



Faculty of Social and Life Sciences

Terese Taylor

Fitness effect of breeding dispersal
among rock pipit males *Anthus petrosus*
littoralis

Effekter på fitness av revirbyte hos skärpiplärkhanar
Anthus petrosus littoralis

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Supervisor: Raimo Neergaard & Björn
Arvidsson
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Abstract

Breeding dispersal can be a way for an individual to improve its fitness. Own reproductive success has been shown to be a cue to dispersal among many bird species. Natural selection should favor dispersal to higher-quality territories and a larger territory is predicted to improve fitness. Data from male rock pipits, *Anthus petrosus littoralis*, on the Swedish west coast indicated, as predicted, that dispersal follows an unsuccessful breeding year. However, no fitness improvement was detected after dispersal, leading to the conclusion that dispersing in itself does not lead to better fitness. Instead it was the acquisition of a larger territory that was the main cause of fitness improvement, unrelated to whether a male returned to an old territory or dispersed to a new one. However, remaining in one's old territory showed to be more beneficial than dispersing. There was a high variation within the rock pipit populations of Nidingen and Malön, due to year-to-year territory quality variation and individual quality among the birds, which could have had a big effect on the outcome of the analyses of the effects of dispersal.

Sammanfattning

Att byta revir kan vara ett sätt för en individ att förbättra sin fitness. Den egna reproduktiva framgången har påvisats påverka beslutet om revirbyte. Naturligt urval borde favorisera byte till ett revir av högre kvalitet och ett större revir förutsägs förbättra fitness. Data från skärpiplärkor, *Anthus petrosus littoralis*, tyder på att ett misslyckat häckningsår leder till spridning. Däremot påvisades ingen förbättring av fitness efter spridning, vilket leder till slutsatsen att spridningen i sig inte leder till bättre fitness. Istället var det anskaffandet av ett större revir som var den huvudsakliga orsaken till fitnessförbättring, orelaterat till om en hanne utökade sitt gamla revir eller flyttade till ett nytt. Däremot visade det sig vara bättre att stanna kvar i sitt gamla revir än att flytta. Det fanns en stor variation bland Nidingens och Malöns populationer av pipilärka, på grund av årlig variation i revirkvalitet och individuell kvalitet bland fåglarna, vilket kan ha haft en stor effekt på resultatet av analyserna av spridningseffekterna.

Introduction

Natural selection favors life histories that result in the most abundant transmission of copies of an individual's genes to future generations. Successful individuals make the appropriate allocation of available limited resources, i.e. they make the right life history decision (Horn and Rubenstein 1984). One such decision that individuals of many species have to make is whether or not to disperse. Dispersal can be divided into natal and breeding dispersal; natal dispersal being the movement from birth site to first breeding location and breeding dispersal the movement from one home range to another between attempts at reproduction (Johnson and Gaines 1990). To change breeding territory between years can be a way for an individual to improve its fitness by acquisition of a higher-quality territory and mate. One benefit of dispersal, both at individual and population level, involve a reduction of the risk of inbreeding depression by having an increased access to unrelated mates (Gandon and Michalakis 2001).

The costs of dispersal involve energetic stress that can have a negative effect on the dispersing individuals in the form of reduced fitness, e.g. the cost in sampling areas prior to the acquisition of a territory (Danchin 2001, Stamps 1994). There can also be higher mortality rates during dispersal and during the settling period in the new territory (Gandon and Michalakis 2001) and fitness can be reduced due to morphological requirements of

