Philopatry, dispersal, and survival of wren (*Troglodytes troglodytes*) in the Faroe Islands

Hvussu músabróðir (*Troglodytes troglodytes*) yvirlivir, spjaðir seg, og hvussu staðbundin hann er í Føroyum

Sven-Axel Bengtson
Museum of Zoology, University of Lund, Helgonav. 3, SE-223 62 Lund, Sweden.
Email: Sven-Axel.Bengtson@zool.lu.se

Úrtak

Reiðrandi músabrøður og floygdir ungar hjá norðuratlantiska føroyska músabróðrinum (*Troglodytes t. borealis*) vórðu í nøkur ár ringmerktir við littum ringum (n=134) á sjey avmarkaðum økjum á seks føroyskum oyggjum. Ein einstakur (ringmerktur tá hann var floygdur) ferðaðist í minsta lagi 50 km og læt seg forða hvørki av oyggjum ella vatni. 61,5% av steggjunum, sum reiðraðust, komu aftur til sama stað á hvørjum ári (n=26), og hetta er ein ábending um at steggin er sera staðbundin. Líkt er til at fleiri føroyskir músabrøður yvirliva samanborið við ringmerkingar-úrslit frá meginlandinum. Væntaði livialdurin hjá steggjum sum reiðrast (t.e. í minsta lagi eitt ára gamlir), var 2,1 ár, og tveir steggjar reiðraðust í minsta lagi fýra fylgjandi ár aftan á at teir vórðu ringmerktir. 15% av teim reiðrandi bøgunum komu aftur (n=20). Av teimum floygdu ungunum komu 10.2% aftur (n=88). Av floygdu ungunum komu munandi fleiri steggjar enn bøgur (vit ganga út frá at kynsbýtið var javnt) aftur hagar, teir vórðu klaktir. Óroyndir steggjar vóru munandi minni hepnir at fáa maka enn teir eldru. Møguligar frágreiðingar, hví bæði kynini spjaða seg ymist, verða viðgjørdar. Eingin munur varð sæddur millum øki ella ár, kanska tí ov fáir fuglar vórðu kannaðir.

Abstract

Breeders and fledglings of the North Atlantic Faroese wren (*Troglodytes t. borealis*) were colour-ringed (n=134) during a number of years in 7 limited areas on 6 of the Faroese islands. Most of the autumn resightings of marked individuals (n=45) were male-biased and made < 2 km from the ringing site and on the same island. One individual (ringed as fledgling) dispersed at least 50 km, passing islands and water-barriers. For male breeders return rate across years and areas was 61.5% (n=26), which implies a high degree of philopatry. The minimum annual survival suggests a significantly higher survival rate than shown by ringing recoveries of mainland wrens. Mean life expectancy of breeding males (i.e. at least one of age) was 2.1 years and two males bred for at least 4 consecutive years following ringing. For female breeders overall return rate was 15.0% (n=20). For fledglings 10.2% (n=88). Among fledglings significantly more males than females (assuming an equal sex ratio) returned to natal areas. In males, first-time breeders were significantly less succesful in obtaining mates than older ones. Possible explanations for the sex-biased dispersal patterns are discussed. No differences between areas or years were discernible, possibly due to very small sample sizes.

Fróðskaparrit 51. bók 2004: 252-263

Introduction

The wren (*Troglodytes troglodytes*) has been remarkably successful in colonizing even the most remote and isolated North Atlantic islands, from the Scottish islands to Iceland. Besides, in a number of cases the island populations are recognized as endemic subspecies (Fig. 1), collectively referred to as "island races" (Armstrong, 1955; Armstrong and Whitehouse, 1977). In contrast to some northern, mainland populations (e.g. Scandinavian) that are migratory, but like most British and Continental wrens the island populations are considered non-migratory, though local and short-distance movements are commonplace (Armstrong, 1955; Hawthorn and Mead, 1975; Armstrong and Whitehouse, 1977; Cramp, 1988). Hence, there is indirect evidence of past long-distance water-crossings and effects of isolation and strong selective regimes that have lead to relatively fast evolutionary changes; indeed, the island races of wren may be viewed as an early stage of adaptive radiation (Williamson, 1981).

