Dispersal of Dunlin *Calidris alpina* in relation to sites of birth and breeding

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Movements from the site of birth to the first breeding site and movements between successive breeding sites are the two ways leading to the dispersion of birds. Dispersal, the process leading to dispersion, promotes the flow of gene material between different parts of a population as well as the occupation of new breeding grounds in a constantly changing environment. An extreme, though very common, case of dispersal occurs when the extent of a movement is very short or zero; a bird then shows site-tenacity or *ortstreue*. Site-tenacity, on the other hand, promotes keeping animals to that very habitat to which they have adapted by genetic variation and natural selection. Knowledge of the dispersal rate thus is fundamental for understanding many phenomena of population dynamics and evolution.

The aim of this paper is to present data on the dispersal of the Dunlin *Calidris alpina schinzii* as revealed by a long-term study of individually marked birds. In an earlier paper of mine (1967) I presented some data on the topic, but a further three years of field study now permit a more detailed analysis. The questions to be answered are as follows: (a) how far from the birth-site does the Dunlin settle to breed for the first time, and (b) how far from the previous nest-site does the Dunlin breed in successive years.

In the following treatment of results, I will label all movements leading to dispersion, irrespective of their causes, as dispersal. For redefinition of dispersal and related terms see JOHNSTON (1961) and BERNDT & STERNBERG (1968).

Study area and methods

The study was carried out over eight seasons, from 1962 to 1969, on the coast near Pori, western Finland (c. 61°30'N, 21°40'E). The study area (Fig. 1) comprises a main study area (60 hectares in size) and four control areas at distances of 1 to 5 km from it. In the study areas the breeding habitat of the Dunlin is an even, shore meadow of short

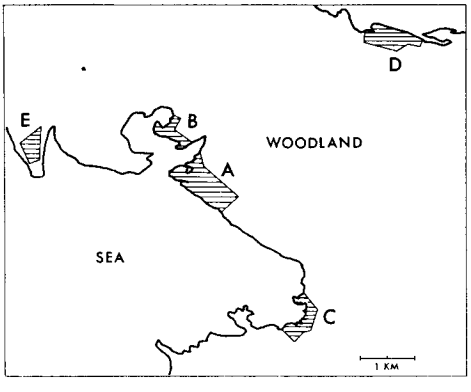

FIG. 1. Location of the main study area (A) and the control areas (B to E) on the coast near Pori, western Finland. *(Päätutkimusalueen (A) ja kontrollialueiden (B—E) sijainti Porin rannikolla.)*

TABLE 1. Annual numbers of breeding Dunlin trapped and ringed or individually recognized in different study areas on the coast near Pori, western Finland. *(Eri tutkimusalueilla Porin rannikolla vuosittain pyydystettyjen ja rengastettujen tai yksilöllisesti tunnistettujen pesivien suosirrien määrä.)*

Study area *Tutk. alue*	1962	1963	1964	1965	1966	1967	1968	1969	Total *Yht.*
A	34	39	45	47	50	53	47	41	356
B	—	—	13	12	13	7	—	6	51
C	2	—	13	13	8	6	—	2	44
D	3	5	1	6	1	16	—	22	54
E	—	—	—	—	—	—	—	7	7
Total *Yht.*	39	44	72	78	72	82	47	78	512

grass and, especially at the very seaside, scattered reed and rush. For a further description of the study area see SOIKKELI (1967).

Annual numbers of Dunlin occupying different study areas have been found as follows:

Study area		No. of pairs
Main study area	A	22 to 27
Control area	B	5 to 8
„	C	8 to 12
„	D	12 to 15
„	E	4*

* Estimation for 1969 only.

The number of pairs (c. 60) within the total study area (A to E) amounts to 95—100% of the whole breeding population of the Dunlin known on the coast near Pori. In recent years, besides the study areas mentioned above, the Dunlin has been found breeding at only one other place on the coast near Pori (E. Haukioja and P. Kalinainen, pers. comm.) and then only one or two pairs.

As the nearest permanent population of the species is located in a coastal meadow some 100 km to the south (SOIKKELI 1964), the population studied is rather isolated from other breeding grounds.

All the breeding birds trapped at the nest were ringed using an ordinary aluminium ring. In addition, those captured in the main study area had an individual combination of one to three coloured rings. In the main study area the Dunlin were under almost daily observation during the breeding seasons, whereas the control of those in the other areas was less intensive; they were only trapped at the nest. The numbers of breeding birds annually trapped and ringed or individually recognized are shown in Table 1.