dispersal (Roff and Fairbairn 2001). Studies of breeding dispersal give a clear indication of birds' tendency of staying in the same territory once dispersed (Paradis et al. 1998); studies like those of Winkler et al. (2004) and Sharon and Stutchbury (2006) show that dispersal does not necessarily occur even if such an opportunity is given. Benefits to remaining in an old territory are apparently at play; such familiarity benefits include experience of a specific site (Forslund and Pärt 1995) and of one's neighbors, especially so where competition for territories among male birds exist (Lambin et al. 2001); being familiar with one's neighbors reduces energy spent on territorial defense, due to knowledge of each individual's boundaries (Temeles 1994). If time spent on patrolling and defending is reduced, more energy is left for other activities such as foraging (Schoener 1987), leading to maximization of energy obtained on the territory. Despite the seemingly high costs of dispersal and high benefits of keeping an old territory, dispersing males should theoretically reproduce more successfully by dispersing, since this is a condition of an adaptive behavior (Brown 1964). Younger birds are more prone to disperse than are older ones (e.g. Serrano et al. 2001, Forero et al. 1999); this can be due to the poorer competitive abilities for resources and territories (Forslund and Pärt 1995) and to the poorer ability to rear young (Emlen 1984) of younger males compared to the older more experienced individuals. Reproductive success of rock pipits in the study area has been shown to increase with age (Arvidsson 1995).

Many studies have shown that birds, both female and male, are more prone to disperse after an unsuccessful breeding year than after a successful one (Ronce et al. 2001). The habitat quality is a cue when deciding upon which territory to disperse to (Danchin et al. 2001, Stamps 1994). In the study area there was a higher degree of philopatry in the high-quality sites in comparison to the low-quality sites (Neergaard 1999). Theoretically, phenotypes able to adjust their dispersal behavior in relation to higher habitat quality should be favored. In conclusion, young males should disperse to a higher-quality territory and improve their fitness after an unsuccessful first breeding year. What is then a high-quality territory? When females are sedentary and spaced uniformly across a landscape and male reproductive success is limited by the amount of females, as is the case with the rock pipits, then natural selection may be favoring the use of large territories (Stamps 1994). Territory size can also be sexually selected, with females preferring males with larger territories as a cue to their quality (Davies and Houston 1984). Theoretical analysis of optimal size of breeding territories predict that territory size should increase with an increase in food abundance (Schoener 1987); the larger the territory occupied the higher the likelihood that there will be enough food to raise the brood (Tullock 1978). Reproductive success has been correlated with territory size among many bird species, including rock pipits (Arvidsson 1995). In the case of the rock pipits, a larger territory means longer coastline and, since the beaches are their feeding area, more food (Neergaard 1999). Another benefit to having a large territory is that proposed by Verner (1997), who suggested that defending a superterritory, that is to say a territory of a size larger than is required for the owner's needs, can bring the benefit of exclusion of competitors from the resources with the result of a higher percentage of the owner's offspring in the population. As was the case with breeding dispersal, territory size is also determined by the costs and benefits. Holding a territory represents not only a gain but also a cost; the larger the amount of land held, the higher the cost of holding each marginal unit (Tullock 1978) and the more energy is lost by the owner from patrolling and defending it (Schoener 1987).

In this paper I test two hypotheses: 1. Fitness improves between breeding years for dispersing rock pipit males and 2. Fitness improves by enlargement of territory. The first hypothesis leads to the predictions: a. Rock pipit males that disperse in year 2 have worse

fitness in year 1 than returning males, b. Fitness is improved between breeding year 1 and 2 for dispersers, and c. The difference in fitness between year 1 and 2 is bigger among dispersing than among returning males. The second hypothesis leads to the predictions: a. Fitness change is correlated to territory size change, and b. Dispersers enlarge their territory between breeding year 1 and 2.

Methods

This study made use of data on rock pipit (*Anthus petrosus littoralis*) populations that were collected for a larger study (Neergaard 1999, Arvidsson 1995) on the two Swedish west coast islands of Malön (57°20'N, 11°58'E) and Nidingen (57°18'N, 11°54'E) during the years of 1981-1993.

Malön (~1 km²) is situated 1 km from the coast and Nidingen (~0.20 km²) 5 km further out. Rock pipit territories cover the entire island of Nidingen, whereas the interior parts of the larger island of Malön are not inhabited by the rock pipit. This is due to the species' preference to sea-shores, especially to the foraging "hotspots" consisting of accumulated seaweed beds which are rich in food.

This territorial migrant passerine species arrives in the study area in March-April and leaves for its wintering quarters along the Atlantic coast from southern England to southwestern France in September. Territories are established by the male upon its arrival in the spring. Females are usually double-brooded, with the first clutch arriving in the beginning of May and the second clutch 6-7 weeks later. Both males and females show strong site-fidelity and mostly return to their previous territory.