As evidenced (though circumstantially) by the seasonal occurrence of wrens in non-nesting areas or in numbers not accountable for by the local populations, intra-island as well as inter-island movements of wrens occur on offshore Scottish islands, the Faroes, and in Iceland (Williamson and Boyd, 1960, 1963; Williamson, 1965; pers. obs.). Presumably these movements are associated with the rigorous environmental conditions prevailing in most of these wind-swept, treeless islands, where the primarily insectivorous wrens often have to track other food resources and, for instance, frequently feed on marine wrack fauna in the intertidal zone. Precise data on the occurrence of such movements, and especially inter-island movements (i.e. the crossing of water barriers), are scarce. Such dispersal patterns have important social and genetic implications for the structure of local populations and differences within and between the archipelagos. In Shetland, mainland wrens (assumedly Scandinavian and/or British that are morphologically distinguishable from the island subspecies) are frequently recorded during migration and inter-island movements occur as inferred from observations of unusually large numbers of wrens on small isolated islands (Williamson, 1965; Cramp, 1988). In the Faroes, assumedly Scandinavian wrens have been captured on three occasions (Sørensen and Jensen, 1999). The existence of inter-island movements in the Faroes is suggested by the continuous presence of small, extinction prone poulations on some of the smallest islands (Bengtson, 2001). As to Iceland no other than the Icelandic subspecies (*islandicus*) has been recorded. In this context it should be noted that a ringed wren observed at Mývatn in NE Iceland in 1963 was, since no wrens had been reported ringed in Iceland in the years before, by Armstrong and Whitehouse (1977:238; also cited in Cramp, 1988:528) considered a possible immigrant that might have been ringed "several hundred miles away across a sea-passage". However, this bird was in all probability one of several Icelandic breeding wrens that had been ringed (using Icelandic rings but not yet reported to the ringing office in Reykjavík at the time of

Fig. 1. *Wren (subspecies* borealis*) on Skúvoy, Faroe Islands. Photo: Daniel Bengtson.*

the observers' enquiry) by the present author earlier in the season at the very same place.

Data on dispersal and survival rates of wren are not easily obtained as recovery rates of birds ringed in Scandinavia, Great Britain and on the Continent are considerably <1% (Mead, 1974; Glutz *et al.*, 1985). Re-sightings (or re-captures) of ringed breeding or wintering wrens have provided some information on site fidelity and minimum survival rate (Armstrong and Whitehouse, 1977; Glutz *et al.*, 1985; Cramp, 1988), but not for any of the North Atlantic island populations. This is one of the reasons for this report based on a rather small sample of colour-ringed wrens ringed on their breeding grounds in the Faroes in 1983-1990. The initial aims of the ringing programme were primarily to be able to identify individual birds within the framework of local population studies and to document possible inter-island and local (i.e. intra-island), seasonal movements, and sex-biased dispersal. The latter objective was at the time influenced by two papers on philopatry and breeding dispersal in birds (Greenwood, 1980; Greenwood and Harvey, 1982) suggesting that in species where essential resources are defendable (e.g. territory) and a prerequisite for obtaining a mate the females would be more likely to disperse. Since the wren is strongly territorial (also in autumn and winter) and the quality of the Faroese breeding sites assumedly varies, there might be differences in site fidelty between the sexes and sites. This supposition regarding differences related to habitat quality was based on suggestions that because of low levels of food resources the island wrens are monogamous, in contrast to their British and Continental counterparts where polygamy is common (Armstrong, 1955; Armstrong and Whitehouse, 1977).