From 1962 to 1968, altogether 511 young Dunlin were ringed in the study areas just after hatching. Before this period, from 1959 to 1961, 55 young were ringed in the same area by Messrs. A. Kaukola, I. Lilja, and myself.

From 1964 to 1969 all young were marked with, besides an ordinary aluminium ring, a coloured ring above the intertarsal joint. Using different colours and combinations with the aluminium ring it was possible to mark every young bird according to its year class. If some dispersal to other distant breeding grounds occurred, the place and year of birth of every Dunlin seen and ringed in this way could be determined simply using binoculars or a telescope.

To get some idea of possible long-distance dispersal, I trapped or inspected using binoculars c. 15 birds (i.e. 60—70%) of the nearest permanent population at Mietoinen, 100 km south of Pori, in 1967. Some other breeding Dunlin have also been inspected using binoculars with the object of finding possible leg rings at other sporadic Finnish breeding grounds, e.g. at Kokkola 280 km north of Pori and in the archipelago of south-western Finland (R. Casén, J. Hakala, O. Hildén, L. and R. Karlson, J. and R. Tenovuo, and the Ornithological Club of Turku, pers. comm.).

Results

Dispersal of first breeding Dunlin

Up to 1969, altogether 57 Dunlin born and ringed in the study areas were later found breeding. Dispersal of these birds

TABLE 2. Distances between first nest-sites of Dunlin and their birthplaces on the coast near Pori, western Finland. *(Ensimmäisen todetun pesäpaikan etäisyys syntymäpaikasta suosirrillä Porin rannikolla.)*

	Km	<0.5	0.5—1.0	1.0—2.0	2.0—5.0	>5.0
Males	N	7	1	6	16	0
Koiraat	%	*23*	*3*	*20*	*53*	*0*
Females	N	6	3	5	13	0
Naaraat	%	*22*	*11*	*19*	*48*	*0*

in relation to their birthplaces is shown in Table 2. Some 70% of the birds were first caught breeding when one or two years old, i.e. at the age when Dunlin normally start breeding (SOIKKELI 1967). The other 30% of the birds had probably bred before found, but because old Dunlin, especially males, are faithful to former breeding-places, as will be shown later, this source of error does not cause any appreciable difference. The division of settled birds according to the distances moved in Table 2 is strongly affected by the distances between different study areas (Fig. 1).

The shortest distance from birthplace to the first breeding-place was 70 m and the longest nearly 5 km. Nearly a quarter of Dunlin found later have settled within 0.5 km or less, and half of the birds within 2.0 km of their birthplaces. Nearly all birds which settled within 1.0 km have returned to the same meadow where hatched. This is because the greatest dimensions of the different study areas scarcely exceed 1.0 km. The following tabulation shows the number of Dunlin settled in the same study area as born and those settled in a different area:

	Same area	Different area
Males	10	20
Females	9	18

Every third Dunlin found had settled in the same meadow as born. This might be slight evidence of the probability that first breeding Dunlin prefer the meadow where hatched. The results shown above are biased, however, because I have worked most intensively in the largest meadow where more Dunlin have been hatched, ringed and recognized than in any other meadow.

The lack of controls outside a radius of 5.0 km is most probably due to the fact that there are no breeding habitats available for Dunlin in the neighbourhood of the study area. The great number of birds found (51%) which have dispersed 2.0 to 5.0 km indicate that in a homogenous habitat, as opposed to a few isolated breeding grounds, the dispersal of first-breeding Dunlin could be much greater than that observed on the coast near Pori. In fact, I have recorded cases of quite distant dispersal of Dunlin ringed elsewhere in Finland. In 1965, I found a female which was born at Kokkola 280 km north in 1963, breeding in my study area, and in 1967 a female, hatched at Mietoinen in 1960, bred on the coast near Pori. In neither of these cases do I know whether the bird had bred elsewhere in previous years, but in the first case at least this seems improbable, because most Dunlin start breeding when two years old (SOIKKELI 1967). Furthermore, there is one observation of long-distance dispersal at the end of a breeding season: a two-year-old female, born and ringed in my study area, was recognized in a migration flock of six Dunlin 280 km *north* of its birthplace 28 June, 1967 (O. Hildén, pers. comm.).

