize suitable habitat. Male separation by age associated with delayed plumage maturation occurs on breeding sites of other North American passerines, where it also correlates with later arrival of subadult males (Lyon and Montgomerie 1986; Hill 1989). In contrast, yearling male indigo buntings (*Passerina cyanea*) arrive with the adults and settle among them (Payne 1991).

The dispersion patterns are influenced by population dynamics. In our study area, the population of redstarts declined dramatically after 1984, correlating with a local decline in reproductive success. Similar corresponding declines were noted in the same 10-year period in New Hampshire, 375 km to the west of our site (Holmes and Sherry 1992; Sherry and Holmes 1992). There the annual return rates for males were somewhat lower, 38% for adults and only 16% for subadults. Males that fledged young returned somewhat more often than those that were not successful, but not significantly so. Those authors argue that the decline in the population of redstarts reflects a failure to recruit young males, in contrast to black-throated blue warblers, *Dendroica caerulescens*, which at the same time had high reproductive success and maintained the population (Holmes and Sherry 1992; Holmes et al. 1992). Based on this reasoning, Sherry and Holmes (1992) predicted a positive correlation between yearling recruitment and total year-to-year differences in male redstart populations. They found a positive but nonsignificant correlation ($r = +0.56$, $P > 0.05$, 7 df). The same calculation from our data yields a nonsignificant negative result ($r = -0.33$, $P > 0.05$, 6 df). By 1995 and 1996, our population showed evidence of increase, in some sites at least.

Evidence from many species shows that fragmentation of the forests may enhance predation (Robinson et al. 1995).

Table 5. Sex ratios of American redstarts at St. Andrews, based on data from Lozano et al. (1996).

Year	Sex ratio	Total males/females	Sex ratio	Total females/adult males
1982	1.37	85/62	1.24	62/50
1984	1.40	74/53	1.04	53/51
1987	1.41	54/32	1.14	32/28
1988	1.28	41/32	1.60	32/20

Note: The number of females was estimated from the number of males on whose territories females had been seen.

Forests in our study area were fragmented and were typified by high nest predation. Forests in Maine, quite near St. Andrews, however, are not as fragmented. Since most recruits to our site come from outside, low recruitment seemingly reflects widespread poor nesting success. If this is not the case, then other factors may be involved, such as high mortality on the wintering ground. Incidentally, parasitic brown-headed cowbirds, *Molothrus ater*, so important in harming reproduction of many small passerines, were inconsequential in our area because of their scarcity.

Conceivably the neighborhoods of males could reflect kinship. At high densities there was evidence that neighboring redstarts had similar songs (Shackell et al. 1988), but the similarities are assumed to result either from copying (Lemon et al. 1994) or from selection of neighbors with similar songs. We did not determine the genetic relatedness among our redstarts, but there are several indications that outbreeding is dominant, rather than kinship. (i) Returns of banded nestlings were only 5%, roughly comparable to the 10% returns of certain other passerines (Nolan 1978; Payne 1991). (ii) No banded nestlings were observed breeding with parents or close relatives. (iii) Total recruitment of males each year was usually over 60%. The largest age-class of males, 1-year-olds, often comprised over 50% of the male population. On the basis of low returns from this age-class, we assume that most of the new adults were 2 years old, having been subadults elsewhere the year previous to their appearance in our area. This argument assumes that mortality rates of adult and yearling males are similar. (iv) Only one-quarter of the 1-year-old males returned as 2-year-olds, a return rate half that of older males, suggesting that as many young males continue to disperse well into their second potential breeding season, assuming no differential mortality by age. This blurs the usual distinction (Greenwood 1980) between "natal" dispersion up to the first breeding season and "breeding" dispersal thereafter.

Only half the number of subadult males returned to the same breeding ground as did adult males; and only half of those that did so regained the territory used in the first year, where their neighbors more often had been subadult males. Those that moved settled among adult males, thereby maintaining an existing adult male neighborhood. These neighborhoods apparently last many years, perhaps as long as habitat quality remains high and the general population large. Success at fledging young may have promoted return, but did not seem overly important at St. Andrews. The fact that date last seen was a better predictor of return for males suggests that the decision to return to the same site is made during the breeding season prior to the following spring migration. The same prediction says also that even some adult males

are willing to disperse again in certain circumstances. We have no estimate of the effects of mortality on the results. We have noted a very few returning individuals who were seen for only a few days, so possibly they continued to move on, or died.