Rock pipits were banded and color-marked on the two islands and the fate of each individual was observed from its arrival in spring until its departure in the fall. The territory borders were determined by a combination of observations of "the parallel walk" display of the males using aggressive body postures and observations of the use of boulders that serve as look-out posts. Territory size was thereafter calculated from field maps with the use of an image analyzer (Quantimet 570). Breeding success was recorded by repeated nest inspections and nestlings were counted and ringed at an age of 8-12 days.

In this study I chose to include only data from each male's first and second year of age since it is between these two first breeding years that most of the breeding dispersal is likely to occur, as mentioned in the introduction.

I define 'breeding dispersal' as movement from one breeding location to another; breeding location in this case being any land occupied by a male during one breeding year. With the help of maps over the two islands where the territories of the pipits had been marked for each year of the study I was able to calculate breeding dispersal distance on an individual level, using two different methods: 1. Calculations of the overlap of the territories of each individual male between its first and second year of age; this was done by making an estimate of how many percent of the territory from year 1 was covered by the territory from year 2; 1 being complete overlap and 0 being no overlap, 2. Calculations of the distance in meters between territory centers between years; this distance was calculated using Pythagoras' theorem on the North-south and East-west coordinates of the territory centers.

As a value for fitness I used, for each individual male and year, number of females (FEMS), number of eggs from all nests associated with the male (CS), hatched eggs (HATCH), fledglings (FLEDGE) and the amount of young that were counted at least two weeks after they had left their nest and were considered to be independent (CONT).

To do the analyses the 114 males used in this study were categorized into a. dispersing males, and b. returning males. The definition of a disperser is a male whose distance between territory centers is at least 111 m. This particular distance was decided upon by calculating the mean of all distances between territory centers of the two islands separately (Malön - 166.6 m, Nidingen - 56.0 m) and then calculating the mean of these two (both islands - 111.3 m). In this way I could get a dispersal distance that would be reasonably accurate for both islands, considering the difference in sizes of the two. The two groups of males arising from this categorization, 18 dispersing and 96 returning males, were used to make a series of analyses.

Excel was used for most of the statistical analyses. SAS 9.1. was used to do a multiple regression analysis on the correlation between the different fitness variables and the territory sizes, overlaps and distances between territory centers.

Results

A t-test showed that the number of fledglings in year 1 was significantly higher among returning males than among dispersers ($t=2.48$, $p=0.01$, $df=112$). However, the other four fitness variables showed no such significant difference between the two groups of males (fig. 1, all p -values > 0.07), although they all indicated the same pattern.

A paired t-test showed no significant change in any fitness variable for dispersers between breeding year 1 and 2 (fig. 2, all p -values > 0.16 , $df=16$), but there was a significant positive change for returning males (fig. 3, $df=94$ in all analyses); FEMS: $t=3.85$, $p=0.0002$, CS: $t=3.46$, $p=0.0008$, HATCH: $t=2.27$, $p=0.03$, FLEDGE: $t=2.13$, $p=0.04$, CONT: $t=1.65$, $p=0.10$.

Table 1. Territory size and dispersal distance characteristics of Nidingen and Malön expressed in averages ($\pm SE$); territory overlap expressed as proportion of territory in year 1 covered by territory in year 2.

	N	Territory size (ha)	Terr. size change (ha)	Territory overlap (%)	Dist. between territory centers (m)
Nidingen	75	0.34 \pm 0.02	0.01 \pm 0.04	0.46 \pm 0.04	55.99 \pm 9.62
Malön	39	1.02 \pm 0.05	-0.07 \pm 0.06	0.44 \pm 0.61	166.60 \pm 51.70
Both islands	114	0.57 \pm 0.03	-0.02 \pm 0.03	0.45 \pm 0.03	94.07 \pm 19.27