As the number of young Dunlin ringed in my study area is perhaps 5 to 10

times greater than anywhere else in the whole of Finland, the lack of recoveries of my birds outside the study area is most probably not due to the lack of distant dispersal, but to low trapping activity. This undiscovered distant dispersal cannot be frequent, however, for I did not find any ringed individuals in the population at Mietoinen in 1967. The number of young Dunlin (11 % of those ringed in 1962 to 1967) found breeding in my study area also indicates a very strong birthsite-tenacity.

There is no difference in dispersal rate between males and females as shown in Table 2 (χ^2-test, $0.50 < P < 0.75$) and the tabulation on the former page.

Dispersal of older Dunlin

For an analysis of the dispersal of older Dunlin (i.e. of birds which have bred before), I will use only data of colour-ringed individuals from the main study area, for their movements have been followed most throughly. Table 3 shows dispersal in relation to the previous nest-site. The cumulative percentages of Dunlin found breeding at different distances are shown in Fig. 2.

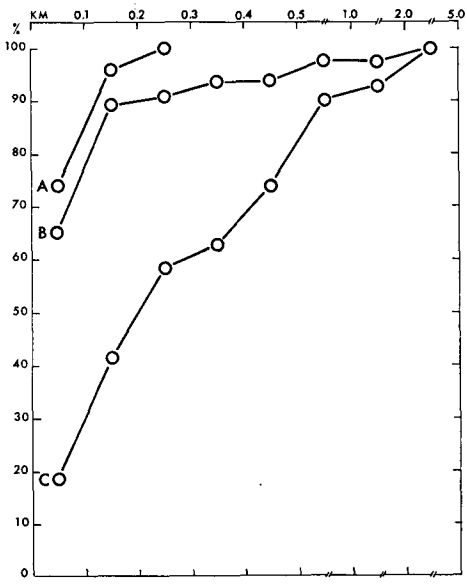

FIG. 2. Cumulative percentages of Dunlin settled at different distances from the former nesting site in successive years. A = mate-faithful birds, B = remated males, C = remated females. *(Perättäisinä vuosina edelliseen pesäpaikkaan nähden eri etäisyyksillä pesineiden suosirrien kumulatiiviset prosenttimäärät. A = pariuskolliset linnut, B = pariaan vaihtaneet koiraat, C = pariaan vaihtaneet naaraat.)*

TABLE 3. Distances between successive nest-sites of Dunlin in different years on the coast near Pori, western Finland. *(Suosirrin perättäisten vuosittaisten pesäpaikkojen välinen etäisyys Porin rannikolla.)*

	Km	<0.1	—0.2	—0.3	—0.4	—0.5	—1.0	—2.0	—5.0	>5.0
Mate-faithful	N	43	13	2	—	—	—	—	—	—
Pariuskolliset	%	*74*	*22*	*3*	—	—	—	—	—	—
Males with new mates	N	30	11	1	1	—	2	—	1	—
Paria vaihtaneet koiraat	%	*65*	*24*	*2*	*2*	—	*4*	—	*2*	—
Females with new mates	N	7	9	6	2	4	6	1	3	—
Paria vaihtaneet naaraat	%	*18*	*24*	*16*	*5*	*11*	*16*	*3*	*8*	—

Note. After renesting, the distance has been measured from the renest to the next year's first nest. *(Uusintapesinnän jälkeen etäisyys mitattu uusintapesästä seuraavan vuoden pesään.)*

TABLE 4. Distances of substitute and second nests of Dunlin from the previous nest in the same years on the coast near Pori, western Finland. *(Suosirrin saman vuoden uusintapesien ja toisten pesien etäisyys edellisestä pesästä Porin rannikolla.)*

	Km	<0.1	—0.2	—0.3	—0.4	>0.4
Mate-faithful	N	25	6	1	1	—
Pariuskolliset	%	*76*	*18*	*3*	*3*	—
Males with new mates	N	4	—	1	—	—
Paria vaihtaneet koiraat	%	*80*	—	*20*	—	—
Females with new mates	N	1	—	1	2	1
Paria vaihtaneet naaraat	%	*20*	—	*20*	*40*	*20*

Dunlin exhibit a strong tendency to nest in the same territory in sucessive years. Nearly three quarters of mate-faithful birds have bred within 0.1 km and all within 0.3 km of the former nest-site. Males paired with a new female show nearly as strong site-tenacity as mate-faithful males; 91 % of them have bred within 0.3 km but two have moved 0.5 to 1.0 and one 3.3 km from the former nest-site. The last bird is the only old male which has been found to move from one study area to another.

