Breeding dispersal and site-fidelity in Dunlin *Calidris alpina* at Tipperne, Denmark

OLE THORUP

(Med et dansk resumé: Spredning hos ynglende Almindelige Ryler på Tipperne)

A returning migratory bird faces the decision: to return to the site where it bred in the previous year, or to try to find a better place. A bird returning to the same site year after year benefits from familiarity with local food resources, suitable nest sites, and predatory regimes. Furthermore, returning to the same site increases the chance to remate, and generally enhances competitive ability due to increased 'self-confidence' of the returned bird within the old home range (Hinde 1956, Oring & Lank 1984). On the other hand, settling at a new site may improve breeding performance if the previous breeding attempt failed due to, e.g., predation or poor habitat quality.

Breeding dispersal in Dunlin and related species is generally very limited (Soikkeli 1970a, Oring & Lank 1984, Jackson 1994, Sandercock 1997). Annual return rates to the breeding site of the previous year are high in Dunlin; four studies found values of 62%, 74%, 83%, and 76%, respectively (Heldt 1966, Soikkeli 1970b, Jönsson 1991, Rösner 1997). Similarly 74-94% of the breeders returned to Tipperne annually (O. Thorup unpubl.).

The present study differs from previous studies (Soikkeli 1970a, Jackson 1994) in being a long-term study covering a fairly large population. This allows, for the first time, an analysis of possible effects of breeding experience on dispersal.

Precise knowledge of dispersal is of major importance in conservation, e.g. in order to secure a proper population management and to ensure a sufficient scale of area protection.

Methods

Study area

The study was performed at the nature reserve Tipperne in western Jylland, Denmark (55°53' N, 8°12' E). The local population of Dunlin (including the adjacent Værnengene; Fig. 1) makes up 110-175 pairs, of which some 75% breed within the reserve. Tipperne holds 15-20% of the Danish Dunlin population (Thorup 1998), belonging to the small and quite isolated population of 'Baltic' Dunlin.

Colour-ringing and resighting

During 1990-1998 208 adult Dunlin were colour-ringed. They were captured on the nest with a heart-shaped walk-in trap and marked with a four ring individual code plus one ring denoting the project. In addition, all birds were ringed with a numbered metal ring from the Zoological Museum, University of Copenhagen.

Colour-ringing with darvic provides excellent possibilities to study various aspects of breeding biology in species breeding in open country. The durability of the colour-rings is high, and, apart from some encrustation of rings during incubation

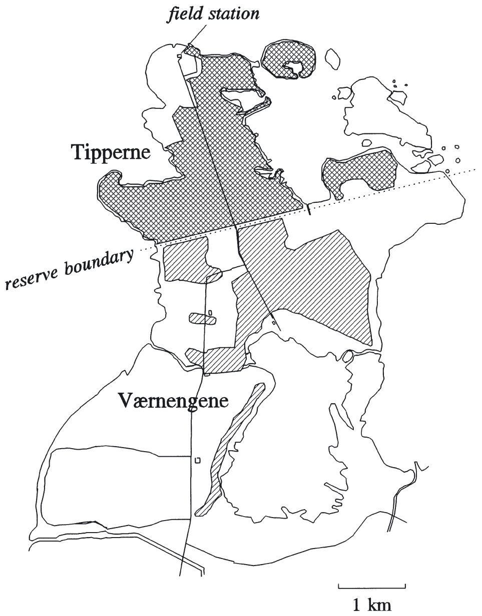

Fig. 1. Distribution of breeding Dunlin at the Tipperne Peninsula. The population at the reserve Tipperne - 80-140 pairs (cross-hatched) - was studied 1990-1998, whereas the population on Værnengene - approx. 30-50 pairs (hatched) - was not covered during this study.
Almindelig Ryles yngleudbredelse på Tipperhalvøen. 1990-1998 undersøgtes de 80-140 par på Tipperne (krydsskraveret), mens de ca. 30-50 par på Værnengene (sidst optalt 1987-1989; skraveret) ikke dækkedes under dette projekt.

Dansk Orn. Foren. Tidsskr. 93 (1999): 255-265

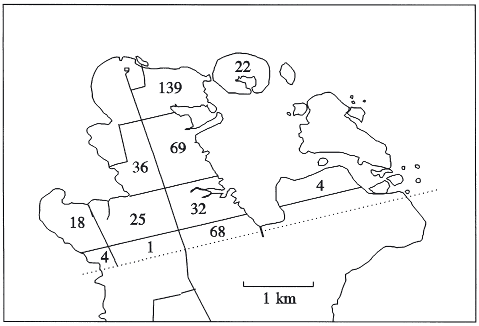

Fig. 2. Distribution of 418 observed individually marked Dunlins with localized nests at Tipperne.
Fordeling på delområder af 418 mærkede Almindelige Ryler med lokaliserede reder på Tipperne.

