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The illusion of monogamy

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PART

IV

Synthesis



**How consistent are patterns of paternity
between different populations
of reed buntings?**

Karen M. Bouwman

Introduction

The extra-pair mating behaviour of reed buntings has been the focus of several PhD-projects over the past 10 years. Sean O'Malley first discovered the high levels of extra-pair paternity (EPP) in a population of reed buntings at Rutland Water in Leicestershire (UK) during the years 1988 to 1990. Andrew Dixon continued O'Malley's study at the same fieldsite during the years 1990 to 1992. Graeme Buchanan (2001) chose a study site at Stawe Grabovnica in Poland during the years 1998 and 1999 and Oddmund Kleven studied a Norwegian population of reed buntings at Øvre Heimdalen. During the years 2000 to 2002 Martin Keiser studied reed buntings in Grande Cariçaie in Switzerland, which is now continued by Stefan Suter. In 2000 I started studying reed buntings in the Lauwersmeer, The Netherlands, but moved my study site to De Biesbosch, The Netherlands, for the subsequent three years (2001-2003). The locations of these study sites are shown in figure 1. In this chapter I will discuss the generality of patterns of EPP in reed buntings, by comparing my main results in the population in De Biesbosch with the results of the other reed bunting projects.

Variation in EPP between populations

High levels of EPP were found in all populations of reed buntings that were studied; only in one year in the Norwegian population was the percentage of EPP relatively low (19%; table 8.1). Most females engaged in extra-pair mating behaviour; the most extreme case being Dixon's study where virtually all females produced at least one extra-pair offspring (table 8.1). As a consequence, EPP occurred in the majority of broods (table 8.1). There was no tendency for second broods to differ from first broods in the proportion of EPP (Dixon 1993; Buchanan 2001; Keiser & Suter, pers.comm.; chapter 2), or for EPP to vary with time of season (Buchanan 2001; Kleven, pers.comm.; chapter 2). Copulations were not observed frequently, since in two to three years of study less than fifty within-pair copulations and only one or two successful extra-pair copulations (EPCs) were witnessed (Dixon 1993; O'Malley 1993; Buchanan 2001; this study). Given the high level of extra-pair fertilisations (EPFs), many copulations (specifically EPCs) occurred out of sight. Males were often seen intruding in other territories (Dixon 1993; O'Malley 1993; Buchanan 2001; Marthinsen *et al.* 2005; this study), but only Buchanan (2001) reported seeing two females make forays into other territories.

Breeding densities were highly variable between populations, ranging from approximately 1 to 10 territories per hectare. Breeding synchrony indices (Kempenaers 1993) of reed buntings in The Netherlands, Poland and Switzerland were

comparable with those of other species of the Fringillidae family (range: 0.17-0.36; Stutchbury & Morton 1995), apart from the synchrony index found in the Norwegian population, which was among the highest found in all studied passerines (range: 0.08-0.73; Stutchbury & Morton 1995). The higher breeding synchrony found in the Norwegian population may be a result of the high latitude. The breeding season will be shorter (day of first egg of first and last nest of the season: Norway: 1 June – 4 July (Kleven, pers.comm.); The Netherlands: 22 April – 20 July (own unpubl.data)), and unlike in the other populations, second broods occur rarely (Kleven, pers.comm.).

Variation in EPP within populations

The difference between the highest and lowest average percentage of EPP in a brood between populations was 25% (table 8.1). When excluding the percentage of EPP of the Norwegian population, which appeared to be an outlier, the variation between and within populations was similar (13% vs. 11%). Also male return rates and breeding synchrony indices showed similar variation between and within populations. The maximum difference in average male return rates between populations was 17%, while within populations this difference was 19% (table 8.2). When including the Norwegian population, the maximum differences in breeding synchrony indices between and within populations were not comparable (37% and 14%), but when excluding the Norwegian population, the difference

Table 8.1. Variation in the mean percentage of offspring resulting from EPP ('%EPP'), mean percentage of broods containing EPP ('%broods'), mean percentage of males that gained EPP in other broods ('%males'), mean percentage of females with EPP in their broods ('%females'), mean breeding density (number of territories per hectare) and mean breeding synchrony index between different populations of reed buntings. Sample sizes are shown in brackets, '-' stands for no data available.