Study areas, material and methods

The wren breeds commonly all over the Faroes, both in the infields (i.e. the inhabited areas and their surrounding managed land) and outfields, the latter including high coastal cliffs as well as inland cliffs and ravines (Bengtson, 2001). Wrens were ringed during the breeding season (June-July) at 7 sites on 6 islands from Mykines in the west to Fugloy in the east (see Bengtson, 2001: Fig. 1):

(i) On Mykines, in an area that includes the settlement and parts of the puffinries immediately west of it. This area supports a dense population of wren and a rich insect life.
(ii) On Koltur, around the two nowadays uninhabited farms each with one breeding pair.
(iii) At Tjörnuvík at the northern end of Streymoy; with 2-5 pairs breeding in the infield and adjacent outfield areas. A secluded and geographically isolated site.
(iv) Immediately south of Haldarsvík, just south of Tjörnuvík on Streymoy. A rather open, exposed outfield area with a relatively low density of breeding wrens and a moderately rich vegetation confined to cliffs and ravines.
(v) At Gjógv at the northern end of Eysturoy; a small settlement with a few breeding pairs and one or two of them in and around the secluded harbour where there are cliffs with luxurious vegetation.
(vi) On Kunoy in the settlement (incl. the plantation) with the same name. Several pairs breed among the buildings and on the outskirts of the settlement.
(vii) Att Kirkja on Fugloy in an area including the infield and the outfields northwest thereof along the coast to Fótur where there is a number of breeding pairs, one in each gully. The infield part has a fairly rich vegetation, contrary to the outfield parts.

Ranking these study areas subjectively (to some extent supported by data on invertebrates from pitfall traps and sticky traps for insects) with respect to their suitability (quality) for breeding wrens leads to the following order: Mykines stands out as being the most suitable followed by Gjógv, Kunoy, Koltur, Tjörnuvík, Fugloy, and Haldarsvík. In at least one respect this ranking may be questioned as it does not take into consideration the presence of feral cats, which occur in many settlements and undoubtedly kill a considerable number of wrens, particularly fledglings.

Altogether 134 wrens were individually ringed with numbered rings and/or coloured plastic rings in the study areas (Tab.

1), mostly in 1984 (n=51)). They were mist-netted on the breeding grounds, often entire family-groups, and only once (on Mykines) was a brood of nestling ringed; nests with young were used for studies of parental food provisioning and therefore too precious to put at risk. The sex of adults was determined from behaviour but that of fledglings could only be established for those that were re-sighted in subsequent year.

The study areas were visited in autumn (mid-August-October) following ringing, and in the subsequent breeding season (June-July) by myself or co-workers. Usually only the study areas and their immediate surroundings (< 300 m) were surveyed, though with highly variable degrees of efficiency. A few birds (none of which was re-sighted) were ringed in sites that were not at all re-visited in the following year (e.g. on Kalsoy) and therefore not included in the analysis. In the Faroes the scarcity of dense, shrubby vegetation and the wren´s habit of approaching and often entering buildings (*músabródir*, "the brother of the mouse") greatly increases its detectability. The wren is familiar to most islanders and therefore public media (newspapers, radio, and TV) were alerted resulting in a number of sightings (from all seasons) of colour-ringed wrens, where in most cases the reported colour-combinations made positive individual identifications possible.

Despite recent methodological advances in statistical techniques and software in analysing ringing recovery and re-sighting data (see e.g. Nichols and Kaiser, 1999), the small sample size of the present study renders comparisons between areas and years meaningless and pooled data are presented descriptivly. From mortality rates (m) the mean life expectancy (MLE) can be calculated using the formula: MLE = $(2 - m)/2m$, and by using minimum annual survival rate (i.e. return rates of marked individuals) instead a conservative (i.e. underestimate) estimate is obtained.

Results

Tab. 1 gives the numbers and frequencies of marked individuals re-sighted during autumn (i.e. within *c.* 3 months of ringing) and in subsequent summer. One fledgling was found dead after a few days where it had been ringed on Fugloy.