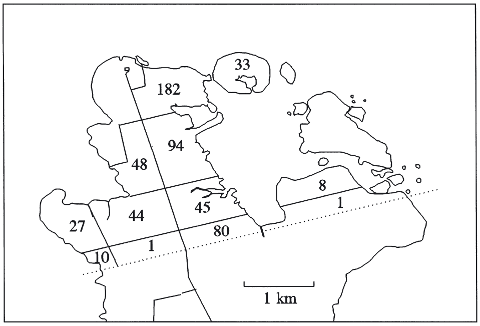

Fig. 3. Distribution of 573 observed individually marked Dunlins with localized territories at Tipperne.
Fordeling på delområder af 573 mærkede Almindelige Ryler med lokaliserede territorier på Tipperne.

and chick rearing, the visibility of the colours is pretty good (Thorup in press).

Thorup (1995) showed that catching and ringing were harmless in most situations. However, during periods of high predation pressure from aerial predators, trapping of incubating adults may increase predation on eggs. Consequently, trapping was avoided in such situations, which is why only 52 adults were ringed in 1995-1998 when predation pressure was much higher than in the previous years. In intensively studied plots, 50 to 65% of the breeders have been individually recognizable since 1992 against 30-40% in other parts of Tipperne. For details of catching method and precautionary measures, see Thorup (1995).

Most birds could be sexed immediately at capture according to bill length (tip to feathering: ♂♂ ≤ 29.0 mm; ♀♀ ≥ 30.0 mm). Some birds were sexed by comparison with their mate; the bill of the female in a pair was consistently ≥ 2.2 mm longer than the male's. Behaviour identified the sex of the rest.

Every year during 1990-1998 all meadows were visited regularly between late April and late June – the study plots every third day, on average. At each visit as many individuals as possible were identified, and all observations together with remarks on the observed behaviour were marked on field maps (scale 1:3500). Territorial behaviour made the identification and mapping of males easier than of females. Unobtrusive behaviour inevitably means that some individuals are overlooked, which is especially true for females; 31 (13%) of 229 males, but 75 (36%) of 210 females were seen only once in a season. Observed males were resighted up to 20, females up to 17 times in a season, with a median of 4 in males, 2 in females.

Less than 40% of the nests were found annually. Distribution of observed colour-ringed Dunlins with a nest is shown in Fig. 2. Inclusion of colour-

Tab. 1. Number of years dispersal distances of individual breeding Dunlin were recorded at Tipperne, based on territories and nests, respectively.
Antal år spredningsafstanden mellem hhv. territorier og reder kunne bestemmes for forskellige ynglende ryler på Tipperne.

Years *År*	1	2	3	4	5	6	7	8	Total
Territories *Territorier*									
♂	30	20	15	4	2	3	2	1	77
♀	26	12	11	4	6	3	0	1	63
Nests *Reder*									
♂	33	7	8	1	3	1	0	0	53
♀	22	13	4	5	2	1	0	0	47

ringed birds with a localized territory improved the coverage (Fig. 3). The following behavioural categories were accepted as indicative of a territory: 1) A bird apparently flushed from a nest or empty nestbowl, 2) A bird flushed or landing at least twice at the same place in suitable breeding habitat, 3) At least two observations separated by at least one week of a bird at the same place on the meadow, away from typical feeding sites, 4) An apparently alert bird watching on the meadow, 5) An alarming bird near newly hatched chicks. If more than one observation was made of territorial behaviour, the territory was marked at the site of the strongest indication, or at the midpoint of the observations. Most birds are represented more than once in the nest and territory data sets (Tab. 1).

The precision in mapping and inter-nest distances was estimated at ±10 m in heterogeneous habitat with gullies and pools, and at ±20 m in more homogeneous habitat. The precision of measured distances between mapped territories was estimated at ±50 m.

A large proportion of nests and territories were localized in the northern and central parts of the reserve (Fig. 2 & 3). This means that short and medium distance dispersals are well covered, whereas possible dispersals farther than 2 km would be underrecorded due to undetected dispersals out of the reserve.

In the assessment of year-to-year dispersal only the site of the first-found nest/territory was used when two or more nests or territories were localized in one season.

Unsystematic checks for colour-ringed Dunlin were performed at some other important breeding sites in the country (Tab. 2).

Site-fidelity and breeding dispersal

Observations at Tipperne of territorial males suggested that typical territories had diameters of 250-300 m. Jackson (1994) and Holmes (1970) found similar values in Scotland and Alaska, respectively. In accordance with the terminology by Greenwood (1980) Dunlins returning to the same or an adjacent territory are considered site-tenacious. Consequently, a distance limit of 175 m (nest-to-nest dispersal) and 200 m (territory-to-territory dispersal) was chosen to define site-fidelity, the difference being due to the higher mapping precision of nests than of territories.

In analysing the relationship between dispersal distance and hatching success, the fate of a nest was determined by the presence of chicks or of eggshell fragments in the nest lining, empty nests without shell fragments being considered indicative of predation (Thorup 1998).

Pair-bonds were determined by the presence of a male and a female together in a territory or – at more than one occasion – at a pool or in the coastal zone; or by a female and a male incubating the same nest or alarming near the same chicks.