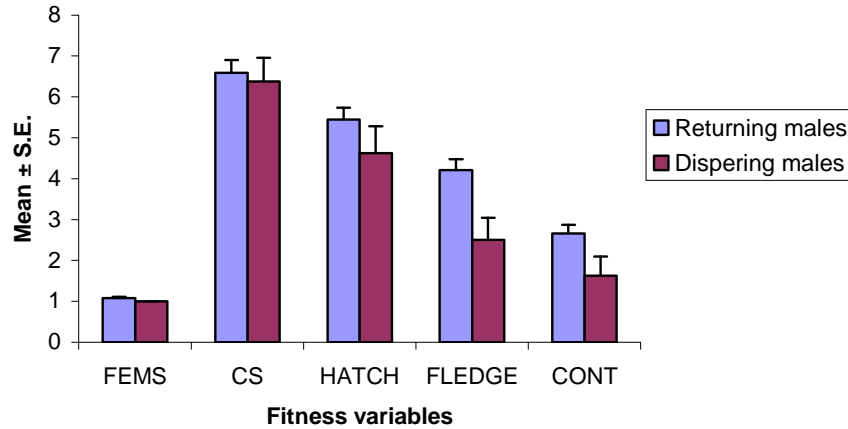


Figure 1. Fitness in year 1 for returning and dispersing rock pipit males. Fitness measured in number of females (FEMS), number of eggs (CS), hatched eggs (HATCH), fledglings (FLEDGE) and independent young (CONT).

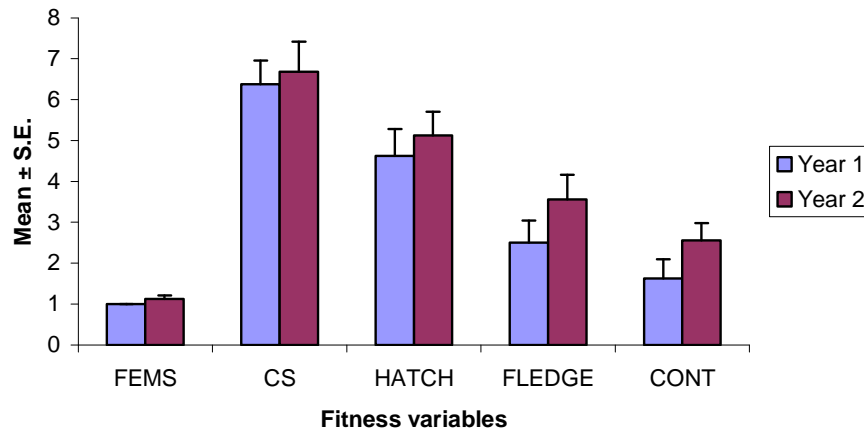


Figure 2. Fitness among dispersing rock pipit males in year 1 and 2. Fitness measured in amount of females (FEMS), number of eggs (CS), hatched eggs (HATCH), fledglings (FLEDGE) and independent young (CONT).

There were substantial differences in fitness change between years for dispersing and returning males, but due to the large within-group variances these differences were not significant (fig. 4, $df=112$ in all analyses); FEMS: $t=0.96$, $p=0.34$, CS: $t=1.36$, $p=0.18$, HATCH: $t=0.43$, $p=0.67$, FLEDGE: $t=0.02$, $p=0.98$, CONT: $t=-0.35$, $p=0.72$.

A multiple regression analysis showed no correlation between territory overlap, distance between territory centers and fitness change (table 2, all p -values > 0.26) but did show a clear correlation between fitness change and territory size change, except for the independent young (table 2).

A paired t -test showed no significant enlargement of territory size neither among dispersers ($t=0.743$, $p=0.469$, $df=16$) or returning males ($t=0.19$, $p=0.85$, $df=94$).