Autumn dispersal

Newly fledged young usually remain in the vicinity of the nest (< 200 m) for the first 8-10 days, but longer movements may occur; e.g. on Mykines one newly fledged young moved 850 m in just short of 3 hours following ringing. About one-forth of the yearlings were observed again before the end of October (mostly in September), nearly all in, or close to their respective natal areas. Four yearlings, two each on Fugloy and at Haldarsvík, that were observed in September had dispersed between 2 and 4 km from the ringing sites. The only case of inter-island dispersal was a fledging ringed on Mykines on 18 July 1984 and reported 25 November on Nólsoy, i.e. 50 km ESE of Mykines. Among breeders a higher, though statistically non-significant proportion of the males than of the females were re-sighted during autumn in the study areas;

Table 1. *Numbers of wrens individually marked as breeders (males and females) or fledglings (on Mykines 7 of them were actually nestlings) in different study areas and re-sighted in the first autumn (15 Aug – 30 Oct) and year (i.e. breeding season) following ringing. The sex-ratio of fledglings returning in the following year is given in brackets. Return rates express the frequency of individuals re-sighted one year after ringing (i.e. minimum annual survival rate).*

Study area	Numbers ringed		Individuals re-sighted			Return rate
			Autumn	Following year	(♂♂/♀♀)	(%)
Mykines:	Males	6	4	4		
1984-1987	Females	11	3	2		
	Fledglings	38	9	5	(4/1)	
	Subtotal	55	16	11		*20.0*
Koltur:	Males	2	1	2		
1984-1990	Females	2	0	0		
	Fledglings	9	2	1	(1/0)	
	Subtotal	13	3	3		*23.1*
Tjörnuvík:	Males	6	4	4		
1983-1990	Females	4	1	1		
	Fledglings	8	3	0		
	Subtotal	18	8	5		*27.8*
Haldarsvík:	Males	3	1	1		
1987-1989	Fledglings	9	2	0		
	Subtotal	12	3	1		*8.3*
Gjógv:	Males	2	1	2		
1985-1986	Females	2	1	0		
	Fledglings	6	2	1	(1/0)	
	Subtotal	10	4	3		*30.0*
Kunoy:	Males	3	2	1		
1984	Females	1	0	0		
	Subtotal	4	2	1		*25.0*
Fugloy:	Males	4	3	2		
1984-1986	Fledglings	18	6	2	(2/0)	
	Subtotal	22	9	4		*18.2*
Pooled	Males	26	16	16		61.5
	Females	20	5	3		15.0
	Fledglings	88	24	9	(8/1)	10.2
	Grand total	*134*	*45*	*28*		*20.9*

the difference not being statistically significant (Chi square = 2.38, df =1, p>0.1). No breeders were re-sighted > 1 km from the ringing site.

Philopatry

The return rate of breeding males in the year subsequent to ringing was higher than for females (61.5% and 15.0%, respectively) and all the re-sightings were made at the place of ringing, or within a few hundred metres. Besides, 8 of 9 fledglings (return rate 10.2%) that were re-sighted in their first breeding year were males returning to their natal area, and assuming an equal sex-ratio at fledging, the difference between sexes was consistent with expectations and statistically significant (Fisher´s exact test, 1-tail, z=1.81, p<0.05). Among these one-year old males 5 were definitely paired and the others were, with a high degree of probability, not (two on Mykines and one in Tjörnuvík), whereas 15 of those that were more than one year old were paired, the difference being statistically significant (Fisher´s exact test, 2-tail, p<0.05).

Survival

Individuals not re-sighted in the following year had either died or emigrated; hence the return rates (Tab. 1) are equivalent to minimum survival rates and when it is as high as in the breeding males it is probably close to the actual survival rate. Out of 16 breeding males being at least two years old (i.e. ringed as breeders) 7 returned to breed in the following year (i.e. 43.8%) and 3 out of 7 (42.9%) being at least 3 years of age returned, and 2 males were still alive at the age of at least 5; thus 3 of 16 males were faithful to the same area for at least 3 consecutive years (Tab. 2). Three of 5 males known to be one year old (i.e. ringed as fledlings) returned in the following year. Thus, for males there is no clear indication of minimum survival rate changing with age after the first year, though the samples are small and individuals ringed as breeders form a heterogeneous group with respect to age. For breeding males the calculated mean life expectancy (using a maximum annual mortality rate of 38.5% as suggested by the return rate across years and study areas) is 2.1 years. As the wrens breed at the age of one the mean longevity is 3.1 years. The return rates for breeding females and fledglings are far too low to reflect actual survival rates.