To analyse for the effect of experience on breeding dispersal, dispersals were grouped into disper-

Tab. 2. Extent of searches (proportion of breeders controlled) for colour-ringed Dunlin 1991-1998 in Danish populations of more than 10 pairs. Breeding population sizes according to Christensen 1984, Kjeldsen 1992, 1997, P.A.F. Rasmussen (in litt. 1997), Thorup 1997, 1998, Grell 1998 and Thorup & Rasmussen 1999.
Omfang af eftersøgninger af farvemærkede ryler 1991-1998 i danske ynglebestande på mere end 10 par.

Site *Lokalitet*	Coordinates *Koordinater*	Distance (km) from Tipperne *Afstand (km) fra Tipperne*	Population (pairs) *Bestand (par)*	Proportion controlled *Andel af bestand undersøgt for farveringe*	Investigators *Observatører*
Rømø Sønderland	55°07'N, 8°30'E	88	20	75-100%	O. Thorup
Rømø Nørreland	55°10'N, 8°30'E	82	15-20	0%	-
Fanø, Grønningen	55°28'N, 8°22'E	47	10-25	50-100%	K. Fischer, O. Thorup
Værnengene	55°52'N, 8°15'E	<5	30-50	10-20%	O. Amstrup, O. Thorup
Bøvling Fjord	56°25'N, 8°08'E	57	10-45	0%	-
Harboør Tange	56°39'N, 8°10'E	85	100	0%	-
Arup/Vesløs Vejle	57°01'N, 8°55'E	133	15-25	30-50%	J.P. Kjeldsen
Bygholm Vejle	57°03'N, 9°06'E	139	60-120	30-50%	J.P. Kjeldsen
Ulvedybet	57°06'N, 9°39'E	160	10-25	0%	-
Læsø, Rønnerne	57°13'N, 11°00'E	226	20	0%	-

Tab. 3. Breeding dispersal in Dunlin at Tipperne. Percentage of site-tenacious birds in nest-to-nest (≤175 m) and territory-to-territory (≤200 m) dispersals, and mean and median dispersal distances. The data set is subdivided into birds with and without hatching success the previous year.
Spredning af ynglende ryler på Tipperne fra år til år. Andel stedtro fugle (≤175 m for reder, ≤200 m for territorier) og spredningsafstand.

	Percentage site-tenacious *Pct stedtro*	Mean dispersal distance *Gennemsnitlig spredningsafstand* m	Median dispersal distance *Median af spredningsafstand* m	n
Nest-to-nest *Rede til rede*				
♂ all *alle*	88	101	60	96
♀ all *alle*	67	246	93	96
♂ hatching failure *uden klækningssucces*	71	129	80	35
♂ hatching success *med klækningssucces*	97	86	55	59
♀ hatching failure *uden klækningssucces*	53	323	180	36
♀ hatching success *med klækningssucces*	77	191	70	57
Territory-to-territory *Territorium til territorium*				
♂ all *alle*	91	108	75	181
♀ all *alle*	66	325	125	155
♂ hatching failure *uden klækningssucces*	88	116	75	72
♂ hatching success *med klækningssucces*	93	103	75	102
♀ hatching failure *uden klækningssucces*	49	428	205	55
♀ hatching success *med klækningssucces*	77	233	93	90

sals after the first year (n+1), after the second year (n+2), and after three or more years of (known) experience (n+3+), n being the year of capture and colour-ringing. Dunlins at Tipperne start breeding in their second to fourth year of age (O. Thorup unpubl.), and n therefore corresponds to a minimum age of two years. Dispersal of birds in the first year after ringing activities were initiated in a sub-area were excluded from analysis since, by definition, all birds were then 'inexperienced'.

Laying takes place from late April till mid-June (Thorup 1998), and clutches or broods lost before mid-June are regularly replaced. In the present analysis of dispersal at replacements, data were only included if both nests were found.

Possible correlations were tested using chi-square tests; Yates' correction for continuity was applied in tests with one degree of freedom.

Results

Breeding dispersal

Dunlin at Tipperne showed a strongly female-biased dispersal (Fig. 4, Tab. 3), the difference between sexes in the proportion of birds showing site-fidelity being significant both for nests ($\chi_1^2 = 10.6$; $p < 0.005$) and territories ($\chi_1^2 = 31.5$; $p < 0.001$).

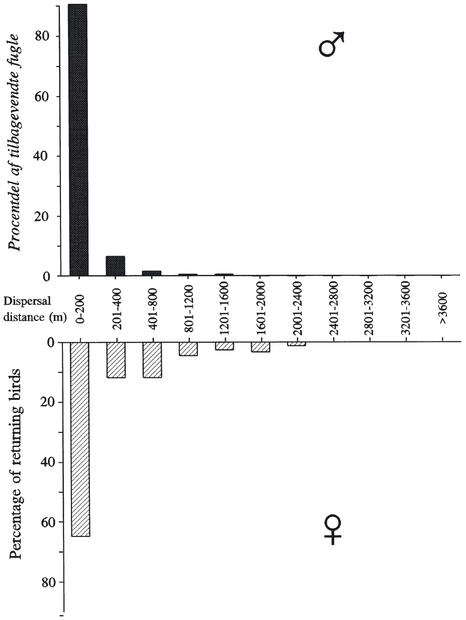

Fig. 4. Breeding dispersal of males (175 territories) and females (145 territories) of Dunlin at Tipperne, 1990-1998.
Spredningen hos hanner (175 territorier) og hunner (145 territorier) af Almindelig Ryle med tidligere yngleerfaring på Tipperne, 1990-1998.