The results suggest that subadult male redstarts represent a dispersive phase of the life history (Root 1962; Ficken and Ficken 1967) during which the aim is to find new habitats and new breeding neighborhoods (see also Greenwood and Harvey 1982; Holmes and Sherry 1992). Yet there is a balance between the tendencies to maintain old neighborhoods on the one hand and to develop new ones on the other. These competing tendencies would be especially important if redstarts exploited highly productive but transient habitats (Studd and Robertson 1985).

The foregoing interpretation emphasizes the competition among males on the basis of primary resources of habitat. Associated also is evidence of strong female selection on males by age. A number of aspects support this interpretation. Females were less common on the breeding ground than males. The biased sex ratio could reflect differences in mortality, with females possibly suffering more during reproduction from predation or other causes. On the wintering ground, all individuals hold separate territories. Members of the two male age-classes may compete equally well (Marra et al. 1993), but appear to dominate females. In Jamaica, male redstarts exploit mangroves whereas females exploit brush, possibly leading to higher mortality among the latter (Marra et al. 1993; Parrish and Sherry 1994). Alternatively, the biased sex ratio could have different bases, genetic or otherwise (Gowaty 1991). Since the heterogametic female birds determine the sex of their offspring, female redstarts might bias production in favor of sons to offset the high cost of dispersal.

Because of the sex ratio, later arriving subadult males often fail to gain mates. If they do gain mates, their reproduction can be less successful, perhaps because of lower quality of the habitat or even of the mate (Lozano et al. 1996). Subadult males appear to be as good as adult males at parenting (Omland and Sherry 1994). The plumage features of adult males can also correlate with reproductive success and with earlier selection by females (Lemon et al. 1992). Subadults and adults show similar agonistic behaviors (Procter-Gray and Holmes 1981), and adults respond strongly to models of each age group (Procter-Gray 1991). Some males are polygynous and even hold satellite territories (Secunda and Sherry 1991). We were not able to age females reliably (Spellman et al. 1987), but some evinced poor choice of nest sites and others lack of expertise in nest construction.

Parentage studies using DNA finger-printing techniques

showed that more than half the offspring on our site were sired by males other than the putative fathers, the territory holders (Perreault et al.).² Neighbors were often the true fathers. Importantly, however, all males new to the area, subadults and even adults, were cuckolded more heavily than returning older adults. Possibly involved in cuckoldry is the practice of sperm storage, of which female redstarts are capable (Briskie and Montgomerie 1993).

In summary, the two sexes of American redstarts have quite different strategies of dispersion. The females aim primarily at immediate reproductive success. They do so by finding males with territories. Once paired (or sometimes sharing a polygynous mate), they have the additional choice of selecting the male that will sire their offspring. Should reproduction succeed, females will often choose to return to the same area, but most often to a new territory and a new mate. Even so, females return less often than do their mates because of further dispersal or mortality.

Males have a different proximal strategy, although having the same ultimate goal of reproductive success. Their initial aim is to find a territory sufficiently good in quality and location to attract a female. In doing so, younger males have several points against them, some involving costs of search while others are social. It takes time to find acceptable breeding sites. For many males the easiest way to locate such sites may be to listen for other singing males (e.g., Mountjoy and Lemon 1991). The later arrival of yearling males may seem at first a disadvantage but in reality may reduce costs associated with searching for and acquiring breeding sites. Delayed plumage maturation may also reduce both these costs, but other warblers show bimodal arrival times probably associated with age (Francis and Cooke 1987) and still do not exhibit greatly delayed plumage maturation.

So the dispersions and movements of males seem to a great extent to be determined by strong sexual selection, both direct and indirect.

Acknowledgments

We thank the staff of the Huntsman Marine Sciences Centre for their hospitality. Many persons helped in this research, and we have thanked them before. Especially helpful in gathering data were R. MacNally, M. Morris, S. Monette, R. Cotter, N. Shackell, L. Date, and D. Weary. We also thank R. Precziosi and H. Tyson for their statistical advice. This work was supported by grants to R.E.L. from the Natural Sciences and Engineering Research Council of Canada.

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