Comparison between study areas

There are no discernible patterns or statistically significant differences between the study areas with regard to return rates.

Discussion

The present study shows that most of the autumn observations (45 of 134 marked individuals, i.e. 34%) were made within < 2 km of the breeding site which, of course, was to be expected as sightings of marked individuals beyond this distance were due to mere chance and not the result of a systematic search. However, 4 yearlings (of 24 re-sighted in autumn) dispersed > 2 km from their natal site during the autumn, but all within the island. In one instance inter-island movements occurred as a fledgling

Table 2. *Number of individual wrens re-sighted in the same area for one or several years following year of ringing.*

Age and sex at time of ringing (year n)	Number of individuals re-sighted	Number of individuals and years of re-sightings			
		n+1	n+2	n+3	n+4
Breeding males	16	9	4	1	2
Breeding females	3	1	2		
Fledged males	8	5	2	1	
Fledged female	1		1		

ringed on Mykines and re-sighted on Nólsoy must have passed over two or more islands and made at least three sea-crossings ("hard edges" *sensu* Wiens *et al.*, 1985), each 2-7 km wide. Thus, in the present study 24 (27.3%, n=88) of the fledglings were re-sighted in autumn close to their natal site (Tab. 1). This is a high figure compared to a Dutch study where 5.1% (n=195) of nestlings ringed were seen in the following winter (Kluijver *et al.*, 1940), and English studies (few nestlings ringed) where none was seen again (Armstrong and Whitehouse, 1977). Hence, the Faroese wrens seem more strongly attached to their natal areas than than mainland ones.

A significant result is that male breeders are considerably more philopatric than females; whether this also holds for yearlings as the male-biased return rates suggest (Tab. 1) depends on the validity of the assumed equal sex ratio in fledglings. As the degree of philopatry is a function of annual survival rate it is markedly higher than the observed return rates. Analyses of English ringing recoveries show that overall annual survival rate is approx. 37% (Hawthorn and Mead, 1975) and for adults 42% (Innis, cited by Cramp, 1988). This is almost identical with the 41% overall minimum survival of adult (both sexes combined) Faroese wrens. Although breeding females invest more energy in the breeding efforts and therefore may have a lower rate of survival than males, the high overall frequency (61.5%) of marked breeding males re-sighted in the following year suggests that the annual survival rate is significantly higher in the Faroes than in England. This, of course, has implications for the actual degree of philopatry (i.e. percentage returning of those alive), which among Faroese breeding males might be well over 90%. As to breeding females, the degree of actual philopatry is undoubtedly considerably higher than the observed return rate, but not high enough to invalidate the significant difference between the sexes. Other studies have demonstrated much lower degrees of site fidelity, though in a study in England at least 40% of the birds returned to the same winter quarters in successive years (Hawthorn *et al.*, 1971).

English and Dutch breeding studies have reported a number of cases of male philopatry, but with low return rates (Kluijver *et al.*, 1940, Armstrong, 1955; Armstrong and Whitehouse, 1977, Garson, cited by Cramp, 1988), and an extensive German ten-year study showed very few recoveries and the wren was considered "nicht besonderes ortstreu", though one polygamous male and 3 females showed faithfulness to their breeding territories in consecutive years (Dallmann, 1987). With regard to the Faroes it would be most interesting to know where the non-philopatric females choose to breed and is the overall relatively high breeding site fidelity in Faroese wrens associated with a reluctance to cross water barriers?