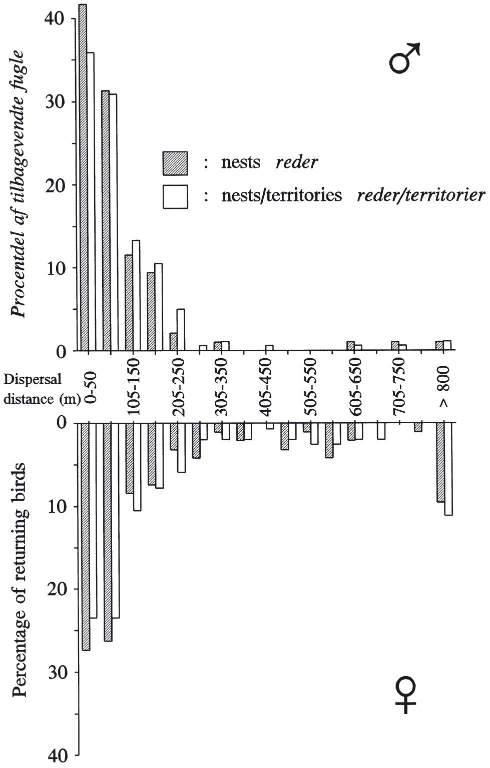

Fig. 5. Breeding dispersal (50 m zones) of males (96 nests, 181 territories) and females (96 nests, 155 territories) of Dunlin at Tipperne, 1990-1998.
Spredningen (i 50 m zoner) hos hanner (96 reder, 181 territorier) og hunner (96 reder, 145 territorier) af Almindelig Ryle med tidligere yngleerfaring på Tipperne, 1990-1998.

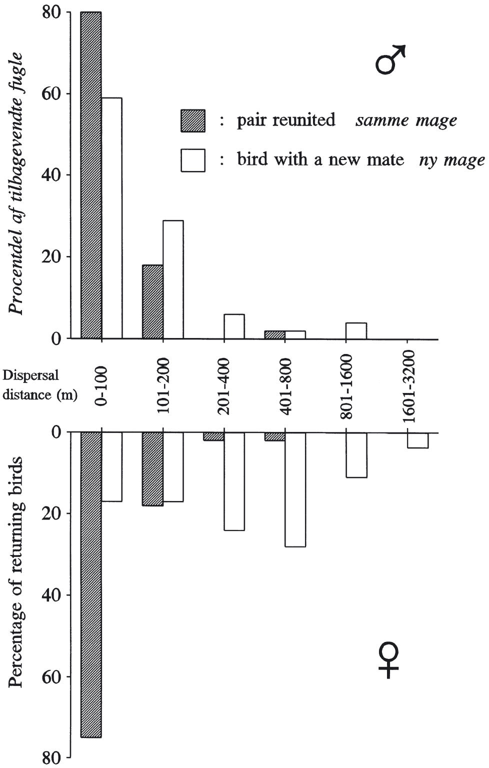

Fig. 6. Breeding dispersal of Dunlin at Tipperne of birds in reunited pairs (n= ♂: 55, ♀: 56), and in birds pairing with a new mate (n= ♂: 51, ♀: 54).
Spredningen fra år til år af Almindelig Ryle på Tipperne af fugle med samme mage som foregående år og fugle med ny mage.

Breeding males only rarely dispersed more than 400 m (3% of all dispersals), whereas females regularly dispersed farther than 400 m (23% of dispersals).

42% of all males showed a very strong site-fidelity by placing their nest less than 50 m from their nest site in the previous year, as did 27% of the females (Fig. 5). A slight difference between nest-to-nest and territory-to-territory dispersal ranges is probably a consequence of the difference in precision at mapping.

Factors affecting breeding dispersal

Effect of previous breeding success. Hatching success had a significant impact on the subsequent dispersal distance (Tab. 3). The difference between failed and successful breeders in the proportion of site-tenacious birds was significant in nest-to-nest dispersal both in males ($\chi_1^2 = 10.2$; $p < 0.01$) and females ($\chi_1^2 = 5.0$; $p < 0.05$). A similar difference was found in territory-to-territory dispersal in females ($\chi_1^2 = 10.4$; $p < 0.01$), but not in males ($\chi_1^2 = 1.0$; $p > 0.1$). Despite the female bias in dispersal, the median dispersal distance of successful females (70 m) was less than the median distance of males with hatching failure in the previous year (80 m).