In females which have changed their mates dispersal is clearly stronger than in males. The difference is significant (χ^2-test, $P < 0.001$). Only 18 % of females settled within 0.1 km and 58 % within 0.3 km of their previous nest-sites. There are five occasions of movements up to nearly 5 km to other meadow: three from area A to area B, one from A to C, and one from A to D. In addition to the material presented above, I have recorded two more females which have moved from a control area (B, C) to the main study area. Because some females have moved from one meadov to another, it is probable that I have not recovered all birds dispersed from the main study area. The real dispersal of females may thus be sligthly greater than shown in Table 3.

During a study[1] of a sandpiper species at Point Barrow, Alaska, in 1968, I trapped and ringed seven breeding Dunlin (race *pacifica*) to get data of their site-tenacity and survival. In 1969, one of them was found dead, two collected, and two or three recognized in the area where they had bred the preceding summer (D. W. Norton, pers. comm.). Thus, five or six out of seven returned. Out of eight breeding Dunlin which Mr. Norton ringed in another nearby area, two were collected later the same season, but at least three (of six) returned in 1969. These observations show that the Dunlin is very faithful to its former area of breeding in the Arctic too.

For comparison, it may be mentioned that not a single Baird's Sandpiper *C. bairdii* of the six individuals I trapped and ringed in the same area at Barrow was seen in 1969, although all breeding Baird's Sandpipers in the area were then captured (D. W. Norton, pers. comm.).

Dispersal of renesting Dunlin in the same year

Table 4 shows the distances of the repeat and true second nests from the first nest or from the previous repeat nest. Three quarters of pairs moved

[1] Supported financially by the Arctic Institute of North America under contractual arrangements with the Office of Naval Research.

less than 0.1 km and no pair settled more than 0.4 km away. The dispersal appears to be similar to that of mate-faithful pairs in successive years. For Dunlin paired with a new mate, females again show stronger dispersal than males.

Mate-faithfulness and site-tenacity

Mate-faithfulness is common in Dunlin. In 1962—1969, 75 % (62 out of 83) of pairs rejoined, if both mates survived till the next season. Up to 1969 three pairs bred together in five, three pairs in four, and seven pairs in three seasons.

Site-tenacity is fundamental for mate-faithfulness. Mates of a pair migrate and return separately, but meet again in the previous year's territory which serves as a rendezvous (SOIKKELI 1967). The reason for pairing with a new mate is mostly the death of the other bird. In the case when both mates survive, changing of mate very often occurs because one of the mates arrives late after spring migration, as revealed by daily observations of returned birds. In 1965 the span of spring arrival was exceptionally long, and less than half of the pairs rejoined. Clearly it is not advantageous for breeding success, if a bird, which has arrived at the normal time, waits long for its former mate which may have died.

In general, males settle in their previous territory irrespective of whether they have paired with a new mate or not. Females also often pair with a new male in their previous territory or in its neighbourhood; 58 % of all remated females settled within 0.3 km of the former nest-site. The dispersal of remated females is similar whether their previous male has returned or not; in both cases 59 and 56 % of females, respectively, settled with a new mate within 0.3 km of the old nesting site. The difference is not significant (χ^2-test, $0.05 < P < 0.1$). Thus, site-tenacity of females in successive years results not merely from faithfulness to a particular male but is, above all, evidence of real faithfulness to a breeding-place.

Discussion

Earlier studies of dispersal in Dunlin

There are observations of dispersal in Dunlin of other breeding grounds too. HELDT (1966) trapped and ringed Dunlin on the German coast of the North Sea very intensively. Only 2.8 % of the 448 young Dunlin ringed in his study area of 4 km^2 were found breeding later. This indicates a greater dispersal than in my area where 11 % of young were later found breeding (and many more seen) around their places of birth. A reason for this difference may be that in the vicinity of HELDT's area, as opposed to mine, there are perhaps other breeding grounds available where first-breeders can disperse.

Also in the tundra, the habit of returning to the birthplace for breeding occurs. HOLMES (1966) found 2 out of 34 ringed nestlings breeding later within a quarter of mile of their places of birth at Barrow, Alaska.