Evolution of social systems and patterns of dispersal is usually considered to be inter-linked and male philopatry and female-biased dispersal as observed in the Faroese wren is consistent with a pattern commonly found in monogamous birds with resource defence (Greenwood, 1980). The island races of wren are territorial through most of the year and, in contrast to the frequently polygamous mainland wrens, monogamy seems to prevail (Armstrong and Whitehouse, 1977); though polygamy has been recorded in the Faroes (Bengtson, 2001 and unpubl.). Over the past decades numerous descriptive and experimental studies have put forward evolutionary explanations for sex-biased dispersal in birds and mammals, mostly invoking inbreeding avoidance and competition (e.g. Pusey, 1987). Inbreeding is generally assumed to have negative consequences at indivual and population levels (e.g. Thornhill, 1993; Keller, 1998) and might be a factor of importance with regard to the local, and often rather small wren island populations. However, inbreeding may not always be detrimental (e.g. Järvinen and Varvio, 1985), for instance with regard to lifetime fitness (e.g. Shields, 1982; Van den Casteele *et al.*, 2003) and may even favour maintenance of local adaptations and coadapted gene complexes (Shields, 1987). Furthermore, the effects of inbreeding may be environmentally dependent (Pray *et al.*, 1994; Bijlsma *et al.*, 1999). In many studies sex differences in competition (intersexual and parent-offspring) are believed to be a driving force (though difficult to distinguish from the relative importance of inbreeding avoidance) behind the evolution of philopatry and sex-biased dispersal. Analyses of dispersal patterns are usually based on asymmetries between males and females in the costs and benefits of being faithful to a site or seek new grounds.

The small sample size from the Faroes is inadequate for any wider conclusions to be drawn. Nevertheless, the observations clearly suggest that males are more philopatric than females, which is consistent with suggestions that in species where males defend resources such as a territory a female-biased dispersal prevails (Greenwood, 1980). Male wrens occupy exclusive territories within which they feed, display and build several nests, and the number of vacant nests seems to be a cue for female mate choice (Garson, 1980; Evans and Burn, 1996). Hence, the significance of being aquainted with suitable nest-sites, which is a highly predictable resource from one year to the next, may be particularly important to the males. In addition, aquaintance with the breeding site is beneficial with respect to the utilization of various other resources and is therefore likely to contribute to enhanced survival and fitness. Moreover, as experience increases with age it seems like a good strategy to be relatively long-lived and highly philopatric, particularly when the environmental conditions are harsh and unpredictable as in the Faroes. These arguments obviously do not help to explain the markedly lower site fidelity observed for the females. A recent phylogenetic study shows that philopatry is associated with low adult mortality, deferred maturation and low reproductive rate (Arnold and Owens, 1998). The Faroese wren is, in contrast to mainland wrens, single-brooded (no second brood has yet been confirmed) and the observed minimum survival rate (across years and study areas) of breeding males corresponds to a mean life expectancy of 2.1 years, which is about twice that of British, less philopatric and multiple-brooded, male wrens (assuming 63% annual mortality; Hawthorn and Mead, 1975). Wrens breed at the age of one year which means that mean longevity of Faroese male wrens is more than three years, and as the re-sightings show at least two males were still alive at the age of five. However, a male of the same age was also recorded in a Dutch and English study, respectively (Kluijver *et al.*, 1940; Armstrong and Whitehouse, 1977). Longlivedness and low recruitment is typical of tropical passerine species compared to their counterparts (equivalent in size) living in the temperate zone (e.g. Lack, 1968; Fogden, 1972; Ricklefs, 1973, 1983; Snow and Lill, 1974), though also for species living in an environment with highly variable food supplies like the tropical Darwin´s Finches (Gibbs and Grant, 1987; Grant and Grant, 1989). The male-biased natal philopatry in yearlings suggested by the re-sightings may be a strategy associated with the prospects of a relatively long life. Many of the one-year old males appear to return to their natal sites and although they seem to be less successful than the older males in obtaining mates. Presumably they gain more in terms of lifetime fitness by being philopatric and competing with relatives for territories, and abiding their time (see e.g. Komdeur and Edelaar, 2001), than by dispersing and competing with conspecific non-relatives. No behavioural observations were made of parent-offspring interactions that could be interpreted as nepotism or parental tolerance, or some kind of parental facilitation (Brown and Brown, 1984). As to female-biased dispersal it is commonly argued that by dispersing females get access to a wider choice of mates (Greenwood, 1980), or that intra-sexual competition and inbreeding avoidance are involved (see e.g. Pusey, 1987). For the Faroese female wrens the very few re-sightings give little indications as to their post-breeding whereabouts, except that just a few females were seen in autumn at the breeding sites (Tab. 1). It is difficult to see why a female should divorce a good male and/or abandon a good area unless it is ousted, but for the time being there are no observations suggesting such behavioural interactions. One may speculate that, while some females exhibit breeding site fidelity, a majority disperse at the end of the breeding season and spend the non-breeding season in, or moving between, any places where conditions are favourable and in the spring mate some distance from natal areas. The islands appear to be saturated with suitable breeding habitats and territorial wrens (Bengtson, 2001 and unpubl.), which may result in a lower site attachment in the females. Ecological constraints on dispersal and the benefits of philopatry may interact (Koenig *et al.*, 1992; Emlen, 1994) and variation in quality between territories may promote variability in dispersing behaviour (Kokko and Lundberg, 2001). Hence a justification for comparing study areas, though the failure to detect any differences between them with respect to dispersal patterns was not surprising considering the small sample sizes.