Effect of mate-faithfulness. Dunlin on Tipperne frequently changed mates; 33% of the pairs divorced (n=82) in years where both mates from the previous year were seen. Divorce-rate was only slightly higher in years following hatching failure, and the difference was not statistically significant ($\chi_1^2 = 1.0$; $p > 0.1$): 70% of successful hatchers remained together, while 60% of failed hatchers did so.

Tab. 4. Dispersal distance in Dunlin obtaining new mates; birds in which the previous mate was not seen, and birds in which the previous mate was present on Tipperne.
Afstand mellem redestedet i to på hinanden følgende år for Almindelig Ryle med ny mage. Opdelt på fugle, hvor den tidligere mage ikke sås det pågældende år, og fugle, hvor den tidligere mage sås på Tipperne.

	Previous mate not seen *Tidligere mage ikke set*		Previous mate present *Tidligere mage til stede*	
	m	(n)	m	(n)
♂ mean *gennemsnit*	167	(17)	150	(27)
♂ median	100	(17)	85	(27)
♀ mean *gennemsnit*	399	(19)	590	(27)
♀ median	375	(19)	360	(27)

The extent of dispersal was much higher in birds that obtained a new mate than in birds that remained together (Fig. 6). Apart from one case in which a pair together moved 635 m between one year and the next, all reunited pairs (55 ♂♂, 56 ♀♀) bred in the same or an adjacent territory as in the previous year. 88% of males with a new mate (n=51) were site-tenacious in contrast to only 33% of the females with a new mate (n=54). Dispersal distance of birds obtaining a new mate was similar in birds whose previous mate was absent and in divorced birds (Tab. 4).

Effect of experience. Breeding experience had no effect on male dispersal, whereas experienced female breeders had a higher dispersal rate than less experienced ones (Tab. 5). Only 19% of the females with only one (known) year of breeding experience dispersed more than 200 m, whereas 43% of females known to have bred for two or more years did so; the difference is statistically significant ($\chi_1^2 = 5.1$; $p < 0.05$). The stronger tendency of experienced female breeders to disperse was apparent both in females that failed and females that successfully hatched a clutch in the previous season.

Dispersal at replacements

Dispersal distance at replacement is known for 29 breeders (Tab. 6). Most replacements involved the original pair, and 20 different nests are represented in the data set. One pair laid a replacement clutch 625 m from the first nest. No other mate-faithful

Tab. 5. Effect of breeding experience on dispersal in Dunlin at Tipperne. The year an incubating bird was colour-marked is denoted 'n', and rates of dispersal (movement of more than 200 m and 350 m, respectively) between subsequent breeding seasons are shown for years n+1, n+2, and later (n+3+). The number of observations in each category is given in brackets.
Yngleerfaringens indflydelse på spredningen af Almindelig Ryle på Tipperne. Året hvor den rugende fugl farvemærkedes er betegnet n, og flytningen er vist for årene n+1, n+2, og de efterfølgende år (n+3+). Antal observationer pr kategori er anført i parentes.

Experience Yngleerfaring	Percentage dispersed (>200 m) *Andel (%) der flyttede >200 m*						Percentage dispersed (>350 m) *Andel (%) der flyttede >350 m*	
	All *Alle*		After hatching failure *Uden klæknings-succes*		After successful hatching *Med klæknings-succes*		All *Alle*	
♂ n+1	10	(41)	11	(9)	6	(31)	0	(41)
♂ n+2	9	(44)	14	(22)	5	(20)	2	(44)
♂ n+3+	11	(75)	14	(36)	8	(37)	4	(75)
♀ n+1	19	(32)	29	(7)	16	(25)	9	(32)
♀ n+2	45	(33)	50	(16)	33	(15)	27	(33)
♀ n+3+	41	(75)	60	(30)	26	(38)	35	(75)

Tab. 6. Dispersal distance between first clutches and replacements in Dunlin at Tipperne.
Spredningsafstand fra førstekuld til omlæg for Almindelig Ryle på Tipperne.

	0-50	55-100	105-150	155-200	205-250	255-300	305-350	355-400	>400	Total
♂ all *alle*	4	4	2	2	2	0	0	0	1	15
♂ new mate *ny mage*	0	0	0	0	2	0	0	0	0	2
♀ all *alle*	4	6	0	2	0	0	0	1	1	14
♀ new mate *ny mage*	0	0	0	0	0	0	0	1	0	1

pair dispersed more than 200 m, whereas two males and one female with new mates moved between 200 and 400 m. The pattern at replacements is very similar to the year-to-year dispersal pattern.

Dispersal at second clutches

Genuine second clutches seem to be very rare. Successful males were never seen to reassume courtship or display activities after leaving their well-grown chicks. On the contrary, most females leave their mate and chicks about one week after hatching, and often they remate. Breeding has been proved twice in such late-established pairs at Tipperne, the nests being 385 m and 70 m, respectively, from the first nests of the females. This is within the normal range of year-to-year breeding dispersal distances in females with new mates (Fig. 6).