location	%EPP	%broods	%males	%females	density	synchrony	reference
Biesbosch	51 (511)	74 (131)	47 (85)	78 (82)	3.1	0.33	chapter 2
Lauwersmeer	49 (70)	88 (17)	67 (9)	86 (7)	1.1	0.19	Own unpubl.data
England I	50 (122)	69 (29)	36 (14)	79 (14)	9.7	-	O'Malley 1993
England II	55 (216)	86 (58)	54 (28)	97 (34)	<8.1	-	Dixon 1993
Poland	44 (217)	70 (59)	72 (29)	74 (42)	1.4	0.32	Buchanan 2001
Switzerland	41 (-)	66 (-)	47 (-)	74 (-)	1.3	0.28	Kaiser & Suter, unpubl.data
Norway	30 (332)	54 (72)	22 (81)	54 (72)	-	0.56	Kleven, unpubl.data

was respectively 14% and 11%. The breeding density appeared to differ between populations, since there was a difference of 8.6 pairs per hectare between the highest and lowest breeding density between populations, while this was only 1.8 pairs per hectare within populations (table 8.2).

These results suggest an important effect of year to year differences within populations, since the differences between years within most populations are comparable to the differences between populations. However, this similarity fails to hold when including the Norwegian population, suggesting that in some cases the differences between populations may be of greater importance than the differences between years. Possibly the differences between the Norwegian and other populations are influenced by the difference in latitude, i.e. climatological factors (figure 8.1).

Although the sample sizes are small, the variation in proportion of EPP within populations appears to be associated with breeding density, but not with male return rates or breeding synchrony indices. On the population level, the highest breeding densities seem to be associated with the highest levels of EPP in four out of four populations, although low breeding densities are found in the year with the lowest level of EPP in three out of four cases (table 8.2). In the case of the highest

Table 8.2. Variation within populations in the percentage of offspring resulting from EPP (%EPP), breeding density (number of territories per hectare), breeding synchrony index, number of males studied (# males) and the percentage of ringed males that returned the subsequent year (% return). Sample sizes are shown in brackets, '-' stands for no data available.

location	year	%EPP	density	synchrony	# males	% return
Biesbosch	2001	47 (38)	-	-	17	-
	2002	55 (262)	3.4	0.27	44	65
	2003	46 (211)	2.7	0.38	35	48
Lauwersmeer	2000	49 (70)	1.1	0.19	11	-
England I	1988	59 (41)	12.58	-	18	-
	1989	42 (81)	6.91	-	11	27
England II	1990	58 (98)	8.11	-	17	59
	1991	45 (40)	<8.11	-	7	-
	1992	55 (78)	<8.11	-	7	-
Poland	1998	39 (96)	1.06	0.38	17	-
	1999	48 (121)	1.65	0.26	26	47
Switzerland	2000	43 (-)	1.49	0.30	-	-
	2001	43 (-)	1.19	0.33	-	36
	2002	36 (-)	1.24	0.23	-	44
Norway	2001	19 (146)	-	0.45	35	-
	2002	38 (186)	-	0.66	46	40



Figure 8.1. Locations of the studied populations of reed buntings in Europe. 1: De Biesbosch (The Netherlands), 2: Lauwersmeer (The Netherlands), 3: England, 4: Poland, 5: Switzerland, 6: Norway. The coloured area indicates the breeding distribution of the reed bunting.

male return rates, the percentage of EPP was highest in the same years in two out of three populations, while for the highest breeding synchrony index this was found in two out of four populations (table 8.2).