Conclusions

In the Faroes, wrens disperse in autumn and during the non-breeding season they occur in habitats not suitable for breeding, for instance the littoral zone. However, the post-breeding movements seem mostly confined to the natal island, though at least one of the colour-marked fledglings dispersed at least 50 km and passed several islands and open water crossings. Dispersal is sex-biased and relatively few adult females returned to the areas where they had bred in the previous year, while the males, which are territorial through most of the year, showed a high degree of philopatry. Males breeding for the first time also show a stronger attachment to their natal areas than females, but appeared to be less successful in obtaining mates than older males were. Mean annual survival rate, and thus length of life span, appears to be higher than in mainland wrens. Evolutionary explanations for the patterns observed require larger samples, extended study areas, more behavioural observations during critical periods of time, and experimental approaches.

Acknowledgements

Funding was received from the Swedish Natural Science Research Council, Dansk-svensk samfunds fond för kultur och vetenskap, Copenhagen, Kungl. Fysiografiska Sällskapet i Lund, and Letterstedska föreningen, Stockholm. Among many local people and others who provided valuable assistance the following deserve special mentioning: Professor Dorete Bloch and her late husband Hans Ólavus Danielsen, Mr Søren Sørensen, Professor Arne Nørrevang, Ms Herdis Joensen, Dr. Pehr H. Enckell, and the ringing-team in 1984, *viz.* Andrew Berry, Tim Anderson, and Chris Dee.

References

Armstrong, E.A. 1955. *The Wren*. London.

Armstrong, E.A. and Whitehouse, H.L.K. 1977. Behavioural adaptations of the wren (*Troglodytes troglodytes*). *Biol. Rev.* 52: 235-294.

Arnold, K.E. and Owens, I.P.F. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proc. R. Soc. Lond.* B 265: 739-745.

Bengtson, S.-A. 2001. Breeding distribution and numbers of wren (*Troglodytes troglodytes*) in the Faroe Islands. *Fróðskaparrit* 49:127-139. Tórshavn.

Bijlsma, R., Bundgaard, J. and Van Putten, W.F. 1999. Environmental dependence of inbreeding depression and purging in *Drosophila melanogaster.* J. *Evol. Biol.*. 12: 1125-1137.

Brown, J.L. and Brown, E.R. 1984. Parental facilitation: parent-offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.* 14: 203-209.

Cramp, S. (Chief Editor). 1988. *The Birds of the Western Palearctic* Vol. 5: 525-542. Oxford and New York.

Dallmann, M. 1987. *Der Zaunkönig*. Wittenberg Lutherstadt.

Emlen, S.T. 1994. Benefits, constraints, and the evolution of the family. *Trends Ecol. Evol.* 9: 282-285.

Evans, M. and Burn, J. 1996. An experimental analysis of mate choice in the wren: a monomorphic, polygynous passerine. *Behav. Ecol.* 7: 101-108.

Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307-343.

Garson, P.J. 1980. Male behaviour and female choice: mate selection in the wren. *Anim. Behav.* 28: 491-502.

Gibbs, H.L. and Grant, P.R. 1987. Adult survival in Darwin´s ground finch (*Geospiza*) populations in a variable environment. *J. Anim. Ecol.* 56: 797-813.