Discussion

Site-fidelity means that a bird returns to a familiar area. There may be different levels of familiarity to search for, however. The entire Dunlin population of the Tipperne peninsula shares common feeding areas at the mudflats in the surroundings, and returning to the peninsula means a return to familiar feeding conditions. During chick-rearing family groups may move several hundred meters, and especially the males gain experience of favorable chick feeding areas during this period. A return within a radius of, e.g., 500 m from the previous nest site would be another possible 'familiarity unit' to choose when defining site-fidelity. In this study the 'action area' during pair formation and incubation period was chosen as the unit to express site-fidelity. It turned out to be a very useful unit to reveal various dispersal patterns. The alternative choice of the entire Tipperne peninsula would highlight the very low degree of flexibility in dispersal, as 100% of the Dunlins would then be site-tenacious.

A possible bias by underrecording long distance dispersals (>2 km), due to undiscovered dispersals outside the reserve, is estimated to be negligible in males and very slight in females, on basis of the observed pattern of short and medium distance dispersal (Fig. 4) and the lack of resightings at other Danish breeding sites (Tab. 2).

There are missing values in both the nest and the territory data because every year several territory owners and nest incubators were not identified. A comparison of dispersal distances of birds localized each year with distances of birds localized in some years only indicates that no systematic bias applies to the missing values – birds did not move gradually in any fixed direction.

Effect of previous breeding success. It is commonly found in birds that individuals disperse farther following breeding failure (e.g. Oring & Lank 1984, Jackson 1994). Jackson (l.c.) found a significantly higher proportion of unsuccessful female Dunlins dispersing more than 100 m from their previous breeding site than successful ones, but was unable to find a similar tendency in males; the dispersal level in male Dunlins is so low that an effect is very difficult to detect. However, by defining site-fidelity as the dispersal of less than 175 m, combined with a precise mapping of nest sites, this study succeeded in showing that males also tend to disperse farther following hatching failure.

Oring & Lank (1984) used Dunlin as an example of a species showing no flexibility in dispersal as a reaction to breeding failure. This holds true at the level of the locality: every Dunlin returns to its former breeding area irrespective of the breeding success in the previous year. At a finer scale, however, both mates react to breeding failure by dispersing, albeit at short distances only, particularly in males. Such small scale flexibility may be advantageous in a heterogeneous habitat in allowing the birds to react on changed predatory regimes, overgrowing of former nest habitat, or the like, without abandoning the benefits from familiar surroundings (feeding grounds).

Effect of mate-faithfulness. The very high site-fidelity of the Dunlin means that dispersal almost inevitably implies a mate change. But divorce rate is not much higher following hatching failure than following hatching success. The combination of a strong correlation between hatching failure and dispersal and a lack of correlation between hatching failure and divorce is possible because a high proportion of divorced breeders settle within 200 m of the nesting site of the previous year. Not only did 88% of divorced males settle with their new mate within the 200 m limit, also 33% of the divorced females settled at the margin of the previous territory or the neighbouring territory, frequently with their former mate as nearest neighbour. Divorce apparently is not a consequence of breeding failure but rather a choice for a better option. Sandercock (1997) found a higher nesting success in pairs of Western Sandpipers *Calidris mauri* that eventually divorced.

In an Oystercatcher *Haematopus ostralegus* study the female was the active partner in a divorce in most cases. As a rule the 'victim' of the divorce lost its breeding status, while the chooser either stayed in the territory or moved to a neighbouring territory (Ens et al. 1993).

The observed divorce pattern in Dunlin at Tipperne is consistent with a system in which it is mainly the female who chooses divorce. She may do so to obtain a better mate or a better territory. Systematic behavioural studies of Dunlin pair-bonds and divorces are lacking, however, making it impossible to substantiate the causes of divorce in this species.

Mate-faithfulness is often calculated by examining divorce-rates of recaptured pairs. This approach may underestimate the true divorce rate because the probability of capturing both members of a divorcing pair is lower than of capturing a reunited pair (Sandercock 1997). Such a bias is unlikely in this study since returning birds were recorded by resightings.

Effect of experience. A marked difference in dispersal between less and more experienced breeders, as was found in this study, has not been reported previously. In their reviews Oring & Lank (1982, 1984) refer to higher return rates in female Temminck's Stint *Calidris temminckii* and female and male Spotted Sandpiper *Actitis macularia* with increasing breeding experience, somewhat contradictory to the present Dunlin data. The two studies did not measure dispersal – they were performed at isolated breeding sites (Hildén 1975, Maxson & Oring 1980), and a dispersal distance of more than a few hundred meters would have marked the bird as 'not returned'.

The observed small rate of dispersal in inexperienced female breeders at Tipperne could be an artifact if a large proportion of unsuccessful females did not return to Tipperne at all after their first breeding attempt. However, the return rate of unsuccessful females was only slightly lower than that of successful ones (O. Thorup unpubl.).

At a first glance increased experience of a territory ought to increase the advantage of site-fidelity. On the other hand, increased breeding experience also means increased knowledge of the entire breeding area, so experienced females may better be able to assess where optimal breeding sites are available than inexperienced females.