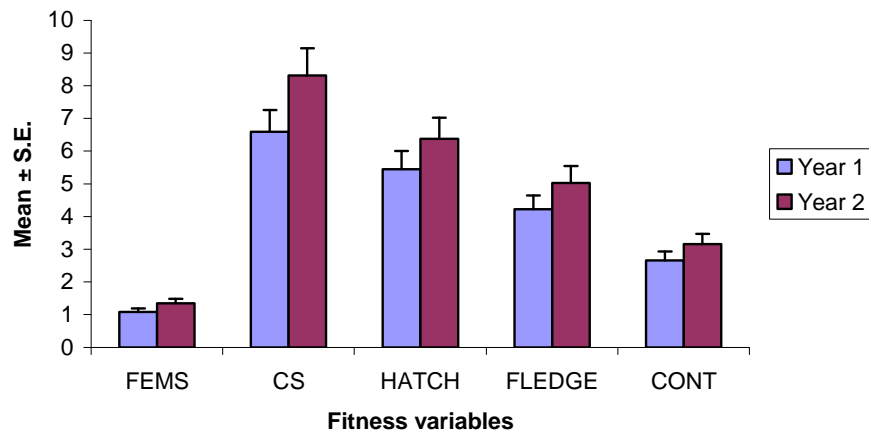


Figure 3. Fitness among returning rock pipit males in year 1 and 2. Fitness measured in amount of females (FEMS), number of eggs (CS), hatched eggs (HATCH), fledglings (FLEDGE) and independent young (CONT).

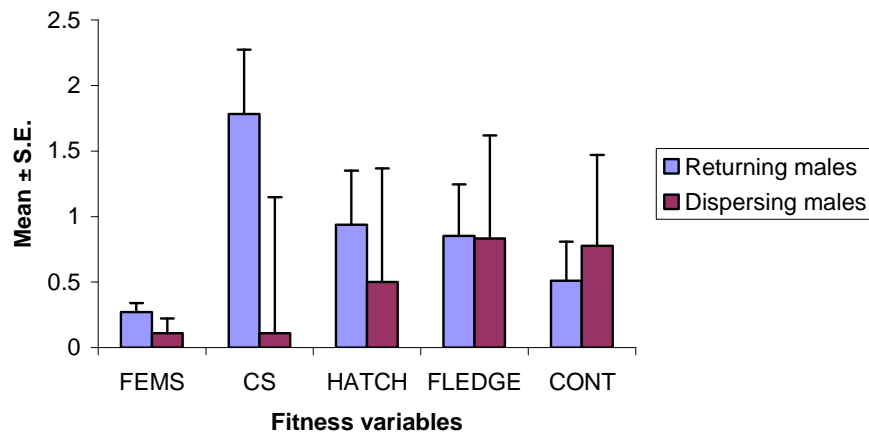


Figure 4. Fitness change among returning and dispersing rock pipit males. Fitness measured in amount of females (FEMS), number of eggs (CS), hatched eggs (HATCH), fledglings (FLEDGE) and independent young (CONT).

Table 2. Multiple regression analysis with five fitness variables as dependent variables and territory size change, territory overlap and distance between territory centers as independent variables. *N* in all analyses = 114.

Fitness variables	Territory size change		Territory overlap		Distance between territory centers	
	t	p	t	p	t	p
No. of females	2.42	0.017	0.59	0.557	0.68	0.495
No. of eggs	2.64	0.001	0.26	0.794	-0.72	0.473
Hatched eggs	3.55	0.0006	-0.42	0.676	-0.18	0.854
Fledglings	2.53	0.013	-0.34	0.734	0.88	0.379
Independent young	1.48	0.143	0.15	0.878	1.13	0.262

Discussion

Of the two hypotheses tested in this paper, the first was rejected and the second was accepted. As many studies have come to the conclusion that birds disperse after an unsuccessful breeding year (e.g. Gowaty and Plissner 1997, Dale et al. 2004), I assumed this to be the case with the rock pipits of Malön and Nidingen as well. There was a significant difference in the number of fledged young between dispersing and returning males in year 1; returning males being the more successful of the two groups. This may explain why some males changed location between years. Own reproductive success has been suggested to be a cue for dispersal in other bird species (e.g. Haas 1998, Blums et al. 2002, Gratto et al. 1985, Forero et al. 1999) and this can be assumed to be the case also with the rock pipits.