Glutz von Blotzheim, U.N., Bauer, K.M. and Bezzel, E. (eds). 1985. *Handbuch der Vögel Mitteleuropas*, Vol. 10: 1022-1060. Wiesbaden.

Grant, B.R. and Grant P.R. 1989. *Evolutionary Dynamics of a Natural Population. The Large Cactus Finch of the Galápagos*. Chigaco and London.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav*. 28: 1140-1162.

Greenwood, P.J. and Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13: 1-21.

Hawthorn, I. and Mead, C.J. 1975. Wren movements and survival. *Brit. Birds* 68: 349-358.

Hawthorn, I, Weston, I., Crockford, R., and Smith, R.G. 1971. Wrens wintering in a reed-bed at Thatcham, Birkshire. *Bird Study* 18: 27-29.

Järvinen, O. and Varvio, S.-L. 1985. Proneness to extinction of small populations of seals: demographic and genetic stochasticity vs. environmental stress. *Finnish Game Res.* 44: 6-18.

Keller, L.F. 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospitza melodia*). *Evolution* 52: 240-250.

Kluijver, H.N., Ligtvoet, J., Ouwelant, C. van den and Zegwaard, F. 1940. De levenswijse van der Winterkoning *Troglodytes tr. troglodytes* (L.). *Limosa* 13: 1-51.

Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.A. and Stanback, M.T. 1992. The evolution of delayed dispersal in co-operative breeders. *Quart. Rev. Biol.* 67: 111-150.

Kokko, H. and Lundberg, A. 2001. Dispersal, migration, and offspring retention in saturated habitats. *Am. Nat.* 157: 188-202.

Komdeur, J. and Edelaar, P. 2001. Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. *Behav. Ecol.* 12: 706-715.

Lack, D. 1968. *Ecological adaptations for breeding in birds*. London.

Mead, C.J. 1974. *Bird Ringing*. BTO, Tring.

Nichols, J.D. and Kaiser, A. 1999. Quantitative studies of bird movement: a methodological review. *Bird Study* 46 (suppl.): 289-298.

Pray, L.A., James, M., Schwartz, C.J., and Goodnight, L.S. 1994. Environmental dependency of inbreeding depression: implications for conservation biology. *Conserv. Biol.* 8: 562-568.

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* 2: 295-299.

Ricklefs, R.E. 1973. Fecundity, mortality and avian demography. *In*: Farner, D.S. (ed.). *Breeding biology of birds*: 366-435. Washington.

Ricklefs, R.E. 1983. Avian demography. *Current Ornithology* 1: 1-32.

Shields, W.M. 1982. *Philopatry, inbreeding, and the evolution of sex*. Albany.

Shields, W.M. 1987. Dispersal and mating systems: investigating their causal connections. *In*: Chepkosade, B.D. and Halpin, Z.T. (eds). *Mammalian dispersal patterns*: 3-27. Chigaco.

Snow, D.W. and Lill, A. 1974. Longevity records for some Neotropical land birds. *Condor* 76: 262-267.

Sørensen, S. and Jensen, J.-K. 1999. Rare birds in the Faeroe Islands in 1993-1996. *Dansk Orn. Foren. Tidsskr.* 93: 65-70 (In Danish with English summary.)

Thornhill, N.W. 1993. *The natural history of inbreeding and outbreeding, theoretical and empirical perspectives*. Chicago.

Van den Casteele, T., Galbusera, P., Schenck, T. and Matthysen, E. 2003. Seasonal and lifetime reproductive consequences of inbreeding in the great tit *Parus major. Behav. Ecol.* 14: 165-174.

Wiens, J.A., Crawford, C.S. and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421-427.

Williamson, M.H. 1981. *Island populations*. Oxford.

Williamson, K. 1965. *Fair Isle and its birds*. Edinburgh and London.

Williamson, K. and Boyd, J.M. 1960. *St. Kilda Summer*. London.

Williamson, K. and Boyd, J.M. 1963. *A Mosaic of Islands*. Edinburgh and London.