Distinguishing between female benefit hypotheses

1. Do females gain genetic benefits through EPP?

DISTRIBUTION OF EPP AMONG BROODS

The studies that investigated patterns of EPP among broods are listed in table 8.3. These patterns were mostly inconsistent with the hypothesis that females seek genetic diversity for their offspring (D), and provide some support for both the good genes (G) and the genetic compatibility (C) hypotheses (chapter 2). First, EPP was not evenly distributed across broods in any of the populations (contra D, pro G + C; table 8.3). Second, the majority of broods, including broods with no

EPP, was sired by a maximum of two different males (contra D, pro G + C; table 8.3). Third, males that sired EPY in other nests were on average more successful at siring offspring in their own nests (contra D + C, pro G; table 8.3). However, there was no relation between an individual male's success at siring offspring in his own and in other nests (contra G, pro D + C; table 8.3). This discrepancy may be explained by a trade-off between mate guarding to protect paternity in one's own brood and seeking EPCs to gain fertilisations in other broods, even though overall these males are more successful. Fourth, a few cases of reciprocal paternity occurred in all populations, i.e. males siring offspring in each others nest (contra G, pro D + C; table 8.3).

Table 8.3. Distribution of EPP among broods. For descriptions of the patterns see text; + indicates that the pattern was found, - indicates the pattern was not found, and the cell is left blank when the pattern was not investigated.

Patterns	Biesbosch	England II	Poland	Switzerland	Norway
Non-random distribution?	+		+	+	
Mainly two sires per brood?	+	+		+	
Low cuckoldry rate = high EPF success other nests? ¹	+			+	
Low individual cuckoldry rate = high EPF succes other nests? ²	-	-	-		
Reciprocal paternity?	+	+	+	+	+

¹ at the population level

² at the individual level

DISTRIBUTION OF EPP AMONG MALES

All studies investigated the relationship between several male characteristics and within- (table 8.4A) or extra-pair fertilisation success (table 8.4B). We found that wing length, song output and badge colour were related to age (chapter 3). In agreement, O'Malley (1993) found a correlation between wing length and song output, suggesting that song output is also an age-related characteristic in the English population.

In the Dutch population, age and most age-related characteristics were found to be negatively related to the proportion of EPP in a male's own brood, so that older males were more successful in siring within-pair offspring, i.e. preventing cuckoldry (table 8.4A; chapter 3). These results were not supported in the other populations (table 8.4A). Dixon even found an opposite trend: older males tended to sire less offspring in their own brood. However, the sample sizes of the Biesbosch population were much larger than those of the most other populations;

Table 8.4. Relation between male reed bunting characteristics and (A) proportion of EPP in a male's own brood and (B) number of extra-pair young sired in other broods. '+' and '-' indicate respectively a positive and negative relationship; 'ns' indicates the relationship was tested, but was non-significant. The cell is left blank when the relationship was not investigated. Sample sizes are shown in brackets. Significant relationships that are consistent with those found in the Dutch population are highlighted.

(A)	Biesbosch	England I	England II	Poland	Switzerland	Norway
Age-related characteristics:						
Age	- (39)		+ (15)	ns (12)		ns (36)
Wing length	- (108)			ns (29)	ns (-)	
Song output	- (43)	ns (17)	ns (15)	ns (12)		
Badge colour	ns (66)	ns (17)	ns (15)	ns (28)		
Other characteristics:						
Tarsus length	+ (108)			ns (28)	ns (-)	
Mass	ns (108)			ns (28)	ns (-)	
Badge size	ns (108)			ns (12)		
Song structure	ns (39)			ns (30)		
(B)	Biesbosch	England I	England II	Poland	Switzerland	Norway
Age-related characteristics:						
Age	+ (26)		ns (15)	ns (12)		+ (46)
Wing length	+ (73)				ns (-)	
Song output	+ (30)	+ (17)	ns (15)			
Badge colour	+ (45)	+ (17)	ns (15)			
Other characteristics:						
Tarsus length	ns (73)				ns (-)	
Mass	ns (73)					
Badge size	ns (73)					
Song structures	ns (26)					

possibly the absence of similar associations in the other populations was a result of a lack of power. In support, in the Polish population, the non-significant associations were in the same direction as the ones that were found to be significant in the Biesbosch. Unfortunately the directions of the associations were not available for O'Malley's data.