No difference in fitness between year 1 and 2 among dispersers indicate that improvement of fitness does not however necessarily follow dispersal. The suggestion that dispersal improves an individual's fitness and that unsuccessful males therefore disperse could be incorrect or more factors, that were not included in this study, could be at play, such as intrasexual competition or divorce (Choudhury 1995). Yearly variation in habitat quality can also play an important role in this analysis. It is possible that fitness improvement is the reason behind dispersing but that the year following dispersal is a less favorable one and has as a result the same or even worse reproductive success than the year before. The high variability in habitat quality between years, because of weather differences (B. Arvidsson, personal communication), leads to a large variance in annual reproductive success in the study area (Arvidsson 1995). This can mean that the cause of dispersal, e.g. unsuccessful breeding in year 1, and cause of choice of territory, e.g. sampling of information during year 1, may not still be relevant in year 2. Also, harem size has been shown to increase with earlier laying date of the primary female and laying date can vary between years due to age of female (Arvidsson 1995) or weather conditions. There was also a big variation in population size between years and this led to variation in territory sizes; big population size led to small territories and vice versa (B. Arvidsson, personal communication). Since data on the 114 males used in this study were collected over a period of more than a decade, year-to-year variation can play an important role in the analyses. A more accurate study could be made by using data from males whose first and second breeding years are of similar habitat quality. In this study however, some of the males' first breeding year might have been a good one, habitat quality-wise, and

their second year a bad one, or vice versa; the different situations resulting in different outcomes of the analyses used in this study.

There is also a high variation in offspring numbers among males (B. Arvidsson, personal communication). It has been shown that lifetime reproductive success of male rock pipits is correlated to birth year and mother (B. Arvidsson, personal communication). The high variation in individual bird quality within the populations can be an explanation to the high variation in the results of this study and to the reason behind the lack of improvement of fitness after dispersal. A more correct analysis can be made by using males born on the same year and from the same female.

The significant improvement of fitness in year 2 among returning males suggests that remaining in an old territory is more beneficial than dispersing. A simple comparison of the amount of males in each group, with more returning than dispersing males, also gives an indication to which of the two strategies is more successful. That birds are more prone to staying than dispersing has been shown by many studies (e.g. Hansson et al. 2002). The results indicate a big difference in fitness change between dispersing and returning males, fitness change being bigger among returning males. This also supports the idea that staying is more beneficial than dispersing, although the variation within the groups is too high for a good analysis (variation can be due to reasons stated above). The multiple regression analysis too showed no correlation between dispersal distance and change in fitness, again indicating no cost or benefit to dispersal.

The results suggest that dispersal in itself does not have an effect on fitness. This is in agreement with studies such as one from Payne and Payne (1993) where lifetime breeding success of indigo buntings was shown to be independent of dispersal. Also site fidelity did not show any relationship with lifetime reproductive output among Cassin's auklets (Pyle et al. 2001). Some other factor other than dispersal itself must be the reason behind improvement of fitness among some male rock pipits. The results showed a clear correlation between territory size and fitness; fitness increasing with enlargement of territories, in agreement with my second hypothesis. The only fitness variable that was not correlated with territory size was the amount of independent young, but this can be explained by the fact that the particular data is the most uncertain due to the difficulty of its acquisition in the field.

Since improvement of fitness seems to be achieved by enlargement of territory I tested if dispersers acquired a larger territory in year 2, but there was no such indication. The same was true for the returning males. These results again suggest that dispersal does not necessarily lead to enlargement of territory and therefore better fitness, but that it is the acquisition of a larger territory that is the reason for improvement of fitness; this being in accordance with earlier studies on the rock pipits (Arvidsson 1995).

There are several reasons why dispersers may be different from residents (Whitlock 2001) and my results do indicate such a difference, given the big improvement of fitness for returning males but not for dispersing males. Results however showed a big variation and did not show a clear picture of the cause and effect of breeding dispersal among the rock pipits of Nidingen and Malön. The method itself of categorizing the birds might have had an effect on the results. The most difficult part of this study was deciding whether a bird was dispersing or staying in order to compare the two groups. Which distance moved away from the former territory should be considered dispersing? My results led me to ask the question: what is the definition of breeding dispersal? Different minimum distance requirements for dispersal have been used by different scientists, e.g. home range distances (Johnson and Gaines 1990), and I came to the conclusion that no dispersal distance would

necessarily be more correct than any other. Due to the big difference between the two islands, it would have been more preferable to do the analyses on the two islands separately but that was unfortunately not possible because of the low number of sample units in each category that would be the result of such a division. A change of the amount of males in each category could possibly have lead to different results.

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