HELDT (1966) reported that c. 20 % of adult females bred farther than 0.1 km from the former nest-site in successive years. On the coast near Pori, nearly 50 % of all females (i.e. both mate-faithful and remated) bred within that distance. The difference between first-breeders observed in HELDT's and my study areas is quite the opposite. I cannot find any explanation for the greater dispersal of females on the coast near Pori. It may be due purely to differences in the methods of field study.

Dispersal of some other wader species

From the annually growing number of recoveries of ringed birds it has become evident that many bird species show a strong tendency to return to their birthplace or former breeding place.

As for wader species, excluding the Dunlin, exact data of dispersal are rather scanty. If data are available, they are often presented in a form unsuitable for comparisons, e.g. only the numbers of birds faithful to the place or of those that have dispersed farther are mentioned without any information as to the size of the study area or distances which the birds have moved.

In the following, I have gathered some data of the dispersal of wader species. In nearly all studies, as in that of mine presented above, results are biassed on the side of the place of ringing, because trapping activity usually is highest just there or near to it.

Haematopus ostralegus. — Adult birds (ringed as adult): DROST (1953) reports 122 cases of breeding-site-tenacity and one case of dispersal of ca. 13 km. According to JUNGFER (1954) the Oystercatcher shows very strong breeding-site-tenacity. Movements of a few hundred metres sometimes occur, but only one bird was later found breeding on a nearby island at a distance of 9 km. Materials used by DROST and JUNGFER were partly the same. GROSSKOPF (1968) recorded breeding-site-tenacity in 144 cases, and only one bird dispersed farther (ca. 10 km).

Young birds (ringed as young): DROST presents 37 cases of birthsite-tenacity *vs.* 9 cases of dispersal to other adjacent islands, up to 60 km from the birthplace. GROSSKOPF mentions 40 cases of birthsite-tenacity and 24 cases of dispersal to adjacent islands.

Charadrius hiaticula. — Adult birds: LAVEN (1940) found that 28 (52 %) out of 54 breeding birds (total of all ringed adults present in three summers) returned the following year; one bird, however, moved 23 km to another breeding ground. Movements of some hundreds of metres, up to 3 km, were common. LAVEN's data are obviously reliable, as he also checked areas close to his study area but found only unringed birds. According to BUB (1962) 30 (70 %) out of 42 ringed birds (total of all birds present in ten summers) returned the following year. Distances between nests in successive years were up to c. 1 km.

Young birds: LAVEN found 3 (4.4 %) out of 68 ringed young breeding later at distances of 6, 6.5, and 11 km from birthplaces. Furthermore, he made observations of three other young which survived. Thus, dispersal of first breeders was probably greater than that observed in the study area. BUB did not see any of 41 young ringed later.

Charadrius dubius. — Adult birds: BUB (1958) recovered 11 birds (38 %) out of 29 ringed adults present in three summers. It is unlikely that all the birds not recovered had succumbed.

Young birds: BUB found only one (1.5 %) out of 67 young ringed later breeding at a distance of 0.5 km from the birthplace. Obviously more than one had survived.

Charadrius alexandrinus. — Adult birds: DROST (1953) mentions only 6 cases of dispersal (out of some hundreds of birds ringed) to adjacent islands a few km away. GROSSKOPF (1968) reports only one movement to another breeding area out of 178 breeders ringed. As RITTINGHAUS (1956, 1961) carried out an intensive study on the same species less than 10 km away, the strong breeding-site-tenacity in this species is apparently genuine.

Young birds: DROST presents 11 cases of dispersal to adjacent islands, up to 35 km, *vs.* an unknown number of birds displaying birthsite-tenacity. RITTINGHAUS (1956) trapped 68 (5.5 %) out of 1220 ringed young breeding on the small island of their birth and supposed that some had dispersed. GROSSKOPF (1968) reported 29 cases of birthsite-tenacity and 23 cases of dispersal.

Tringa totanus. — Adult birds: According to GROSSKOPF (1959, 1968) male Redshanks are highly faithful to former territories, but movements up to some hundreds of metres may occur. Females change their breeding-places more often, mostly as a result of pairing with a new male on adjacent feeding grounds (not in breeding territory as Dunlin do). No long-distance movements are known, but the species is little ringed and trapped elsewhere on the German coast.

Young birds: GROSSKOPF got 33 recoveries showing birthsite-tenacity.