In the Dutch population, age and age-related characteristics were also associated with the number of extra-pair young a male sired: older males were more successful (table 8.4B; chapter 3). Similar results were found in the English

(during O'Malley's study) and Norwegian populations, but no indication of older males being more successful was found in the English (during Dixon's study) or Polish population (table 8.4B). Again, this may be a result of too low sample sizes, since the sample sizes used in our Dutch study were much larger than those in the English and Polish study, and the non-significant associations were again in the same direction. Unfortunately reed buntings are difficult to age using plumage characteristics; only Buchanan used such a method (Buchanan 2001). The other studies based the age classification on the high site fidelity of individuals (O'Malley 1993; chapter 3), and assumed new arriving (i.e. unringed) adults to be young and returning birds to be old (Dixon 1993; O'Malley 1993; Kleven & Lifjeld 2004; Kaiser & Suter, pers.comm.; chapter 3). Thus differences in return rates may be associated with differences in fertilisation success between populations, since with lower return rates, a larger proportion of males is expected to be young and have a lower probability of gaining EPFs. However, male return rates hardly differed between populations (table 8.2) and did not appear to be related to the percentage of males that gained EPFs; return rates for the Polish and Norwegian population were comparable (respectively 47% and 40%; table 8.2), but the percentage of males that gained EPFs in these populations were the opposite maxima of the range found (respectively 72% and 22%; table 8.2).

The differences in results between the two studies of the English population suggest either variation in associations between years, or differences in methodology applied by O'Malley and Dixon. Variation in associations between years may be expected, since local circumstances that may affect extra-pair mating behaviour, such as breeding synchrony, food availability and weather conditions, may also differ between years. Although the same methodology to measure song output was used by O'Malley and Dixon, Dixon included the residuals of song output over time of season in his analysis, while O'Malley used the uncorrected measure. For measuring badge colour, a slightly different methodology was applied in both studies, since O'Malley divided the range into six categories, while Dixon used nine categories.

DIFFERENCES BETWEEN WITHIN-PAIR AND EXTRA-PAIR OFFSPRING

When comparing extra-pair young and their maternal half-siblings in broods of mixed paternity, we found that extra-pair offspring had significantly longer tarsi than within-pair offspring (chapter 3), a trend that was also found in the Swiss reed bunting population (table 8.5). Although this may be a result of high quality paternal genes, we suggested that it is more likely to be a consequence of extra-pair young hatching earlier than within-pair young and thus being slightly older (chapter 3). No other differences between maternal half-siblings were found (table 8.5). Long-term fitness consequences of EPP were not available from any of the populations, as recruitment rates of reed buntings are low.

Table 8.5. Differences in nestling characteristics between maternal half-siblings in broods of mixed paternity. ‘+’ indicates a positive relationship; ‘ns’ indicates the relationship was tested, but was non-significant. The cell is left blank when the relationship was not investigated. Sample sizes are shown in brackets.

	Biesbosch	Poland	Switzerland	Norway
Tarsus length	+ (34)		+ (-)	
Mass	ns (34)	ns (39)	ns (-)	
Heterozygosity	ns (34)			ns (30)
Immunocompetence				ns (19)

TO SUMMARISE: DO FEMALE REED BUNTINGS GAIN GENETIC BENEFITS THROUGH EPP?

Dixon (1993) argued that indiscriminate female copulatory behaviour associated with the genetic diversity hypothesis best explained his observation that almost all females participated in extra-pair copulations (EPCs; 97%). However, gaining genetic diversity is not likely to be an adaptive strategy, since there are no obvious advantages to individuals (Birkhead 1998). Generally, the observed patterns did not support the genetic diversity hypothesis, and we therefore discard this hypothesis as a likely female benefit.

In three out of five populations indications were found that males that were successful in siring offspring were older than unsuccessful males. This supports the predictions of the good genes (Kempnaers & Dhondt 1993) and fertility insurance hypothesis (Sheldon 1994b), but not necessarily the predictions of the genetic compatibility hypothesis (Griffith *et al.* 2002). The absence of a relationship between male age and fertilisation success in some populations may be a result of limited sample sizes, differences between years in local circumstances affecting extra-pair mating behaviour or differences in methodology.