Oring & Lank (1984) hypothesized that females disperse farther than males because females face the risk at arrival of finding their previous male already mated and the former territory thus defended both by the male and the new female. However, less experienced (more site-tenacious) female Dunlins at Tipperne hardly arrive earlier than experienced females, and neither does the stronger dispersal of unsuccessful females appear explainable by arrival time.

The underlying causes notwithstanding, the observed dispersal pattern does not suggest that females are forced to divorce or disperse. Increased dispersal with experience probably reflects an improvement in the females' ability to increase reproductive success by taking advantage of variability in breeding habitat, as has been suggested in a number of passerine species (cf. Oring & Lank 1982). It appears likely, for example, that experience increases 'self-confidence' and/or status and, consequently, the possibility to choose a preferred mate or territory.

Implications for conservation

The high site-fidelity of breeders together with a dispersal pattern closely linked to previous breeding success highlight the Dunlin's need of stable and predictable breeding areas. This implies stable management practices concerning, e.g., grazing schemes and mowing schedules at breeding sites. Such management practices may inflict a substantial egg and chick mortality to late breeding species like Dunlin but are also important in creating suitable breeding habitat (Thorup 1998).

The Tipperne data do not allow an assessment of natal dispersal which might make it possible to estimate the ability of the species to establish

Dunlin. Photo: Poul Reib.
Almindelige Ryler er meget stedtro, men hunnerne vælger oftere nye ynglesteder end hannerne, og både hanner og hunner, der har mistet yngelen, er tilbøjelige til at flytte til et nyt territorium året efter.

breeding populations in restored meadow areas. However, two long-distance natal dispersals observed in Finland (Soikkeli 1970a) do indicate that young breeders have some flexibility. Natal philopatry, in terms of chicks returning to their birth site, is well developed in Dunlin as well as in several other shorebird species (e.g. review in Oring & Lank 1984, Kruk et al. 1998).

Strong site-fidelity (together with natal philopatry) generates a strong attachment of Dunlins to their breeding grounds, leaving little opportunity for forced dispersal as a response to changes in local breeding conditions (e.g. an abrupt change of management). Such changes may lead to local catastrophes to populations. In this respect Baltic Dunlin shares conditions with other shorebirds associated with cultural grasslands, such as Black-tailed Godwit *Limosa limosa* and Redshank *Tringa totanus* (Thompson & Hale 1989, Groen 1993, Kruk et al. 1998).

To ensure viable populations of Baltic Dunlin it is of major importance to safeguard all major breeding sites. Dispersal patterns are, without any doubt, evolved to ensure survival in a stable environment, and without core areas with predictable breeding conditions the small and decreasing population of less than 2000 pairs (Thorup 1998) is threatened with extinction.

Acknowledgments

Jan Drachmann, Kaj Kampp, Jørgen Peter Kjeldsen and Hans Meltofte made valuable comments on an earlier version of this paper. The Danish Ministry of Environment and Energy – through Skov- og Naturstyrelsen and Danmarks Miljøundersøgelser (NERI) – gave permission to undertake research at Tipperne and provided accommodation and equipment for the study. The staff at Tipperne – especially Ole Amstrup – made a large number of the resightings of colour-ringed birds. Jørgen Peter Kjeldsen, Vejlerne, and Kim Fischer, Fanø, checked many Dunlins for colour-rings in their respective study areas.

Resumé

Spredning hos ynglende Almindelige Ryler på Tipperne

En fugl, der vender tilbage til sit gamle yngelsted, kan drage fordel af sit kendskab til velegnede redesteder, velegnede fourageringsområder og prædationsforhold. På den anden side kan en fugl ved at flytte forbedre sine ynglemuligheder, hvis den finder et mere velegnet yngleområde.

Fugle, der som Almindelig Ryle er monogame og hævder territorium, er normalt meget ynglestedtro. Hovedparten af de voksne ryler, der er i live, vender tilbage til samme ynglelokalitet, som de ynglede på året før. På Tipperne genfindes mellem 74% og 94% af ynglefuglene fra året før, hvilket må være meget nær alle de fugle, der har overlevet. Spredningen af erfarne ynglefugle foregår altså først og fremmest inden for den en gang valgte ynglelokalitet.

Mellem 110 og 175 par ryler er udbredt på næsten alle engene på Tipperne og på de fugtigste dele af Værnengene (Fig. 1). Denne undersøgelse er foretaget inden for reservatets grænser, men på en række andre vigtige yngleområder for Almindelig Ryle i Danmark er der ledt efter farvemærkede fugle (Tab. 2). Uden for Tipperne er der foreløbig kun fundet farvemærkede fugle på Værnengene.

1990-1998 er der farvemærket 208 voksne ryler. Siden 1992 har 40-50% af Tippernes ynglefugle været farvemærket.

De vigtigste ryleområder på Tipperne er i gennemsnit besøgt hver tredje dag mellem sidst i april og sidst i juni, og så mange fugle som muligt er individbestemt og kortlagt med bemærkninger om adfærd. Fuglene, især hunnerne, optræder dog så diskret, at der hvert år har været fugle, der er blevet overset, og 13% af de observerede hanner og 36% af hunnerne er kun set én gang i løbet af en sæson.