All the five wader species mentioned above seem to show relatively strong tenacity for the sites of birth and breeding. The Little Ringed Plover apparently is least *ortstreu,* which may be associated with the ability of the species to rapidly exploit new natural and cultural habitats (VOIPIO 1956).

When compared with the Dunlin, most wader species appear to show, as far as is known, equally strong tenacity for places of birth and breeding. But there are a few interesting exceptions in

northern Europe. MEAD *et al.* (1968) and EVANS (1968) reported many cases of long-distance dispersal, mostly in directions between E and NE, of British and Dutch Lapwings *Vanellus vanellus*. If the high rate of dispersal is characteristic for the whole palaearctic population of the Lapwing, this coincides with the monotypic subspeciation of the species. The Ruff *Philomachus pugnax* is perhaps another wader species with a high dispersal rate of offspring. For example, in the Finnish bird ringing reports (NORDSTRÖM 1962) a bird born in Finland and found three years later at the end of May 1680 km ENE of its birthsite is mentioned.

The Dunlin, on the other hand, is apparently relatively *ortstreu* in its whole circumpolar area of distribution and, correspondingly, shows clear variation in size, colour patterns etc. between different semi-isolated populations (DEMENT'EV & GLADKOV 1954, WITHERBY *et al.* 1958, SOIKKELI 1966).

Summary

This paper deals with the dispersal of the Dunlin. Out of 57 Dunlin ringed as young and later found breeding, nearly a quarter settled to breed within 0.5 km and a half within 2.0 km of their birthplaces. No bird which was ringed when young was later found breeding farther than 5.0 km from the birthplace, mostly due to the lack of suitable habitats in the neighbourhood of the study area. Some long-distance dispersal of first-breeders, however, probably occurs, though this was not revealed in this study.

Almost three quarters of mate-faithful birds bred within 0.1 and all within 0.3 km of the previous nest-site. Only 9 % of remated males changed their nest-sites more than 0.3 km, but 42 % of remated females moved farther than 0.3 km.

The Dunlin was also found to exhibit strong tenacity for the former breeding-place in arctic tundra habitats.

Site-tenacity is fundamental for mate-faithfulness, as mates meet and pair after spring arrival in the old territory. In eight seasons 75 % of surviving pairs rejoined.

The Dunlin shows a polytypic subspeciation in its semi-isolated circumpolar populations, which coincides with its relatively low dispersal rate.

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Selostus: **Suosirrin syntymä- ja pesimäpaikkauskollisuudesta.**

Kahdeksan vuoden aikana Porin rannikolla suoritetussa tutkimuksessa selvitettiin mm. kysymystä, kuinka lähelle syntymäpaikkaansa tai entistä pesimäpaikkaansa suosirrit palaavat pesimään. 57 poikasena rengastetusta ja myöhemmin pesivänä tavatusta linnusta lähes neljännes pesi 0.5 km:n säteellä ja puolet 2.0 km:n säteellä syntymäpaikastaan. Pisin todettu syntymä- ja pesimäpaikan välinen etäisyys oli vain 5.0 km, koska tätä kauempana tutkimusalueen lähellä ei ole suosirrille sopivia pesimäpaikkoja. Pitempiäkin siirtymisiä todennäköisesti esiintyy, mutta ne eivät ole yleisiä päätellen syntymäseudulleen palanneiden lintujen suuresta määrästä.

Ennen pesineistä, pariuskollisista linnuista lähes kolme neljännestä pesi 0.1 km:n ja kaikki pesivät 0.3 km:n päässä aikaisemmasta pesäpaikastaan. Puolisoa vaihtaneista koiraista vain 9 % siirtyi yli 0.3 km, mutta naaraista 42 %.

Suosirri palaa myös tundralla entisen pesimäpaikkansa lähelle, kuten havainnot Alaskasta osoittavat.

Kahdeksan vuoden aikana 75 % elossa säilyneistä pareista liittyi uudelleen yhteen. Pariuskollisuuden perustana on pesimäpaikkauskollisuus, sillä puolisot muuttavat erillään, mutta tapaavat ja muodostavat jälleen parin entisessä pesimäpiirissä.

Suosirrin circumpolaarisella levinneisyysalueella erotetaan useita alalajeja. Lajin maantieteellisen muuntelun yhtenä tehostajana on suhteellisen voimakas paikkauskollisuus.

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