Extra-pair young were generally not different from their maternal half-siblings. Only tarsus length appeared to be longer in extra-pair young in both studies where it was measured (chapter 3; Kaiser & Suter, pers.comm.). This may be a result of superior paternal genes, however, evidence was found in the Dutch population that this was more likely to be a result of a small difference in age between within- and extra-pair young, due to a bias in hatching order (chapter 3). This interesting bias towards early hatching of extra-pair offspring was not tested in any of the other populations. The intrusion behaviour of extra-pair males observed by O'Malley provides a plausible explanation for the bias in hatching order; intrusions peak during the three days before the first egg is laid, and thus the first laid eggs are more likely to be fertilised by extra-pair sires than the last eggs (O'Malley 1993).

Earlier hatched eggs may have a fitness benefit (reviewed by Krebs 1999), and thus it may be adaptive for both extra-pair males and females to bias extra-pair offspring to eggs laid early in a clutch. However, no such peak close to egg-laying was observed in the Norwegian population (Marthinsen *et al.* 2005).

Because fitness benefits may be revealed on a long-term basis, and only short-term benefits have been measured in reed buntings due to low recruitment rates, we have not been able to test the genetic benefits hypotheses rigorously. Although the difference in tarsus length between within- and extra-pair offspring may be related to future fitness benefits, so far we conclude that no support was found for the genetic benefit hypotheses.

2. Do female reed buntings gain direct benefits through EPP?

Buchanan (2001) suggested that female reed buntings may be trading EPCs for foraging access on other territories, as females with more sires per brood foraged on more male territories. In 2002, we studied foraging behaviour of adults during the nestling phase in the Dutch population. Both males and females collected most food either on neutral grounds (males: 54%, $n = 269$ foraging trips; females: 48%, $n = 474$ foraging trips) or on their own territory (males: 43%; females: 37%). Females collected significantly more food on other territories than males (16% vs. 3% of foraging trips; $\chi^2 = 22.7$, $df = 1$, $p < 0.001$). There was a significant positive relationship between the distance to neutral foraging grounds and the proportion of foraging trips to other territories ($r_s = 0.39$, $p = 0.021$, $n = 35$), which was also found in the Polish population (Buchanan 2001). We found no correlation between the proportion of foraging trips made to other territories and the proportion of EPP in a brood ($r_s = -0.04$, $p = 0.82$, $n = 32$), nor between the proportion of foraging trips made to other territories and the number of sires per brood ($r_s = -0.13$, $p = 0.49$, $n = 32$). Unlike Buchanan (2001), we found no correlation between the number of extra-pair sires and the number of other territories the female foraged on ($r_s = 0.17$, $p = 0.56$, $n = 14$).

There was no difference in the proportion of feeding trips to neutral foraging grounds between the populations (Dutch vs. Polish: 48% ($n = 474$) vs. 45% ($n = \pm 581$); $\chi^2 = 0.01$, $df = 1$, $p = 0.94$), but females from the Dutch population foraged more in their own territories compared to other male territories than females from the Polish population (71% ($n = 474$) vs. 58% ($n = \pm 581$); $\chi^2 = 9.22$, $df = 1$, $p < 0.01$). This is not a result of higher territory densities, since breeding densities were lower in the Polish than in the Dutch population. Furthermore, fewer extra-pair males sired offspring in a brood in the Dutch than in the Polish population (1.4 ± 0.1 ($n = 88$) vs. 1.8 ± 0.1 ($n = 37$); $t = 3.14$, $df = 123$, $p < 0.01$), and a smaller proportion of the broods containing EPP were sired by three or more different males (17% ($n = 88$) vs. 66% ($n = 37$); $\chi^2 = 27.75$, $df = 1$, $p < 0.001$). Possibly females from the Polish population have less

foraging opportunities in their own territory and thus are more likely to forage in other male's territories, for which they may have to engage in EPCs with the territory owner. However, this explanation was not supported by Buchanan's finding that the territories visited by females did not centre on males siring extra-pair offspring in the brood (Buchanan 2001).