Rederne er så godt skjult, at mindre end 40% er fundet. Fordelingen af lokaliserede farvemærkede fugle med reder er vist i Fig. 2, mens Fig. 3 viser udbredelsen af fugle, hvor territoriet blev kortlagt. Ved opmåling af afstanden mellem to reder vurderes usikkerheden til ± 10 m i områder med loer og pander og ± 20 m i mere homogene områder. Ved opmåling af afstanden mellem territorier vurderes usikkerheden til ± 50 m. Mange individer indgår i materialet flere gange, da alle flytninger er medtaget (Tab. 1).

Erfarne ynglefugle viste en signifikant større spredning hos hunner end hos hanner (Fig. 4, Fig. 5, Tab. 3); 42% af hannerne placerede deres rede mindre end 50 m fra redestedet året før, mens det tilsvarende tal hos hunnerne var 27%. Forskellen på de målte spredningsafstande mellem reder og mellem territorier afspejler den større præcision ved redekortlægningerne.

Fugle, der flyttede deres rede mindre end 175 m og deres territorium mindre end 200 m, betragtes her som stedtro. Signifikant flere både hanner og hunner, hvis æg klækkede det foregående år, var stedtro, end ryler, der mistede deres kuld (Tab. 3). Det er tidligere vist, at hunner uden ynglesucces er mere tilbøjelige til at flytte (Jackson 1994), men den aktuelle undersøgelse påviser for første gang, at dette også gælder de mere stedtro hanner.

Monogame fugle, der udviser en høj grad af stedtrohed, er normalt også meget partro. I denne undersøgelse opløstes dog 33% af alle parforhold, hvor begge mager var konstateret i live. Årsagen til opløsningen af parforholdet er sjældent manglende ynglesucces (Tab. 4); forskellen på fugle med og uden succes er ikke særlig stor: 70% af par med klækningssucces og 60% uden klækningssucces genforenedes. Da territoriet er det sted, hvor pardannelsen finder sted, er det ikke overraskende, at spredningen er størst hos fugle, der fik en ny mage (Fig. 6); kun i ét tilfælde flyttede et par et langt stykke sammen, mens alle øvrige genforenede par bosatte sig mindre end 200 m fra forrige års redested.

For at undersøge om øget yngleerfaring havde nogen indflydelse på spredningsmønstret, opdeltes alle registrerede flytninger efter hvor mange år efter mærkningen, de fandt sted. Rylerne er dog ikke nødvendigvis mærket det første år, de ynglede, og for at undgå de mest oplagte fejl, medtages fugle ikke det første år efter mærkningsstarten i et delområde.

Der fandtes ikke noget mønster i hannernes spredning, men hos hunnerne sås, at fugle med mere erfaring spredte sig i langt højere grad end fugle med mindre erfaring (Tab. 5). En sådan ændring af spredningsmønstret med tiltagende erfaring er ikke tidligere påvist hos nogen vadefugleart, og den antyder, at opløsning af parforhold og spredning hos hunnen er udtryk for et valg (som foreslået for Strandskade af Ens et al. (1993)), og ikke er påtvunget af omstændighederne (som foreslået af f.eks. Oring & Lank (1984)).

Omlægskuld placeredes i de fleste tilfælde mindre end 200 m fra første kuld, hvis parret holdt sammen, mens de placeredes mellem 200 og 400 m fra første kuld, når parret var nyetableret (Tab. 6). Denne spredning svarer til den fundne år-til-år spredning.

Regulære andetkuld er meget sjældne. Succesfulde hanner er aldrig set yngleaktive efter at de har forladt ungerne, mens succesfulde hunner ofte forlader ungerne ca en uge efter klækningen og danner par med en ny mage. Kun to gange er ynglen hos sådanne sent etablerede par dog dokumenteret; reden fandtes hhv. 70 og 385 m fra hunnens første kuld. Spredningen falder altså indenfor rammerne af år-til-år spredningen hos hunner med ny mage.

Fugles spredningsmønstre bestemmer génudvekslingen mellem bestande og regioner og derfor også, hvordan bestandene udvikles. Præcis viden om spredning er derfor afgørende for muligheden for at foretage en passende beskyttelse af en bestand. Den baltiske ryle er i dag en lille bestand, der de seneste ti-år har været udsat for en voldsom tilbagegang (Thorup 1998). Den baltiske ryles høje grad af stedtrohed viser en tilpasning til et stabilt miljø og en manglende evne til at reagere på forringelser af yngleområdet. Den baltiske ryles overlevelse er derfor afhængig af, at bestandens få tilbageværende kerneområder nyder udstrakt beskyttelse. En sådan beskyttelse inkluderer en stabil landbrugsmæssig drift, f. eks. hvad angår kreaturgræsning og høslæt; to driftsformer, der forkert udført medfører en stor dødelighed hos æg og unger, men som samtidig er nødvendige for at opretholde habitater med kortgræssede enge, som rylen er afhængig af.

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Accepted 11 September 1999

Ole Thorup
V. Vedsted Byvej 32, 6760 Ribe