Costs of EPP to females

One of the best examples of females suffering a cost through engaging in EPP was found in reed buntings. Using two broods of the same pair within one season, Dixon *et al.* (1994) showed that males provisioned less to broods in which they sired a lower proportion of the offspring. However, this result could not be repeated in the Dutch (chapter 4) or Polish population (Buchanan 2001). In the Polish population the relationship between paternal provisioning rate and paternity was in the same direction, however not significant ($p = 0.14$), whereas in the Dutch population the relationship was in the opposite direction and far from significant ($p = 0.8$). The reason why males differed in their provisioning behavior as a function of their paternity levels between the populations in England, Poland and the Netherlands remained unclear. Sample size, levels of EPP, feeding rates and male share of feeding rates (England: 0.40; Poland: 0.37; the Netherlands: 0.41) appeared to be similar between the studies, although males showed larger variation in provisioning rates between broods in the Dutch and Polish than in the English population (chapter 4).

Constraints on the occurrence of extra-pair paternity

Breeding density and synchrony

Breeding density and synchrony may limit the number of potential extra-pair partners available, and thus influence whether individuals engage in extra-pair mating behaviour (Westneat & Sherman 1997; Møller & Ninni 1998). Only in the English population an effect of breeding density was found on EPP. O'Malley (1993) described a positive relation between breeding density and the number of extra-pair offspring a male sired, while Dixon (1993) reported a tendency for the proportion of EPP in a brood to increase with breeding density. No effect of breeding density on EPP was found in the Dutch (chapter 6), Polish (Buchanan 2001) or Swiss population (Kaiser & Suter, pers.comm.) when investigating individual cases. Breeding densities were approximately five times higher in the English population than in the other populations combined (9.2 vs. 1.8 territories per hectare), which is likely to have affected the extra-pair opportunities.

Breeding synchrony has been calculated both on the population level, and on a local scale (Kempenaers 1993). No effect of breeding synchrony on a local scale was found in the Dutch (chapter 6) and Swiss population (Kaiser & Suter, pers.comm.), while no effect of breeding synchrony on the population level was found in the Dutch, Polish (Buchanan 2001), and in one year in the Swiss population (Kaiser & Suter, pers.comm.). However, in 2002, both the probability of EPP and the proportion of EPP in broods increased when individuals were breeding more synchronously in the Swiss population. As a consequence, following predation, replacement broods had low levels of EPP (Kaiser & Suter, pers.comm.). In the Dutch population, replacement broods did not differ in levels of EPP from first broods (chapter 6).

Male mate guarding

Males in many species attempt to protect their paternity by closely following their mate, to either prevent her from seeking EPCs (Lifjeld *et al.* 1994), or to prevent other males from gaining EPCs (Beecher & Beecher 1979). Whether or not the female has an active role in seeking EPCs will largely determine the effectiveness of male mate guarding behaviour with regard to preventing cuckoldry (Lifjeld *et al.* 1994). Opposing results with regard to the effectiveness of mate guarding have been reported in different reed bunting studies. Dixon (1993), reported only weak mate guarding behaviour in the English population of reed buntings, as he found no differences between the fertile period and other stages of the breeding cycle in the proximity between male and female and the number of flights where the male follows the female. However, O'Malley (1993) showed in the same population that mate guarding did occur during the fertile period of the female, but that it was not related to the proportion of EPP in the brood. This result supported the hypothesis that guarding occurs in low quality males, which are trying to make 'the best of a bad job' (Lifjeld & Robertson 1992). On the other hand, Marthinsen *et al.* (2005) found mate guarding to be effective in the Norwegian population of reed buntings: higher levels of mate guarding were associated with lower levels of cuckoldry.

The differences in effectiveness of mate guarding between populations may be a result of differences in the female role in seeking EPCs, as was found in red-winged blackbirds (*Agelaius phoeniceus*). In an eastern population of red-winged blackbirds, males initiated EPCs by intruding onto female territories, usually when social males were not present to guard their mate, and females accepted or rejected these EPC attempts; females rarely made forays to seek EPCs themselves (Westneat 1992; Westneat 1994). In contrast, in a western population, females often forayed away from their territory to solicit copulations, while social males rarely guarded their fertile mate (Gray 1996). Since neither the English or the Norwegian studies report seeing female reed buntings actively soliciting EPCs, the

role of the female is not expected to be different between the populations, although due to the covert behaviour of female reed buntings, EPC solicitations may have passed unobserved. However, also the quality of mate guarding observations may have been affected by the covert behaviour of females and low visibility of pairs due to dense reed vegetation.

Weather conditions

In a Norwegian population of bluethroats (*Luscinia s. svecica*) evidence has been found that extra-pair mating behaviour can be constrained by adverse weather conditions, such as low temperatures. The Norwegian population of reed buntings was studied at the same site as the bluethroats, and was the only population to encounter extreme adverse weather (i.e. snow) during the fertile period in 2001. Possibly this is associated with the relatively low levels of EPP found in that year. In the Dutch population of reed buntings we found the opposite relation with minimum temperature (range: 4.4 - 13.1°C), so that more EPP was found in broods where the minimum temperature during the fertile period was high (chapter 7). We suggested that in our relatively mild climate, time-consuming behaviours such as mate guarding are constrained, while less time-consuming behaviours such as gaining EPCs are less constrained. In harsh conditions such as encountered in Norway, all behaviours that are a trade-off with self-maintenance are likely to be constrained.

Conclusion

Most patterns of EPP appear to be consistent between populations of reed buntings. Generally the percentage of offspring resulting from EPP is high, and EPP occurs in the majority of broods. Since in most the cases the variation in EPP within a population is similar to the variation between populations, the effect of year appears to play an important role in determining the level of EPP. Both within and between populations, we found indications that breeding density is related with the level of EPP observed, while between populations, factors associated with a difference in latitude may be important. In three out of five populations, male reproductive success is related to age. The absence of a relationship between male age or age-related characteristics and within- or extra-pair fertilisation success in some populations, or between years in the same population, may be a result of differences between years, differences in methodology or limited sample sizes. The differences between within- and extra-pair offspring within broods of mixed paternity were consistent between populations, however, whether the observed difference in tarsus length is a result of females gaining genetic benefits for their offspring, remains to be determined.

Recommendations for future studies on EPP in reed buntings

So far, the role of female reed buntings in initiating extra-pair mating behaviour remains unclear. In order to understand the mechanisms behind extra-pair mating behaviour, it is crucial to study female behaviour in more detail. Using radio transmitters we may be able to determine whether females make covert extra-territorial forays to extra-pair male territories, for instance before dawn, as was seen in the superb fairy-wren (*Malurus cyaneus*; Double & Cockburn 2000). In complete darkness, male reed buntings sing before other birds commence their dawn chorus (pers.obs.); this early songpeak may be related to female extra-territorial behaviour. Furthermore, we occasionally observed females sitting conspicuously in reed stems while making contact calls. The possibility that these are fertile females calling for extra-pair partners needs to be explored. Also the behaviour of the fertile female with respect to intruding males needs to be documented in greater detail. Through temporary removal of the social male, we may be able to determine whether females actively accept and reject EPCs attempts of intruding extra-pair males, without these males being deterred by the social male.

The importance of different age-related male characteristics in gaining fertilisations can be determined by manipulating characteristics that may be used as a cue, either by females, if they actively select their partner, or by males in male-male competition. Age as such cannot be manipulated, but badge colour or song output may be altered by for instance painting the badge or temporarily muting a male (Smith 1976; Westcott 1992). In order to rigorously test the genetic benefit hypothesis, longterm fitness benefits need to be recorded. However, due to low recruitment rates of offspring and a decreased survival of reed buntings (Newton 2004), this will be difficult to accomplish. In first instance it will be interesting to see whether also in other populations extra-pair offspring have longer tarsi than their half-siblings, and whether this is actually a result of a bias in laying or hatching order.

The study of EPP on reed buntings in different years and in different populations provides us with the unique possibility to determine the variation in levels of EPP which is explained by local ecological factors. Therefore, combining our data in a 'reed bunting database' and performing a meta-analysis to determine factors that explain variation in EPP in reed buntings should be our next step, which will be a large contribution to understanding variation in EPP within species.

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